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DIFFERENT FRACTIONS OF PRIMARY PRODUCTION IN LARGE SHALLOW EUTROPHIC LAKE VÕRTSJÄRV, ESTONIA

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Abstract. Different fractions of primary production (PP) were measured weekly with ^{14}C assessment in shallow highly eutrophic Lake Võrtsjärv, Estonia (area 270 km^2, mean depth 2.8 m, max depth 6 m). The particulate PP was 200 g C m^{-2} yr^{-1} with peaks in May, June, and August. Its measured mean rate was 50 ± 7 mg C m^{-2} h^{-1}. The share of the > 40 µm fraction in PP was negligible, while chlorophyll *a* in that fraction comprised 23% of the total chlorophyll *a*, indicating the low productivity of large cells. The dissolved fraction constituted on an average 37% of the total PP. In the seasonal aspect, the proportion of exudated PP was determined by phosphorus limitation or phytoplankton species composition rather than by light conditions: it was higher at higher total N/P ratios and when diatoms were dominating and lower during the prevalence of blue-green algae. The efficiency of light utilization and assimilation number were strongly dependent on light intensity.

Key words: phytoplankton, primary production, chlorophyll, fractions, shallow eutrophic lake.

List of abbreviations

AD = average depth of the lake;
AN_{part} = chlorophyll *a* specific PP (assimilation number);
BAC% = percentage of diatoms in phytoplankton biomass;
Chl*a* = chlorophyll *a* concentration;
COD_{Cr} = chemical oxygen demand determined by means of dichromate oxidation;
CY% = percentage of blue-greens in phytoplankton biomass;
DL = length of the light day;
DOC = dissolved organic carbon;
E_{part} = efficiency of light utilization in particulate PP;
I_{mix} = irradiance of mixed water layer;

I_0 = total solar irradiance on water surface;
I_0day = I_0 per day;
I_0hour = I_0 at midday;
K = attenuation coefficient of water for scalar PAR;
maxP_{part} = vertical maximum of particulate PP in the water column;
N_{org} = organic nitrogen;
$P_{disstot}$%, $P_{disspart}$% = percentages of labile fractions in P_{tot} and P_{part};
$P_{disstot}$, $P_{disspart}$ = labile fractions of P_{tot} and P_{part};
PP = primary production;
P_{part}, $P_{part}40$ = particulate PP (total and in the fraction < 40 µm);
$P_{partacid}$, $P_{partacid}40$ = acid treated particulate PP dried at 60 °C;
PPhour = PP per hour at midday;
P_{tot} = total PP;
S = water transparency by Secchi disc;
SRP = soluble reactive phosphorus;
TN = total nitrogen;
TP = total phosphorus.

INTRODUCTION

Phytoplankton production represents a major synthesis of organic matter in aquatic systems, which initiates the food chains and forms a basis of the trophological pyramid. It is well known that part of the primary production (PP) of phytoplankton is released into water as dissolved organic carbon (DOC). This phenomenon, noticed already in the 1970s (Schindler et al., 1972; Burris, 1977; Wiebe & Smith, 1977), was regarded as a methodological artifact (Sharp, 1977); Nowadays the role of phytoplankton as the producer of easily degradable DOC is widely recognized. The active release of DOC may be the result of photo-respiration and serves as a defence mechanism of cells against surplus accumulation of oxygen and photoassimilates at high irradiance or nutrient limitation (South & Whittick, 1987). DOC may be released also in the course of cell autolysis, sloppy feeding of zooplankton, bacterial or virus attack, or as passive diffusion through the algal membrane (Chrost, 1983; Bjørnsen, 1988; Münster & Chrost, 1990; Sundh, 1991).

Exudated DOC may consist of relatively small (< 1000 D) molecules such as glycolate and other organic acids, amino acids, and sugars; however, also big molecules such as proteins, polysaccharides, nucleic acids, toxins, vitamins, etc. can be excreted (Chrost, 1981; Chrost & Faust, 1983; Wetzel, 1983; Sundh, 1992). The composition and amount of exudates are determined by environmental conditions (Sharp, 1977; Zlotnik & Dubinsky, 1989) and by the species structure of phytoplankton (Sundh, 1991, 1992). The share of exudates ranges from 0.3 to 90% (Wetzel, 1983), in most cases from 5 to 45% of the total PP (Berman & Gerber, 1980; Chrost, 1981; Chrost & Faust, 1983; Bell & Kuparinen, 1984; Chrost et al., 1989; Lignell, 1990; Baines & Pace, 1991), being lower in more eutrophic conditions (Round, 1981; Sundh, 1989).

The released DOC is an important substrate for heterotrophic bacteria (Bell & Sakshaug, 1980; Berman & Gerber, 1980; Chrost, 1983; Chrost & Faust, 1983; Tamminen et al., 1984), satisfying for up to 100% of their carbon requirement (Münster & Chrost, 1990). Bacterial assimilation returns DOC to the planktonic food web, which allows its further utilization in the so-called microbial loop (Chrost et al., 1989; Tranvik, 1992).

Bacteria, considered formerly mostly as decomposers, are ever more recognized also as mobilizers of organic matter (mainly DOC). The role of the release of DOC, as well as its mobilization, cannot be neglected in constructing a model of an ecosystem. In a strongly eutrophic lake such as Võrtsjärv where the detrital food chain is prevalent (Nõges et al., 1998) also the microbial loop must be extremely important. The links of the classical food chain have been quite well studied in this lake during the last 10 years; however, a thorough study of the microbial loop is still lacking. The aim of the present paper is to analyse the seasonal dynamics of PP and its potential exudation, providing thus a basis for further quantification of the role of the microbial loop in the trophic structure of Võrtsjärv.

MATERIAL AND METHODS

Weekly sampling was performed at a station in the vicinity of the deepest area of Võrtsjärv, a shallow and highly eutrophic lake (area 270 km^2, mean depth 2.8 m, max depth 6 m) in Estonia (Nõges, 1992). The sampling period lasted from December 1994 to the end of 1995.

Water transparency (*S*) was measured with a Secchi disc. The concentration of chlorophyll *a* (Chl*a*) was determined in two size fractions: total and < 40 µm (after 40 µm sieving). Seston was collected on Whatman glass fibre filters (GF/C). Chlorophyll was extracted with 90% acetone and analysed spectrophotometrically (Strickland & Parsons, 1972; Edler, 1979).

Chemical analyses to determine total nitrogen (TN) and total phosphorus (TP) were performed using standard methods described by Grasshoff et al. (1982). Total organic carbon was determined as chemical oxygen demand (COD_{Cr}) by means of dichromate oxidation (Ahlgren & Ahlgren, 1975).

The attenuation coefficient of water for scalar PAR (*K*) was measured with a 4π underwater light absorption meter as described by Reinart et al. (1995). The average water column irradiance in the mixed layer was calculated according to Riley (1957):

$$I_{mix} = I_0 \times (1 - e^{-K \times AD}) / (K \times AD), \quad (1)$$

where I_0 is total solar irradiance on water surface and AD is average depth of the lake.

Phytoplankton PP in different fractions was estimated according to the $^{14}CO_2$ assimilation technique introduced first by Steeman-Nielsen (1952). Water from 0 m, 0.25, 0.5, 1, 2, and 3S was poured into 36 mL glass scintillation vials, 100 µL of sterile $NaH^{14}CO_3$ (Izotop, St. Petersburg) solution (2–3 µ Ci per vial) was added to achieve final activity 0.083 µ Ci mL^{-1}. After that the vials were incubated for 2 h at midday (usually from 11 a.m. to 1 p.m.) in the lake, at the same depths from where the water was sampled. Non-photosynthetic carbon fixation was measured in dark vials with water from the surface layer and from the depth of 3S. After incubation, 6 mL of water from every vial was poured into a new clean plastic scintillation vial, and was acidified (pH < 2) by adding 150 µL of 0.5 N HCl per 1 mL. Inorganic ^{14}C was assumed to be removed during 24 h (Niemi et al., 1983; Hilmer & Bate, 1989; Lignell, 1992). Next, the sample was dried at 60 °C. Additional measurements in 1996 revealed that no organic material (COD_{Cr}) was lost at 60 °C drying of lake water when HCl was added in final concentration of 0.012 N, as used in PP assessment. The radioactivity of the remaining precipitate was measured in toluene–PPO–POPOP cocktail using LSC RackBeta 1211 (Wallac, Finland) and external standardization for DPM calculations. The value of total primary production (P_{tot}) per 1 m^3 in different water layers was calculated from the radioactivity of the precipitate according to the standard formula (Nielsen & Bresta, 1984). Dark assimilation was determined separately, and subtracted from light assimilation to avoid the biases caused by possible resting activity of commercially available $NaH^{14}CO_3$ (Bresta et al., 1987) as well as by the absorption of inorganic $^{14}CO_2$ on the walls of the plastic scintillation vials (Søndergaard, 1980). The trapeze integration over depth and time was applied for calculating values per 1 m^2 and per year, respectively. Daily PP values were calculated using the equation relating daily PP (PPday; mg C m^{-2} day^{-1}) with PP at midday (PPhour; mg C m^{-2} h^{-1}) and the length of the light day (DL; h):

$$PPday = PPhour / (0.230 - 890 \times 10^{-5} DL); R^2 = 0.66, p < 0.01. \quad (2)$$

The regression was found on the basis of 14 series of seasonal measurements of PPday as the sum of 2-hour values over the whole day, performed in Võrtsjärv in 1989 (unpublished). Particulate PP (P_{part}) was measured with two methods in two size fractions (total and < 40 µm) (Fig. 1). *The first method*: 6 mL of water from both fractions was filtered through membranes of 0.45 µm pore size (Millipore HA), the filters were treated with concentrated HCl fumes for 5 min to remove the excess of inorganic ^{14}C. Values for air-dried P_{part} and $P_{part}40$ were obtained. The effect of the duration of HCl fuming (5 and 30 min) was tested in a separate experiment. No significant influence of fuming time on the retained radioactivity was found.

The second method: 6 mL of water was treated with 150 µL of 0.5 N HCl for 24 h prior to filtration (analogously to the assessment of P_{tot}), then filtered through membranes of 0.45 µm pore size which were exposed at 60 °C like the

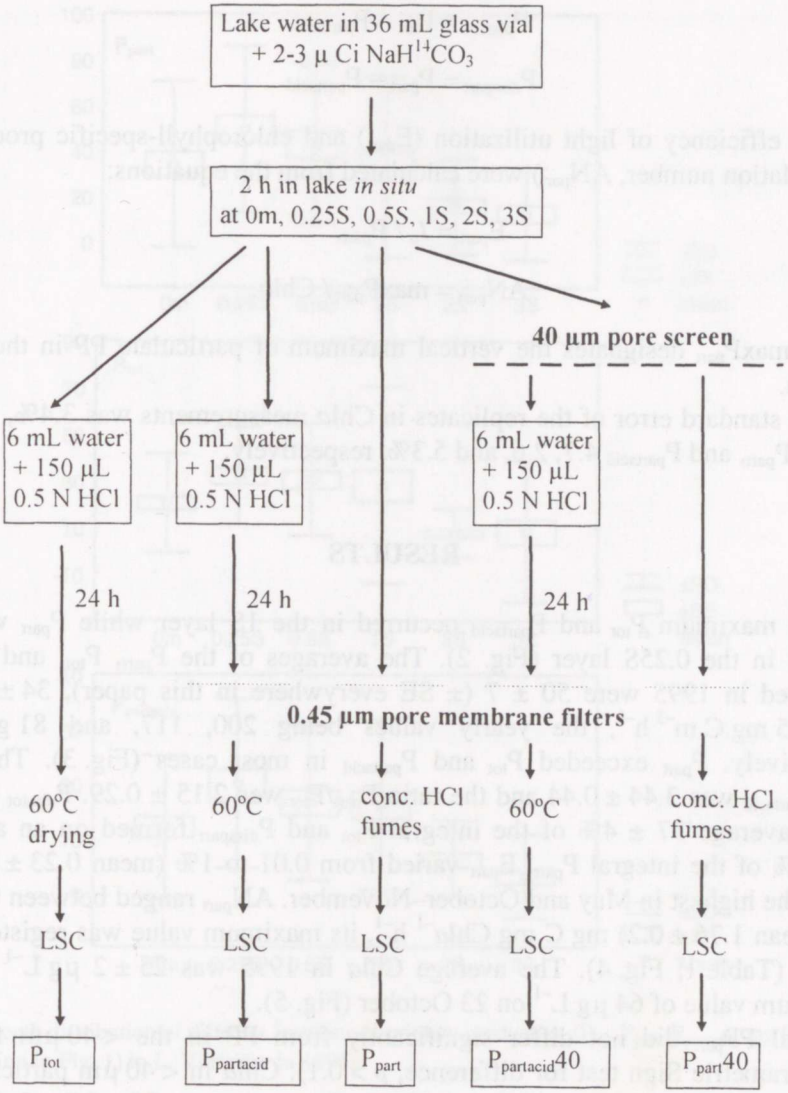

Fig. 1. Scheme of primary production measurements in L. Võrtsjärv in 1995.

water for P_{tot}. Values for total and < 40 μm acid treated particulate primary production dried at 60 °C ($P_{partacid}$ and $P_{partacid}40$, respectively) were obtained. Additional experiments showed that drying of filters at room temperature yielded the same values as the 60 °C treatment.

Two different parameters expressing the amount of the dissolved organic matter produced were calculated:

$$P_{disstot} = P_{tot} - P_{partacid}, \quad (3)$$

$$P_{disspart} = P_{part} - P_{partacid}. \quad (4)$$

The efficiency of light utilization (E_{part}) and chlorophyll-specific production (assimilation number, AN_{part}) were calculated from the equations:

$$E_{part} = I_o / P_{part}, \quad (5)$$

$$AN_{part} = \max P_{part} / \text{Chl}a, \quad (6)$$

where $\max P_{part}$ designates the vertical maximum of particulate PP in the water column.

The standard error of the replicates in Chl*a* measurements was 3.4%, in case of P_{tot}, P_{part}, and $P_{partacid}$ 4.7, 2.6, and 5.3%, respectively.

RESULTS

The maximum P_{tot} and $P_{partacid}$ occurred in the 1S layer while P_{part} was the highest in the 0.25S layer (Fig. 2). The averages of the P_{part}, P_{tot}, and $P_{partacid}$ measured in 1995 were 50 ± 7 (± SE everywhere in this paper), 34 ± 6, and 18 ± 2.5 mg C m^{-3} h^{-1}, the yearly values being 200, 117, and 81 g C m^{-2}, respectively. P_{part} exceeded P_{tot} and $P_{partacid}$ in most cases (Fig. 3). The ratio $P_{part}/P_{partacid}$ was 3.44 ± 0.44 and the ratio P_{part}/P_{tot} was 2.15 ± 0.29. $P_{disstot}$ formed on an average 37 ± 4% of the integral P_{tot} and $P_{disspart}$ formed on an average 58 ± 3% of the integral P_{part}. E_{part} varied from 0.01 to 1% (mean 0.23 ± 0.03%) being the highest in May and October–November. AN_{part} ranged between 0.1 and 5.4 (mean 1.76 ± 0.2) mg C mg Chl*a*$^{-1}$ h^{-1}, its maximum value was registered on 9 May (Table 1, Fig. 4). The average Chl*a* in 1995 was 25 ± 2 µg L^{-1} with a maximum value of 64 µg L^{-1} on 23 October (Fig. 5).

Total PP_{part} did not differ significantly from PP in the < 40 µm fraction (nonparametric Sign test for difference, $p > 0.1$). Chl*a* in < 40 µm particles was significantly lower than total ($p < 0.0001$). On an average 77 ± 2% of the total Chl*a* passed the 40 µm sieve (Fig. 5). Phytoplankton cells remaining on the 40 µm mesh did not prove very active, making an insignificant contribution to the overall particulate production.

Seasonal variations of integral P_{part}, P_{tot}, $P_{partacid}$, $P_{disspart}$, and $P_{disstot}$ were significantly correlated (Table 2). The dynamics of all fractions of integrated over depth PP (mg C m^{-2} h^{-1}) were correlated with the total solar irradiance on water surface (I_o) while the correlations with I_o per day ($I_o$day) were stronger than those with I_o at midday ($I_o$hour), at the time of actual PP measurement. The correlation of Chl*a* with the vertical maximum of PP (mg C m^{-3} h^{-1}) was stronger than with the integral PP. The daily mean I_{mix} showed strong negative correlation with E_{part}, the correlation of absolute values of PP and I_{mix} was weak. The

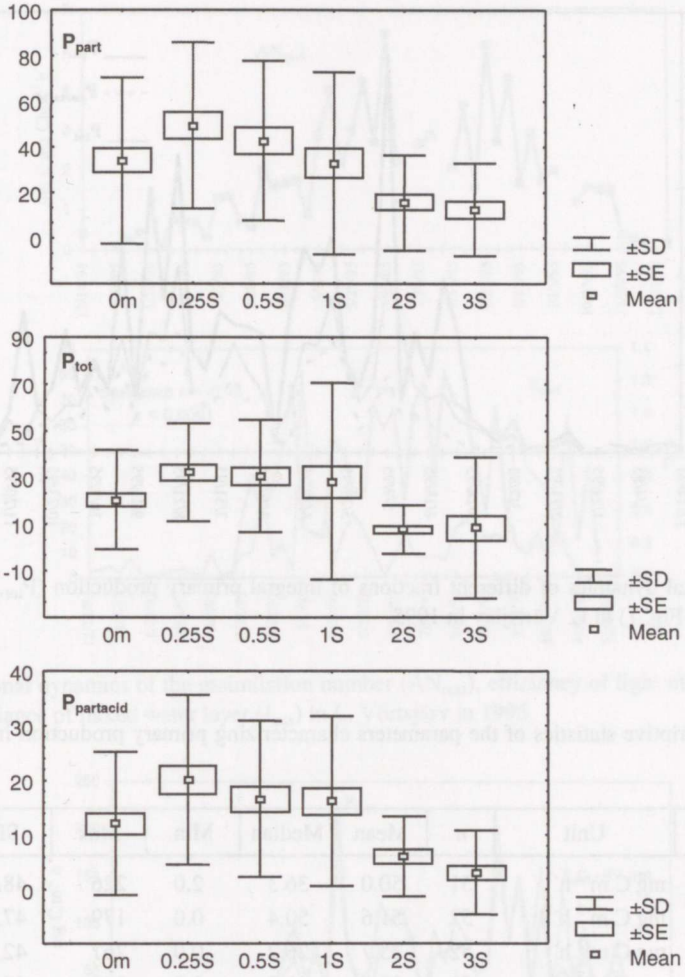

Fig. 2. Depth distribution of different fractions of primary production (P_{tot}, P_{part}, $P_{partacid}$, mg C m^{-3} h^{-1}; explanation in Fig. 1) in L. Võrtsjärv in 1995.

percentages of labile fractions $P_{disstot}$% (=$P_{disstot}/P_{tot}$) and $P_{disspart}$% (=$P_{disspart}/P_{part}$) as well as the ratios $P_{part}/P_{partacid}$ and P_{part}/P_{tot} were correlated neither with light nor with Chl*a*.

$P_{disstot}$% from the beginning of the year up to the end of May (Fig. 6) was higher than for the period June–October (Tukey HSD test for unequal *n*, *p* for difference < 0.01). Diatoms, which dominated up to the end of May, were replaced by blue-greens in June (P. Nõges, unpublished). The correlation of $P_{disstot}$% with the percentage of blue-greens in phytoplankton biomass (CY%) was negative, and that with the percentage of diatoms (BAC%) positive. $P_{disspart}$% was positively correlated with the TN/TP ratio in water (Table 2).

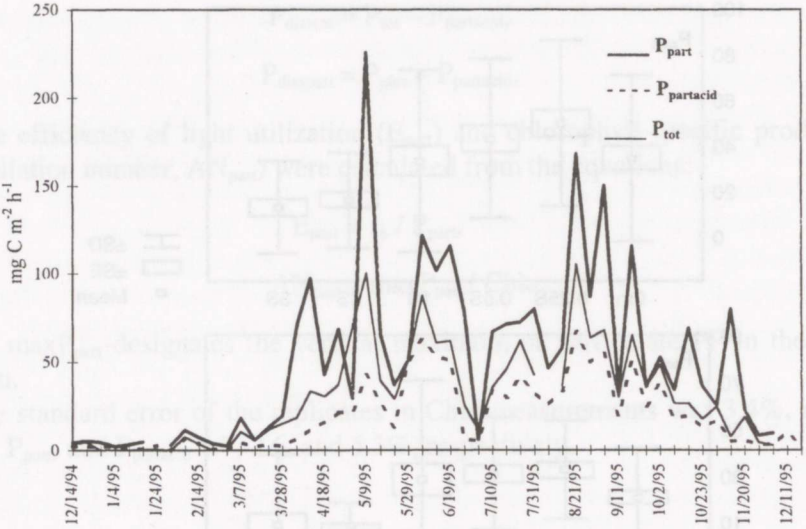

Fig. 3. Seasonal dynamics of different fractions of integral primary production (P_{tot}, P_{part}, $P_{partacid}$; explanation in Fig. 1) in L. Võrtsjärv in 1995.

Table 1. Descriptive statistics of the parameters characterizing primary production in L. Võrtsjärv in 1995

Parameter	Unit	*n*	Mean	Median	Min	Max	SD	SE
P_{part}	mg C m^{-2} h^{-1}	51	50.0	36.3	2.0	226	48.7	6.8
max P_{part}	mg C m^{-3} h^{-1}	52	51.6	50.4	0.0	179	47.4	6.6
P_{tot}	mg C m^{-2} h^{-1}	52	33.7	26.2	0.0	261	42.2	5.9
max P_{tot}	mg C m^{-3} h^{-1}	51	33.1	20.8	0.0	243	40.6	5.7
$P_{partacid}$	mg C m^{-2} h^{-1}	53	19.4	12.9	0.0	67.2	19.3	2.7
max $P_{partacid}$	mg C m^{-3} h^{-1}	53	17.8	11.0	0.0	65.5	17.9	2.5
P_{part} / $P_{partacid}$		52	3.4	2.4	0.0	16.0	3.2	0.4
P_{part} / P_{tot}		47	2.1	1.6	0.0	10.3	2.0	0.3
$P_{disspart}$%		51	0.58	0.59	0.0	1.0	0.22	0.03
$P_{disstot}$%		44	0.36	0.3	0.0	0.9	0.3	0.0
$P_{disspart}$	mg C m^{-2} h^{-1}	53	28.7	16.5	-10.2	183.3	35.1	4.8
$P_{disstot}$	mg C m^{-2} h^{-1}	49	14.7	8.9	-3.3	235.2	34.4	4.9
Secchi	m	53	1.1	0.9	0.5	2.4	0.5	0.1
Chl*a*	mg m^{-3}	49	24.8	23.9	2.1	64.0	15.6	2.2
K	m^{-1}	50	1.9	1.7	1.1	3.2	0.5	0.1
I_{mix}	W m^{-2}	30	43.1	42.3	7.2	109.7	26.1	4.8
E_{part}	%	50	0.23	0.14	0.0	1.0	0.24	0.03
AN_{part}	mg C mg Chl*a*$^{-1}$ h^{-1}	46	1.76	1.6	0.1	5.4	1.4	0.2

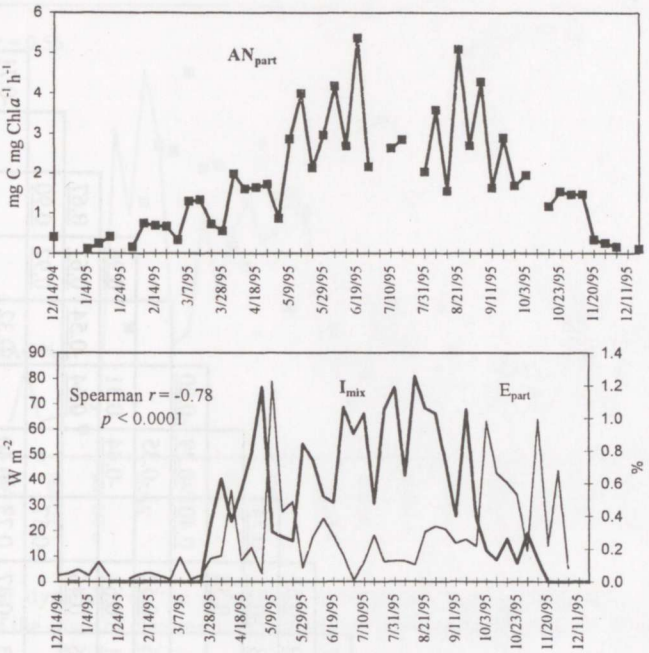

Fig. 4. Seasonal dynamics of the assimilation number (AN_{part}), efficiency of light utilization (E_{part}), and the irradiance of mixed water layer (I_{mix}) in L. Võrtsjärv in 1995.

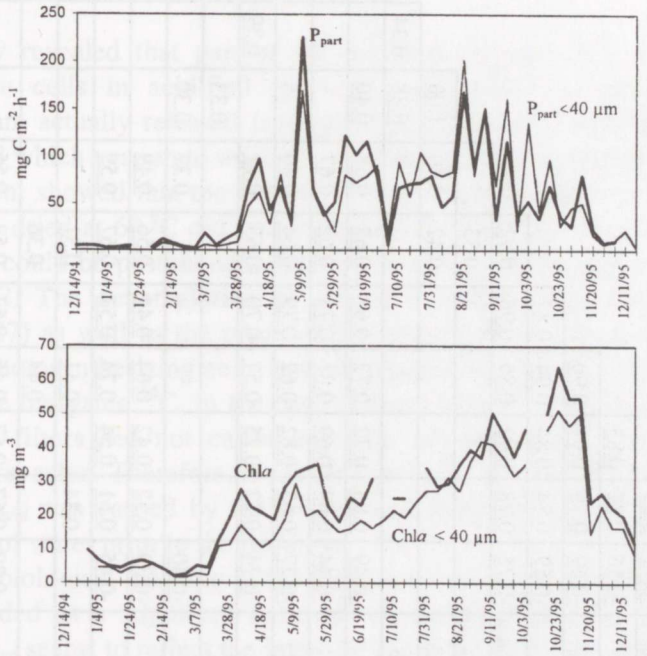

Fig. 5. Particulate primary production (P_{part}) and chlorophyll *a* concentration (Chl*a*) in all particles and in the < 40 µm fraction in L. Võrtsjärv in 1995.

Table 2. Spearman rank correlation coefficients of measured parameters in L. Võrtsjärv, $p < 0.01$ underlined

	S	P_{part}	max P_{part}	P_{tot}	max P_{tot}	$P_{partacid}$	max $P_{partacid}$	$P_{part}/P_{partacid}$	$P_{disspart}$ %	$P_{disstot}$ %	$P_{disspart}$	$P_{disstot}$	Chl*a*	TN/TP	BAC%	CY%	I_o hour	I_o day	AD	I_{mix}	E_{part}
P_{part}	-0.54																				
max P_{part}	-0.71	0.83																			
P_{tot}	-0.56	0.82	0.83																		
max P_{tot}	-0.69	0.75	0.94	0.90																	
$P_{partacid}$	-0.59	0.84	0.84	0.94	0.87																
max $P_{partacid}$	-0.75	0.78	0.92	0.89	0.96	0.92															
$P_{part}/P_{partacid}$						-0.33															
$P_{disspart}$%						-0.42	-0.40	1.00													
$P_{disstot}$%								0.38	0.34												
$P_{disspart}$	-0.49	0.85	0.72	0.72	0.67	0.67	0.68	0.40													
$P_{disstot}$	-0.44	0.69	0.69	0.81	0.73	0.62	0.67			0.60	0.77										
Chl*a*	-0.77	0.63	0.82	0.62	0.79	0.64	0.80				0.59	0.57									
TN/TP	0.74	-0.52	-0.75	-0.57	-0.70	-0.63	-0.71		0.39		-0.38	-0.36	-0.74								
BAC%								0.33		0.56		0.38									
CY%	-0.40						0.37	-0.30		-0.32			0.40	-0.39	-0.80						
$I_o$hour	-0.39	0.52	0.42	0.64	0.44	0.56	0.49				0.46	0.52		-0.35							
$I_o$day	-0.45	0.61	0.54	0.74	0.57	0.67	0.59				0.51	0.61		-0.44	0.31		0.96				
AD		0.34		0.41		0.31				0.38	0.36	0.46			0.64	-0.54	0.61	0.67			
I_{mix}				0.44		0.36							-0.37				0.92	0.90			
E_{part}	-0.39	0.67	0.67	0.45	0.57	0.52	0.55				0.63	0.47	0.73	-0.40		0.32				-0.71	
AN_{part}	-0.51	0.86	0.88	0.86	0.82	0.87	0.83				0.67	0.64	0.51	-0.57			0.64	0.77	0.51		0.49

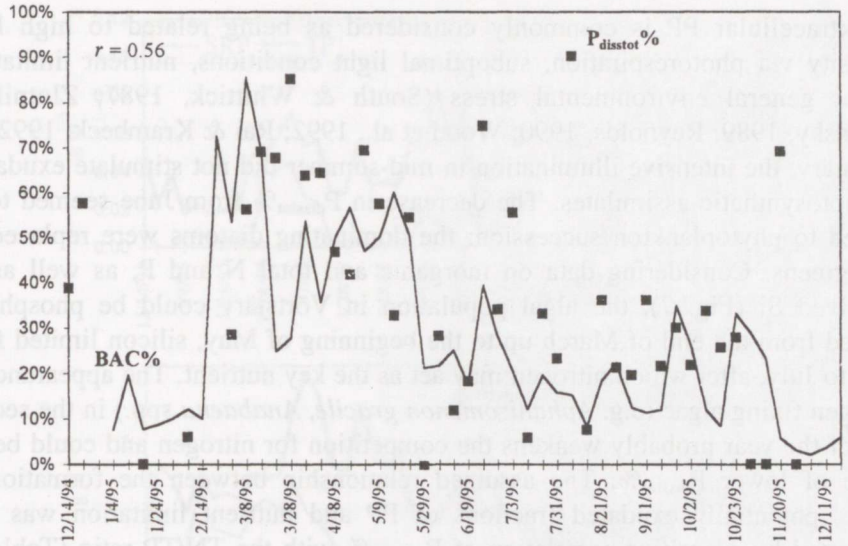

Fig. 6. Seasonal dynamics of the proportion of exudated fraction in total primary production ($P_{disstot}$%) and of the share of diatoms in phytoplankton biomass (BAC%) in L. Võrtsjärv in 1995.

DISCUSSION

Our study revealed that part of the bounded carbon (^{14}C) was lost from phytoplankton cells in acidified ($pH < 2$) water. We do not know which compounds are actually released from phytoplankton cells when the sample is acidified, and which evaporate when the acidified sample is dried at 60 °C. Since our experiment showed that the content of total organic carbon (COD_{Cr}) of the water sample dried at 60 °C did not depend on the presence of acid, the loss of radioactivity could be postulated as caused by the excretion and evaporation of inorganic ^{14}C. The accumulation of excess CO_2 into algal cells (Burns & Beardall, 1987) as well as the precipitation of carbonates due to high pH near intensively photosynthesizing cells can be regarded as causes of the appearance of nonvolatile inorganic ^{14}C. In the case of measuring P_{part} and $P_{partacid}$ the 60 °C treatment of filters did not cause any loss of radioactivity as the control experiments revealed. Therefore, it can be concluded that the difference between P_{part} and $P_{partacid}$ was caused by the loss of radioactivity from cells due to the acidification of water prior to the filtration.

As to the biological meaning of the indicators measured, the parameter $P_{disstot}$ can be regarded as a stipulated indicator of exudated photosynthetic carbon, whereas $P_{disspart}$ seems to reflect the intensity of the formation of the cellular pool of labile organic compounds, and probably also inorganic ^{14}C.

Extracellular PP is commonly considered as being related to high light intensity via photorespiration, suboptimal light conditions, nutrient limitation, and/or general environmental stress (South & Whittick, 1987; Zlotnik & Dubinsky, 1989; Reynolds, 1990; Wood et al., 1992; Rai & Krambeck, 1992). In Võrtsjärv, the intensive illumination in mid-summer did not stimulate exudation of photosynthetic assimilates. The decrease in $P_{disstot}$% from June seemed to be related to phytoplankton succession: the dominating diatoms were replaced by blue-greens. Considering data on inorganic and total N and P, as well as on dissolved Si (Fig. 7), the algal population in Võrtsjärv could be phosphorus limited from the end of March up to the beginning of May, silicon limited from May to July, after which nitrogen may act as the key nutrient. The appearance of nitrogen fixing algae (e.g. *Aphanizomenon gracile, Anabaena* spp.) in the second half of the year probably weakens the competition for nitrogen and could be the cause of lower $P_{disstot}$%. The assumed relationship between the formation of labile, potentially exudated fractions of PP and nutrient limitation was also supported by a positive correlation of $P_{disspart}$% with the TN/TP ratio (Table 2). An increase in TN/TP, reflecting the strengthening of phosphorus limitation, brought about a more intensive exudation of photoassimilates in Võrtsjärv. This is in good accordance with the data of Myklestad (1977), which suggest that in comparison with N limitation, P limitation stimulates the release of a larger proportion of PP.

On the other hand, some investigations have shown that phytoplankton communities dominated by blue-greens excrete smaller molecules than the communities dominated by diatoms (Sundh, 1991, 1992). Although we did not study the chemical composition of exudated matter, our results indirectly confirm this statement. The fact that smaller organic molecules (< 1000 D) are much more easily accessible to bacteria and are assimilated as soon as they are exudated (Tulonen et al., 1992) could be the cause of the lower $P_{disstot}$% during the dominance of blue-greens. Besides, there exists also evidence that the water level acts as an important controller of phytoplankton in Võrtsjärv, realizing its impact through changes in the mean water column irradiance in this very shallow polymictic lake (Nõges, 1995). Since the drop in the water level in the second half of the vegetation period brings about an improvement of light availability and reduces light limitation, lower $P_{disstot}$% can reflect also better living conditions of phytoplankton. The correlation of the AD and $P_{disstot}$% was positive, although no correlation occurred between the share of exudated PP ($P_{disstot}$% and $P_{disspart}$%) and the direct indicators of light availability (I_o, I_{mix}) (Table 2). The last parameters influenced strongly the efficiency of light utilization and assimilation number. It is surprising that AN_{part}, which was in strong positive correlation with I_o, had no correlation with I_{mix} and E_{part}, on the contrary, had strong negative correlation with I_{mix} and no correlation with I_o. Negative correlation of E_{part} and I_{mix} and positive correlation between E_{part} and Chl*a* reflects the higher utilization efficiency at the lower light intensities and at higher phytoplankton biomass.

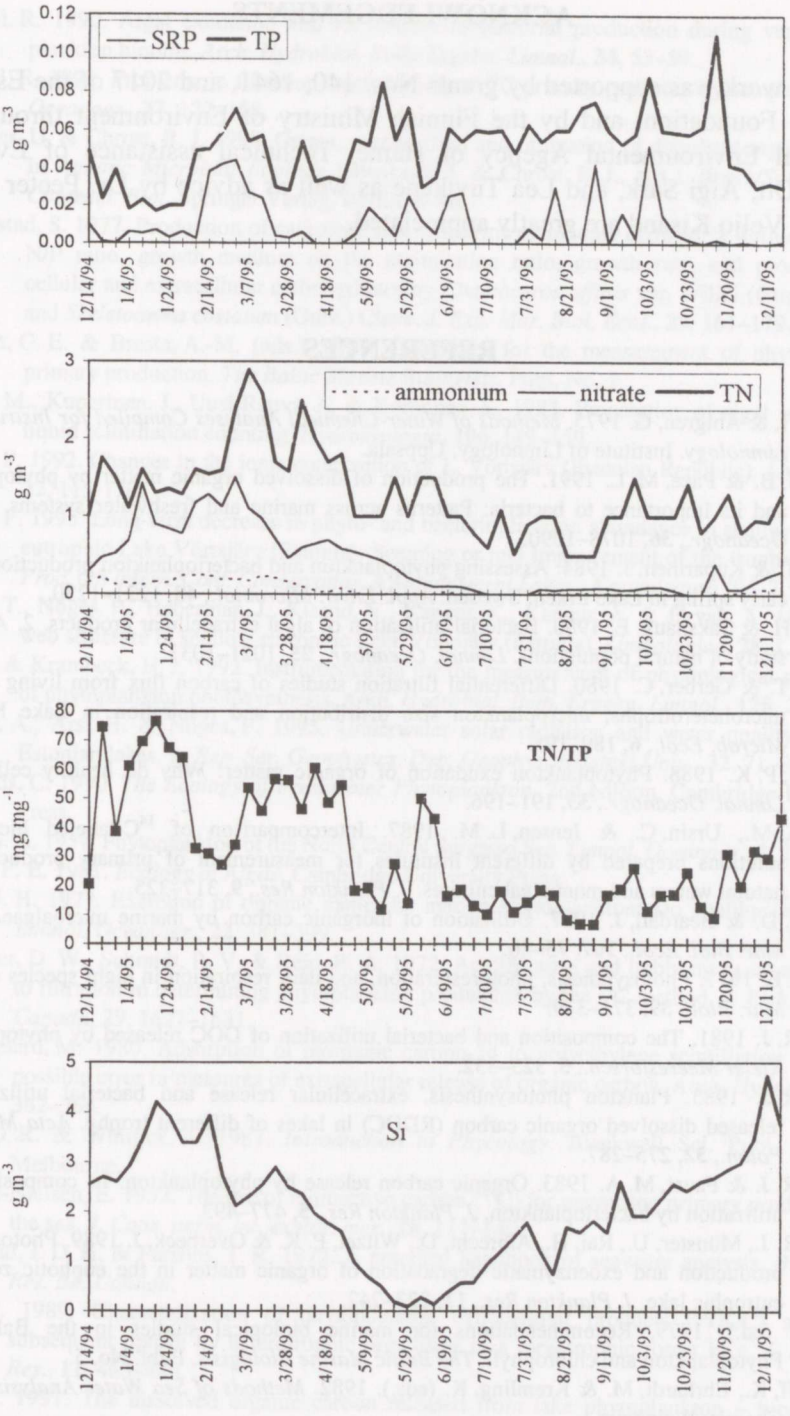

Fig. 7. Seasonal dynamics of soluble reactive phosphorus (SRP), total phosphorus (TP), ammonium, nitrate, total nitrogen (TN), TN/TP ratio, and dissolved silicon in L. Võrtsjärv in 1995.

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PRIMAARPRODUKTSIOONI FRAKTSIOONID VÕRTSJÄRVES

Tiina NÕGES

Primaarproduktsiooni mõõdeti suures madalas eutroofses Võrtsjärves 1995. aasta jooksul kord nädalas. Uuriti radioaktiivse märgise (^{14}C) lülitumist planktoni erinevatesse suurusfraktsioonidesse (< 40 µm, > 40 µm) ja lahustuvasse fraktsiooni. Aasta jooksul lülitati fütoplanktoni rakkudesse 200 grammi süsinikku ruutmeetri kohta, keskmine tunniprodukt sioon keskpäeval oli 50 ± 7 mg C m^{-2}. Klorofüll *a* kontsentratsiooni alusel hinnates moodustasid 40 µm-st suuremad rakud 23% fütoplanktoni koguhulgast, kuid nende produktsioonikiirus oli väiksemate rakkudega võrreldes väga madal. Lahustuv fraktsioon oli keskmiselt 37% koguproduktsioonist. Sesoonselt määrasid lahustuva primaarproduktsiooni osakaalu eelkõige fosfori limitatsioon ja fütoplanktoni liigiline koosseis. Lahustuva fraktsiooni osakaal oli suurem kõrgematel üldlämmastiku ja üldfosfori suhte (TN : TP) väärtustel ning ränivetikate domineerimise ajal; madalam siis, kui valdasid sinivetikad (tsüanobakterid). Võrtsjärves näib valguse osa lahustuva esmasproduktsiooni tekkel olevat üsnagi väike. Samas oli valgusel oluline roll assimilatsiooniarvu ja valguse kasutamise efektiivsuse kujunemisel.