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ECOLOGICAL RELATIONS OF MAIN PLANKTON COMPONENTS IN THE PELAGIAL OF LAKE PEIPSI

Abstract. The seasonal dynamics of water chemistry, temperature, adenosintriphosphate (ATP), and chlorophyll *a* (Chl) concentration, and the biomass and production of phyto-, zoo- and bacterioplankton was investigated during the vegetation periods of 1985 and 1986. Statistical analysis revealed that the intensity and balance of production processes were chiefly affected by water temperature. Seasonal observations of ATP and Chl concentrations showed an accumulation of "dead" chlorophyll in autumn. This was evidently caused by the predominance of large algae, non-edible for zooplankton, and reduced destruction activity in cold water. The decay of the algal mass during winter may cause oxygen deficiency and the appearance of H_2S on the bottom of the lake. The average production values per vegetation period for the years studied were as follows: phytoplankton — 203.5 g C $\cdot$ m^{-2}; bacterioplankton — 37.9 g C $\cdot$ m^{-2}; filter-feeding zooplankton — 20.6 g C $\cdot$ m^{-2}; and predatory zooplankton — 1.5 g C $\cdot$ m^{-2}. Herbivorous zooplankton production constituted 10.1% of primary production. This ratio indicates that filtrators feed mostly on living algae while the detrital food chain seems to be of little importance. Bacteria meet on an average 11% of zooplankton food requirements. The mean destruction activity (D) was 2.166 g C $\cdot$ m^{-2} $\cdot$ day^{-1}. D exceeded gross primary production in almost all cases. Evidently, the sharp peaks of primary production were missed because of long measuring intervals; the organic matter, produced during these peaks, raises D for a longer period. Moreover, the early phytoplankton maximum during the under-ice or ice-break period was not observed, which could cause an underestimation of the yearly phytoplankton production value.

Key words: Lake Peipsi, plankton, productivity, ATP, chlorophyll *a*, destruction activity, trophic relations.

Introduction

Trophic chains are responsible for transformation of matter and energy in the ecosystem. The grazing chain is characterized by the direct consumption of plant biomass by herbivores while the detrital chain contains an additional link between primary producers and consumers, i. e. the bacterial loop. Among the trophic chains in the pelagial of a waterbody, three main types might be distinguished:

1. The transformation phytoplankton→fish is the shortest and the most effective, but the rarest way; it does not exist in Estonian waterbodies. Only few species of fish in the world are able to feed on phytoplankton.

2. The transformation phytoplankton→zooplankton→fish is the classical grazing chain. The indispensable condition for this kind of transformation is the suitability of phytoplankton as food for herbivorous zooplankton.

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3. The transformation phytoplankton→detritus+bacteria→zooplankton→fish takes place if live phytoplankton is not consumable for zooplankton due to its unsuitable size, chemical composition, etc. This detrital food chain consists of the greatest number of links and therefore here the efficiency of energy transformation from autotrophs to top predators is the lowest.

The phytoplankton—zooplankton interface is a crucial point in the determination of the type of trophic chain in a pelagic ecosystem.

The main task of our studies in Lake Peipsi was to determine the general type of energy transformation in the pelagial of this large waterbody. Results of complex hydrochemical and hydrobiological investigations are analysed in the present paper to resolve this problem.

Description of Lake Peipsi

Lake Peipsi is situated on the border of Estonia and Russia. It consists of three different parts. The biggest, northern part is also called Lake Peipsi *sensu strictu*. Its area is 2611 km^2, mean depth 8.3 m, and greatest depth 12.9 m. The southern part is Lake Pihkva (708 km^2, mean depth 3.8 m). These two parts are connected by the narrow river-shaped Lake Lämmijärv (236 km^2, mean depth 2.6 m) (Loopmann, 1984). By its area, Lake Peipsi occupies the fourth position among the lakes of Europe.

According to the classification of Mäemets (1974), which was made for Estonian lakes, Lake Peipsi *s. str.* belongs to unstratified eutrophic lakes with mesotrophic features, Lake Lämmijärv has some dyseutrophic features, while Lake Pihkva is a typical unstratified eutrophic lake.

The amount of water in Lake Peipsi is 25 km^3. The water in the part of the lake belonging to Estonia makes up 89% of the surface fresh-water supply and gives 95% of the fresh-water fish catch of the republic. Nowadays Lake Peipsi is considered to be a promising source of water supply for North-East Estonia and Tallinn. The water resources of Lake Peipsi can be estimated as practically inexhaustible for Estonia; moreover, this lake has great importance from the aspect of fishery and recreation.

North-East Estonia is one of the most developed industrial regions of the republic, where the oil-shale industry occupies the first position. The waste waters and gaseous emission of toxic sulphur and nitrogen oxides, hydrogen chlorine, and carcinogenic compounds from the power stations operating on pulverized oil-shale have a considerable influence on the chemical composition of water in Lake Peipsi. Waste waters from oil-shale mines accumulate in the lake through the Rannapungerja River. The majority of phosphorus and nitrogen compounds are carried into the lake by the waters of the rivers Velikaya and Emajõgi. In 1985 the content of total phosphorus in these rivers was close to ecologically permitted concentration (100 mg $P \cdot m^{-3}$) or seldom even exceeded it (Lindpere et al., 1987). The strongest harmful influence from the aspect of nutrient load is coming from the River Suur Emajõgi and in particular from the town of Tartu, which up to now has no sewage purification plant.

The lake was thoroughly investigated in 1962—1963 by scientists of the Institute of Zoology and Botany of the Estonian Academy of Sciences. Plankton, fish fauna, and higher vegetation of the lake were investigated in the course of several expeditions. The water chemistry has also been measured from the 1960s. As the result of these investigations, Lake Peipsi, and especially its biggest part, was identified as a waterbody in which the features of oligotrophic, mesotrophic, and eutrophic type were combined in a characteristic way. The water was very pure in microbiological aspect. In phyto- and zooplankton, benthos, and fish fauna the indicators of mesotrophic and eutrophic lakes were prevalent. The mean fish catch during the period 1931—1972 was 29 $kg \cdot ha^{-1}$, often reaching 36 $kg \cdot ha^{-1}$. This is a very high value and exceeds that of all other large lakes in North Europe. The hydrochemical and hydrobiological conditions in Lake Peipsi give reason to assume it to be a promising waterbody for eel introduction (Mäemets et al., 1982).

The complex investigations of Lake Peipsi carried out in the early 1980s showed that the situation of this waterbody had been changing for the worse. As compared with the 1960s, the ion content of water had changed markedly. The concentration of sodium and potassium had increased 5.1 times (up to 22.5 mg $\cdot l^{-1}$), that of sulphate ions 4.8 times (up to 47.5 mg $\cdot l^{-1}$), and chloride ions 3.3 times (up to 10.3 mg $\cdot l^{-1}$) while the concentration of calcium ions remained more or less on the same level (26—40 mg $\cdot l^{-1}$) (Lokk et al., 1988). The fluctuation range of oxygen and CO_2 concentration also increased. The blue-green algal blooms caused by *Aphanizomenon flos aquae*, *Aphanothece saxicola*, *Microcystis pulverea* or *Gloeotrichia echinulata* took place in the summer phytoplankton. Great fluctuations of oxygen content in warm water caused the fish-death event in summer 1988. It was evidently the result of algal bloom. In April 1990 the pH of water increased up to 9.5; obviously due to the bloom of the diatom *Melosira islandica* ssp. *helvetica*. Such events are undoubtedly alarming, indicating to the critical situation in the ecosystem of the lake.

In 1984 a complex research programme was worked out in which more than 20 institutions of Estonia and some of Russia took part. The main task of investigations was to estimate the present state of the ecosystem of the lake and to prognosticate its future, taking into account the influence of natural factors and human impact.

The characteristics analysed were the following:

$t°$ — water temperature, °C;
pH — water reaction;
HCO_3 — total alkalinity, mg$\cdot l^{-1}$;
S — water transparency by the Secchi disk, m;
O_2 — oxygen concentration, mg$\cdot l^{-1}$;
POC — particulate organic carbon concentration, g C$\cdot m^{-3}$;
Chl — chlorophyll *a* concentration, mg$\cdot m^{-3}$;
Pheo — concentration of pheopigments, mg$\cdot m^{-3}$;
Detr — detritus concentration, mg C$\cdot m^{-3}$;
ATP — adenosine triphosphate concentration, mg$\cdot m^{-3}$;
B_{phyto} — phytoplankton biomass, mg C$\cdot m^{-3}$;
B_{bact} — bacterial biomass, mg C$\cdot m^{-3}$;
B_{zoop} — total zooplankton biomass, mg C$\cdot m^{-3}$;
B_{filt} — biomass of herbivorous (filtrative) zooplankton, mg C$\cdot m^{-3}$;
Fil% — relative content of herbivorous forms in zooplankton biomass;
P_{tot} — total phosphorus concentration, mg$\cdot m^{-3}$;
N_{tot} — total nitrogen concentration, mg$\cdot m^{-3}$;
N/P — N_{tot}/P_{tot};
D — destruction activity, mg C$\cdot m^{-2}\cdot day^{-1}$;
PP — primary production;
PP_{max} — primary production in a water layer under optimum light conditions, mg C$\cdot m^{-3}\cdot h^{-1}$;
PP_{int} — integral primary production under 1 m^2 surface, mg C$\cdot m^{-2}\cdot day^{-1}$;
PP_g — gross primary production, mg C$\cdot m^{-2}\cdot day^{-1}$;
PP_n — net primary production, mg C$\cdot m^{-2}\cdot day^{-1}$;
$AN = PP_{max}/Chl$ — assimilation number;
Q — total irradiance of 1 m^2 water surface, kJ$\cdot m^{-2}\cdot day^{-1}$;
$Eff = PP_{int}/Q$ — efficiency of photosynthesis;
P_{bact} — bacterial production, mg C$\cdot m^{-3}\cdot day^{-1}$;
P_{filt} — filtrative zooplankton production, mg C$\cdot m^{-3}\cdot day^{-1}$;

P_{pred} — predatory zooplankton production, mg $C \cdot m^{-3}$ day^{-1};
C_{filt} — filtrative zooplankton ration (food requirement), mg $C \cdot m^{-3} \cdot day^{-1}$;
C_{pred} — predatory zooplankton ration, mg $C \cdot m^{-3} \cdot day^{-1}$;
GR_{phyto} — zooplankton grazing rate on phytoplankton, mg $C \cdot m^{-3} \cdot day^{-1}$;
GR_{bact} — zooplankton grazing rate on bacterioplankton, mg $C \cdot m^{-3} \cdot day^{-1}$.

Among these indicators Q and $t°$ are purely abiotic factors; pH, HCO_3, and O_2 are affected by production and destruction processes. Intensive photosynthesis causes an increase in their values, while the prevalence of destructive processes brings about a decrease. Water transparency is an abiotic factor influencing light conditions in water; transparency itself depends on the amount of seston and, consequently, on primary production.

Among the biotic parameters those belonging to the first group — Chl, ATP, B_{phyto}, B_{zoop}, B_{filt}, Pheo, B_{bact}, POC, Detr, P_{tot}, N_{tot} — characterize the amount of various groups of organisms. Chl characterizes the phytoplankton biomass; ATP consists only of live cells and in this way reflects the amount of all living organisms: bacteria, microalgae, and microzooplankton. Pheopigments are the destruction products of chlorophylls. P_{tot} and N_{tot} reflect the amount of biogenes connected with plankton metabolism.

The second group of biotic parameters characterize the intensity and balance of metabolic processes. PP_{max}, PP_{int}, PP_g, PP_n, P_{bact}, P_{filt}, and P_{pred} are indicators of productivity; C_{filt} and C_{pred}, of the food requirement of organisms. AN reflects the photosynthetic capacity of the chlorophyll *a* unit. Eff indicates the relative amount of solar energy bound by primary producers. The N/P ratio permits to forecast which element will limit photosynthesis (Forsberg et al., 1978; De Haan and Moed, 1984). The Chl/ATP ratio increases according to the escalation of autotrophic processes in an ecosystem (Paerl et al., 1976; Burns et al., 1984). The interrelation P_{filt}/PP_{int} characterizes the role of nonpredatory zooplankton in a trophic net.

Material and Methods

The material for the analyses was collected in 1985—1986 by the working group of the Võrtsjärv Limnological Station during expeditions on Lake Peipsi. We investigated the central area of the largest part of Lake Peipsi (2611 km^2) with a mean depth of 8.3 m. All parameters were measured twice a month (from May to November) at two stations (Fig. 1) and four depth horizons.

A Secchi disc was used to measure *S*. In order to determine Chl, Pheo, ATP, and POC, 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. The Holm-Hansen method was applied for ATP measurements (Holm-Hansen and Booth, 1966; Holm-Hansen and Paerl, 1972; Nõges, 1989). Before filtration water was strained through a 150 μm net to remove zooplankton. Filters were boiled in 5 ml Tris buffer (0.02 M; pH 7.8) for 3 min, then frozen and stored at −20 °C prior to analysis. The ATP content was determined by the luciferin—luciferase method using an LKB-Wallac Luminometer 1251, the ATP monito-

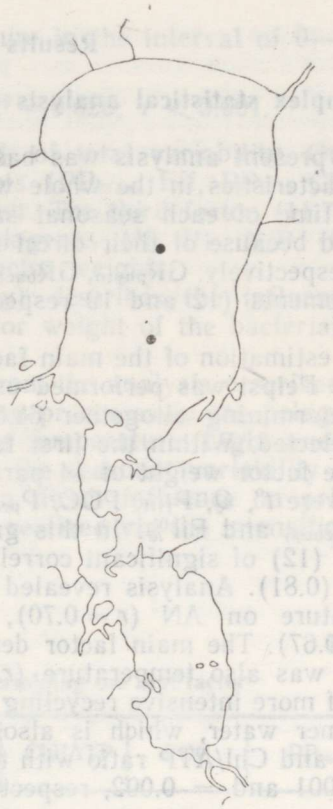

Fig. 1. Sampling stations in the pelagial of Lake Peipsi.

ring reagent, and ATP standard (LKB Instruments). In order to determine N_{tot} and P_{tot}, organic compounds were mineralized, with persulphate, into nitrite and phosphate. Standard photometric analysis was then applied (New Baltic Manual . . . , 1972). All biomasses were calculated on the basis of microscopically measured bivolumes using cell density 1 $g \cdot ml^{-1}$. PP_{max} and PP_{int} were measured by the radiocarbon method, PP_g, PP_n and D by the oxygen light- and dark-bottle method (Greeson, 1977).

P_{filt} and P_{pred} were calculated using the physiological method (Винберг, 1968, 1979; Waters, 1977; Методические . . . , 1984; Иванова, 1985; Nõges et al., in press).

P_{bact} was measured by the direct count of increment in test bottles in prefiltered water (pore size 2.5 μm for removing predators) and calculated using the formulae:

$$g = t \times \log 2/(\log B_t - \log B_o); \quad P = B \times \ln 2/g,$$

where g — generation time, h; t — exposition time, h; B_o — initial bacterial concentration in a test bottle; B_t — final bacterial concentration in a test bottle; P — bacterial production; B — average bacterial biomass (Иванов, 1955; Sorokin and Kaddota, 1972; Гак, 1975; Методические. . . , 1982).

POC was measured by means of the wet combustion of seston on glass fiber filters (Методические . . . , 1981). Organic matter was oxidized with 0.1 N $K_2Cr_2O_7$ in concentrated sulphuric acid. POC was calculated from the oxygen consumption rate using the equation 1 mg O_2 = 0.69 mg organic matter = 0.300 mg C.

Detr was estimated as the difference between POC and the sum of B_{phyto}, B_{bact}, and B_{zoop}.

Zooplankton grazing experiments were carried out in a specially constructed twin bathometer (according to Gliwicz, 1968, 1969; Haney, 1971, 1973; Roman and Rublee, 1981; Hart and Christmas 1984; Nõges, in press).

The following coefficients were used in calculations: for B_{phyto} and B_{bact}: 1 mg wet biomass = 0.1 mg C = 1 cal = 4.187 J (Nauwerk, 1963; Vollenweider et al., 1974; Гак, 1975; Бульон, 1976); for B_{zoop}: 1 mg wet biomass = 0,056 mg C = 0.6 cal = 2.5 J (Mullin, 1969; Винберг, 1979).

Results and Discussion

1. Complex statistical analysis

The present analysis was based on the mean values of the majority of characteristics in the whole water column, measured at both stations at the time of each seasonal sampling ($n = 42$). C_{filt} and C_{pred} were excluded because of their direct mathematical relationship with P_{filt} and P_{pred}, respectively. GR_{phyto}, GR_{bact}, and D were excluded because of too few measurements (12 and 10 respectively) in comparison with other parameters.

The estimation of the main factors determining the plankton dynamics in Lake Peipsi was performed using factor analysis. Four strongest factors, determining altogether 68.5% of variability of all characteristics, were selected. Within the first factor (responsible for 31.7% of variability) the factor weight of 14 parameters out of 27 was greater than 0.6. These were $t°$, Q, P_{filt}, POC, P_{pred}, Chl/ATP, B_{bact}, month, AN, PP_{int}, S, Detr, B_{zoop}, and Fil%. In this group water temperature had the highest number (12) of significant correlations (Table 1) and the greatest factor weight (0.81). Analysis revealed the strongest influence ($P < 0.0001$) of temperature on AN ($r = 0.70$), on Fil% ($r = -0.67$), and on POC ($r = -0.67$). The main factor determining the dynamics of primary production was also temperature ($r = 0.59$; $P = 0.0002$). This might be the result of more intensive recycling of organic matter and mineral nutrients in warmer water, which is also reflected by the decrease of the POC amount and Chl/ATP ratio with the increase of $t°$ ($r = -0.67$ and -0.54; $P < 0.0001$ and $= 0.002$, respectively).

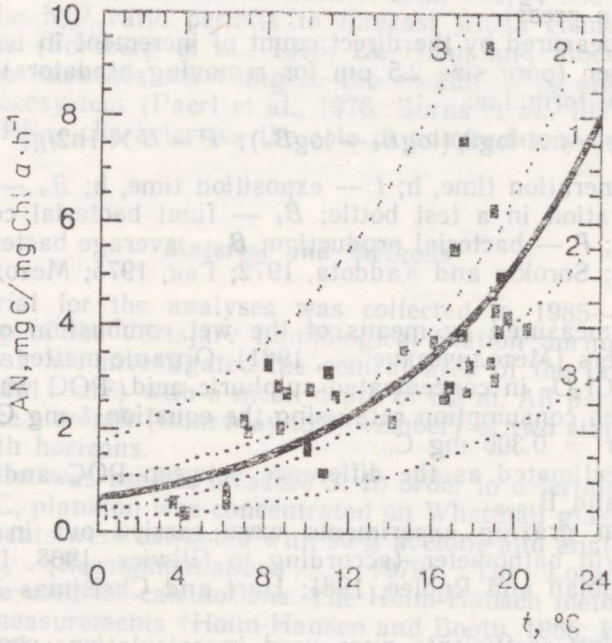

Fig. 2. Regression between assimilation number and water temperature (*1*) in the pelagial of Lake Peipsi in 1985 and 1986. Borders indicate probability levels $P=0.05$ (*2*) and $P=0.01$ (*3*).

AN was determined by water temperature in the interval of 0—24 °C with the exponential function (Fig. 2):

$$AN = EXP\ (-0.444 + 0.105\,t°);\ R^2 = 0.628;\ P < 0.001.$$

The second factor accounted for 15.9% of total variability. On the basis of the greatest (>0.6) factor weights (PP_{max}, Eff, PP_{int}, Chl) it can be regarded as the phytoplankton factor. The third factor (11.7% of variability) describes the influence of biogenes (N, P). N/P (0.84), P_{tot} (−0.60) and N_{tot} (0.51) had great factor weights.

The fourth factor (9.2% of variability) describes the influence of bacteria on plankton metabolism. The factor weight of the bacterial biomass was −0.9.

The most important conclusion drawn from the analysis described was that the intensity and balance of production processes in the pelagial of Lake Peipsi were chiefly affected by water temperature. Light and temperature are the main factors determining the seasonal variability of all processes in ecosystems. Irradiation has a direct influence on primary production, the influence of temperature is realized via the intensification

Table 1

Correlation matrix of parameters determining the first factor

	S	*t°*	AN	Chl/ATP	POC	PP_{int}
Month	−0.7	−0.39	−0.28	0.61	0.5	−0.2
P_{filt}	0.24	0.53	0.65	−0.34	−0.44	0.68
P_{pred}	0.23	0.52	0.35	−0.27	−0.49	0.39
B_{bact}	−0.46	−0.36	−0.11	0.66	0.25	−0.34
Fil%	−0.35	−0.67	−0.29	0.29	0.51	−0.14
Detr	−0.26	−0.50	−0.37	0.17	0.71	−0.57
B_{zoop}	0.13	0.26	0.34	−0.25	−0.41	0.42
Q	0.65	0.63	0.46	−0.59	−0.62	0.29
PP_{int}	0.18	0.59	0.74	−0.31	−0.28	
POC	−0.62	−0.67	−0.43	−0.45		
Chl/ATP	−0.51	−0.54	−0.41			
AN	0.22	0.70				
t°	0.48					

	Q	B_{zoop}	Detr	Fil%	B_{bact}	P_{pred}	P_{filt}
Month	−0.9	−0.23	0.14	0.18	0.52	−0.26	−0.35
P_{filt}	0.48	0.79	−0.55	−0.32	−0.43	0.74	
P_{pred}	0.38	0.82	−0.62	−0.67	−0.45		
B_{bact}	−0.49	−0.36	0.30	0.32			
Fil%	−0.35	−0.33	0.43				
Detr	−0.27	−0.62					
B_{zoop}	0.32						

Underlined figures indicate correlation coefficients, significant on the >95% level.

of phosphorus and nitrogen remineralization (Golterman, 1976). In case the assimilation number and primary production are limited by water temperature, the primary production rate can be assumed as caused by the availability of biogenes (Sommer, 1988). In such a case the productivity of the lake has not achieved the maximum possible level of the latitude.

Further analysis was aimed at determining general types of relations in a plankton community. Temperature and radiation were excluded as parameters influencing all other indexes. The rest of the characteristics were again subjected to factor analysis. The strongest factor was responsible for 26.6% of variability, within this factor P_{filt}, P_{pred}, POC, Detr, B_{zoop}, Fil%, PP_{int}, AN, and Chl/ATP had the greatest (>0.6) factor weights. Consequently, the relationships of phytoplankton and zooplankton were mainly determined by this factor. The intensification of PP brought about an increase in P_{filt} ($r = 0.68$, $P < 0.0001$), the latter in its turn caused a growth of P_{pred} ($r = 0.74$, $P < 0.0001$) (Table 1).

Detr, too, turned out to be quite a good characteristic of the processes taking place in a plankton community. The correlation coefficients of Detr with P_{filt} and P_{pred} were negative and significant on the level $P < 0.01$ (Table 1), which indicates an important role of zooplankton in decreasing the concentration of dead organic material. Phytoplankton-zooplankton relations proved to be another important determinant in the ecosystem of Lake Peipsi. Their detailed analysis will follow in Chapter 5.

Statistical analysis left the role of ATP, Chl, and Chl/ATP ratio as characteristics of the status of an ecosystem unclear. A detailed analysis will be presented in Chapter 2.

2. Estimation of the state of the phytoplankton community during the vegetative period, based on ATP and Chl

The determination of ATP in microplankton was introduced by Holm-Hansen and Booth (1966). Living organisms have a comparatively constant ATP content, accounting on an average for about 0.4% of the organic carbon content (Holm-Hansen, 1970; Holm-Hansen and Paerl, 1972). This fact serves as a basis for the determination of the microplankton biomass using ATP assays. Assuming that adenosine triphosphate is contained only within live cells and decomposes rapidly after their death, the method permits the estimation of the live seston component. Chlorophyll *a* is a specific photosynthetic pigment, but since its decomposition after the cell's death is much slower, the overestimation of the phytoplankton biomass on the account of detrital chlorophyll is probable.

If one considers that the biomass of phytoplankton in Lake Peipsi exceeds considerably those of zooplankton and bacterioplankton (Fig. 3), ATP has to be in a good correlation with the biomass of live phytoplankton as well as with PP_{max}. The results of all seasonal measurements performed in 1985 and 1986 expressed no close relationships between PP_{max}, ATP, and Chl. A hypothesis was set that the character of interdependence varied in the course of plankton development.

As seen in Fig. 4, changes in ATP during the first period of vegetation (from May to August) were in a good agreement with changes in Chl and PP. Later Chl showed a tendency to increase while ATP diminished. The summer—autumn increase of Chl was not accompanied by an increase in PP. The latter, on the contrary, decreased according to the decline of ATP. The intensity of destructive processes in Lake Peipsi decreased in autumn (see Fig. 5, Table 2), which can be explained by a sharp temperature fall (Fig. 4). Probably, non-decomposed chlorophyll

in dead cells (the so-called detrital chlorophyll) starts accumulating under these conditions. This is evidently caused by the domination of large algae non-edible for zooplankton, e. g. *Melosira* spp. and *Aphanothece saxicola*, and the reduced destruction activity in cold water.

The differences of correlative relationships between ATP, Chl, and PP, depending on the period of plankton development, were also revealed. From May to August PP_{max} correlated strongly with Chl ($r = 0.68$; $P < 0.001$). Chl in the range of 0—24 mg · m^{-3} determined the PP value up to 61.7% according to the regression equation:

$$PP_{max} = EXP(2.39 + 0.27\,Chl); \quad R^2 = 0.617; \quad P < 0.001.$$

The correlation between PP and ATP during this period was insignificant.

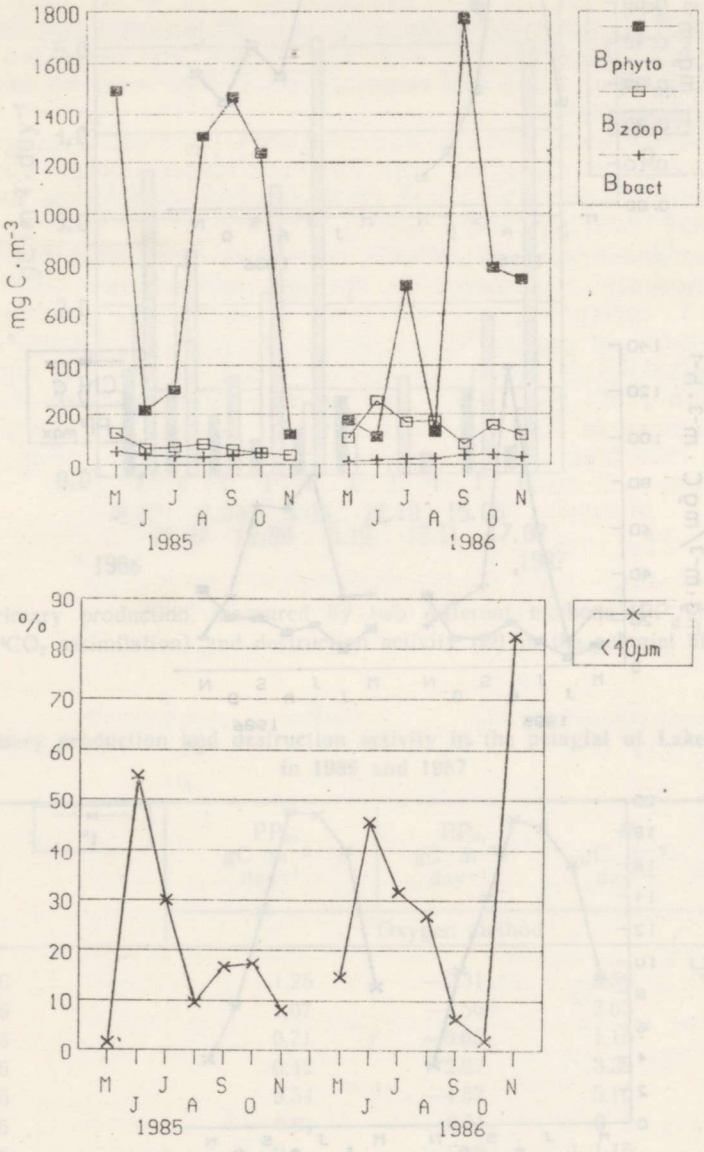

Fig. 3. Seasonal dynamics of phyto-, zoo- and bacterioplankton biomasses and the percentage of consumable phytoplankton (<40 µm) biomass in the pelagial of Lake Peipsi in 1985 and 1986.

From September till November the situation had changed: the correlation between Chl and PP_{max} was insignificant; the latter was strongly dependent on ATP ($r = 0.52$; $P = 0.08$). Consequently, during the period when destructive processes are of low intensity, the ATP in seston is a better measure of phytoplankton productivity than Chl (see also Nõges, 1989; Ныгес et al., 1989).

The accumulation of detrital chlorophyll in late autumn indicates that the organic matter produced in this period will precipitate after the

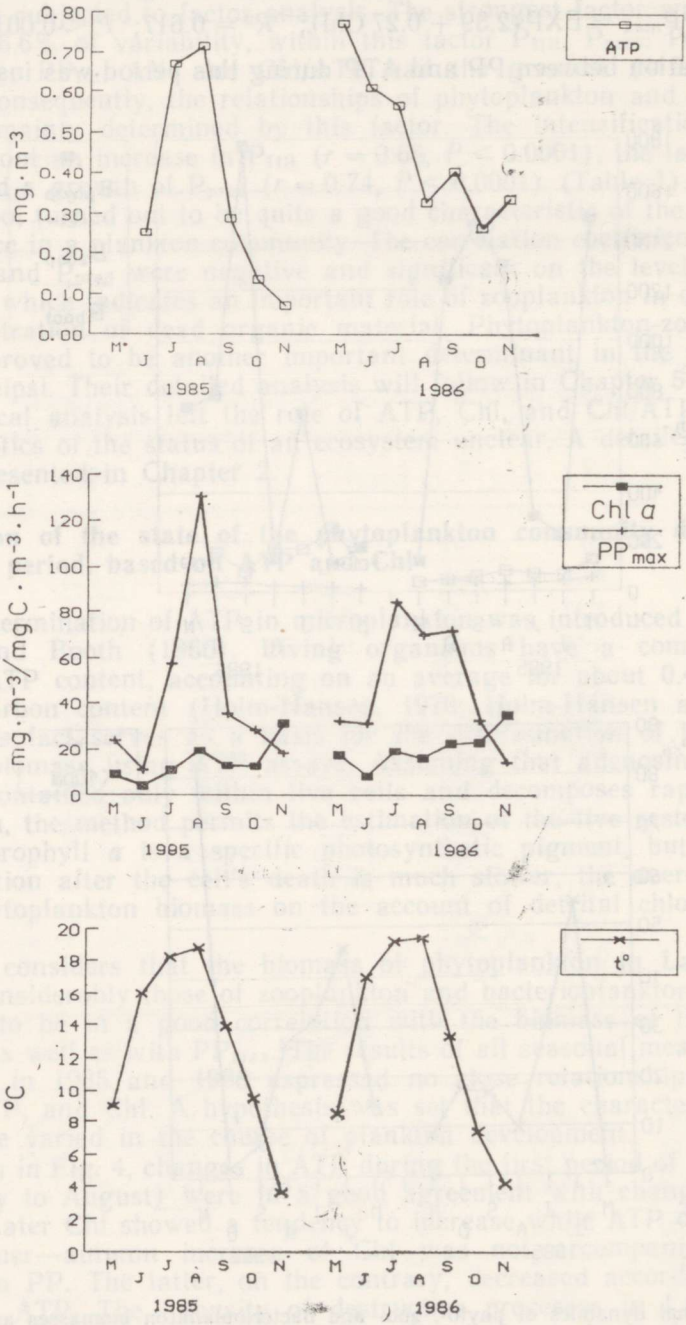

Fig. 4. Seasonal dynamics of Chl, ATP, PP, and water temperature in the pelagial of Lake Peipsi in 1985 and 1986.

appearance of the ice cover. The decay of the algal mass and detritus during winter may cause oxygen deficiency on the bottom of the lake. Taking into account that the concentration of sulphates in Lake Peipsi has grown (Mäemets and Tiidor, 1982) due to the inflow of water from oil-shale mines and air pollution (Raia et al., 1987), the oxygen depletion increases the risk of H_2S formation on the bottom of the lake. According to Pihlak et al. (Пихлак et al., 1987), the highest concentrations of sulphates in Lake Peipsi approach the value of 50 $mg \cdot l^{-1}$ above which the rate of sulphate reduction depends only on the availability of organic substrates (Горленко et al., 1977).

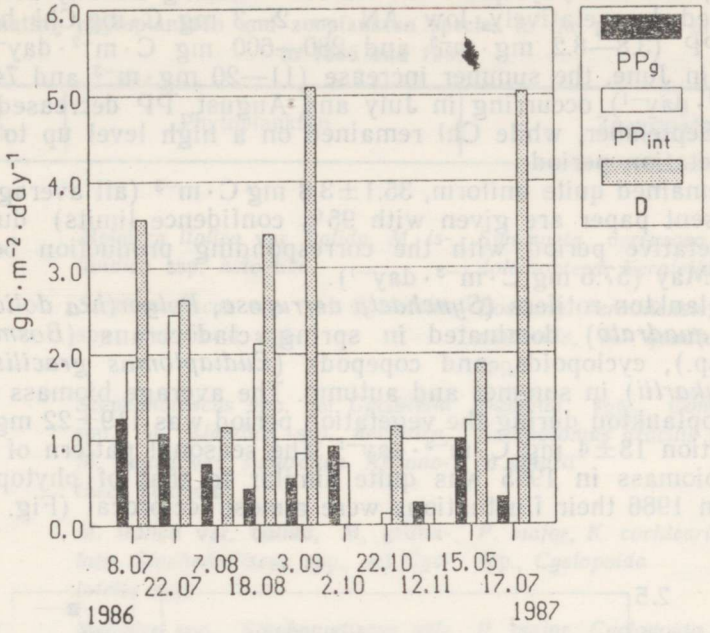

Fig. 5. Primary production, measured by two different methods (PP_g by O_2 release, PP_{int} by $^{14}CO_2$ assimilation) and destruction activity (D) in the pelagial of Lake Peipsi.

Table 2

Primary production and destruction activity in the pelagial of Lake Peipsi in 1986 and 1987

Date	PP_g, $gC \cdot m^{-2} \cdot day^{-1}$	PP_n, $gC \cdot m^{-2} \cdot day^{-1}$	D, $gC \cdot m^{-2} \cdot day^{-1}$	PP_{int}, $gC \cdot m^{-2} \cdot day^{-1}$
	Oxygen method			^{14}C method
08. 07. 1986	1.25	−2.31	3.56	1.91
22. 07. 1986	1.07	−1.56	2.63	2.46
07. 08. 1986	0.71	−0.65	1.15	0.53
18. 08. 1986	0.42	−2.97	3.39	2.12
03. 09. 1986	0.54	−4.57	5.10	0.84
02. 10. 1986	0.91	0.91	0	0.71
22. 10. 1986	0	−1.15	1.15	0.13
12. 11. 1986	0.25	0.25	0	0.18
15. 05. 1987	1.00	−0.87	1.87	1.22
07. 07. 1987	0.32	−4.72	5.04	0.75

3. Seasonal dynamics of phyto-, zoo- and bacterioplankton

In phytoplankton diatoms (mostly the *Melosira* spp.) were dominant during the whole vegetation period. The abundance of smaller centric diatoms (*Stephanodiscus*, *Cyclotella*) reached their peak densities in June. In summer and autumn blue-green algae (*Aphanothece saxicola*, *Microcystis aeruginosa*) supplemented the species list (Table 3). The rapid development of phytoplankton began in early spring, just after or even during the ice-drift (at the end of April or at the beginning of May). In mid-May Chl (10—20 mg·m^{-3}) was already quite high, while PP was only moderate (370 and 670 mg C·m^{-2}·day^{-1} in different years; Fig. 6). The assumption that phytoplankton started declining already in mid-May is supported by relatively low AN — 2—3 mg C·mg Chl·h^{-1}. Low Chl and PP (3.8—8.2 mg·m^{-3} and 280—600 mg C·m^{-2}·day^{-1}) were registered in June, the summer increase (11—20 mg·m^{-3} and 740—2100 mg C·m^{-2}·day^{-1}) occurring in July and August. PP decreased significantly in September, while Chl remained on a high level up to the end of the vegetation period.

B_{bact} remained quite uniform, 35.1±3.8 mg C·m^{-3} (all average values in the present paper are given with 95% confidence limits) during the whole vegetative period with the corresponding production being the highest in May (57.6 mg C·m^{-3}·day^{-1}).

In zooplankton rotifers (*Synchaeta verrucosa*, *Polyarthra dolichoptera*, *Keratella quadrata*) dominated in spring, cladocerans (*Bosmina* sp., *Daphnia* sp.), cyclopoids, and copepods (*Eudiaptomus gracilis*, *Mesocyclops leukartii*) in summer and autumn. The average biomass of filter-feeding zooplankton during the vegetation period was 119±22 mg C·m^{-3}, the production 13±4 mg C·m^{-3}·day^{-1}. The seasonal pattern of the zooplankton biomass in 1985 was quite similar to that of phytoplankton; however, in 1986 their fluctuations were almost reciprocal (Fig. 3).

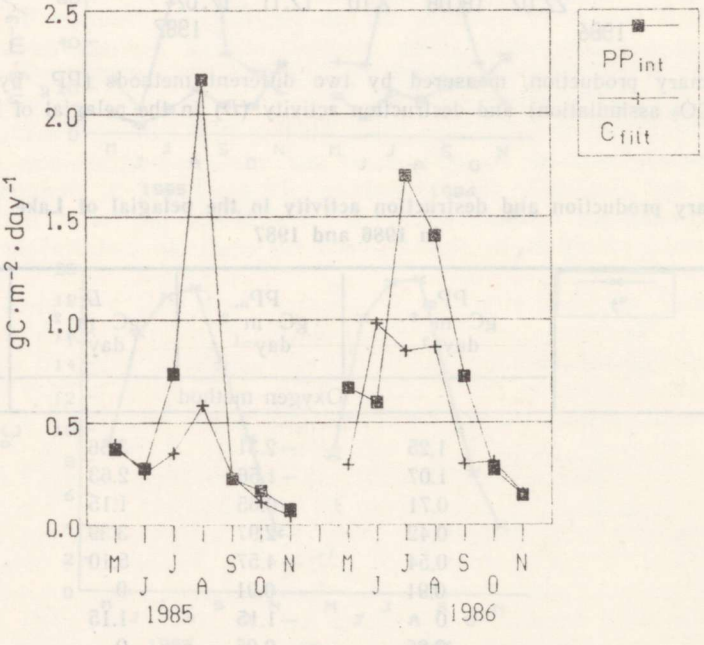

Fig. 6. Seasonal dynamics of primary production and filtrative zooplankton ration in the pelagial of Lake Peipsi in 1985 and 1986.

4. Primary production and destruction

The seasonal dynamics of PP was measured in 1985 and 1986 using the radiocarbon method. D, PP_g, and PP_n were measured 10 times in 1986 and 1987 using the oxygen method. On the average, the radiocarbon method resulted in 68% higher PP values than oxygen release method in the case of PP_g (0.988 and 0.588 g $C \cdot m^{-2} \cdot day^{-1}$, respectively). The mean D was 2.166 g $C \cdot m^{-2} \cdot day^{-1}$. D exceeded PP_g in almost all cases (Table 3, Fig. 5).

Table 3

The dominating phytoplankton and zooplankton species in the pelagial of Lake Peipsi in 1985 and 1986

Year, Month	Phytoplankton	Zooplankton
1985		
May	*Melosira italica* var. *valida*, *M. islandica* ssp. *helvetica*	*Synchaeta verrucosa*, *Polyarthra dolichoptera*, *Keratella quadrata*
June	*Stephanodiscus* spp. vel *Cyclotella* spp., *Tabellaria* spp.	*Bosmina berolinensis*, *Conochilus unicornis*, *K. quadrata*, *Daphnia* spp.
July	*Stephanodiscus* spp. vel *Cyclotella* spp., *M. islandica* ssp. *helvetica*, *M. italica* var. *subarctica*, *Aphanothece saxicola*	*Daphnia* spp., *Conochilus* spp., *Eudiaptomus gracilis* juv., *Leptodora kindtii*
August	*M. italica* var. *valida*, *M. granulata*, *Stephanodiscus* spp., vel *Cyclotella* spp.	*P. major*, *K. cochlearis*, *Conochilus* spp., *Cyclopoida*
September	*Melosira* spp., *Stephanodiscus astraea*, *Aphanothece saxicola*	*P. major*, *Cyclopoida*, *B. coregoni*, *B. berolinensis*
October	*Melosira* spp., *A. saxicola*	*B. berolinensis*, *B. coregoni*, *Cyclopoida*
November	*Melosira* spp., *A. saxicola*	*B. berolinensis*, *Cyclopoida*
1986		
May	*Melosira* spp.	*S. verrucosa*, *P. dolichoptera*, *K. quadrata*
June	*Melosira ambigua*, *Stephanodiscus astraea*, *Coelastrum microporum*	*Asplanchna priodonta*, *B. berolinensis*, *Cyclopoida*, *K. quadrata*
July	*Melosira* spp., *Fragilaria contorta*, *Stephanodiscus* spp.	*Daphnia* spp., *Cyclopoida*, *E. gracilis*, *P. major*, *L. kindtii*
August	*Melosira* spp., *A. saxicola*, *Microcystis aeruginosa*, *S. astraea*	*Daphnia* spp., *P. major*, *E. gracilis*, *Cyclopoida*, *A. priodonta*, *Dreissena* (*nauplii*)
September	*A. saxicola*, *Melosira* spp., *Stephanodiscus* spp.	*Cyclopoida*, *D. galeata*, *Bosmina* spp., *P. major*
October	*Melosira* spp., *S. astraea*	*Bosmina* spp., *D. galeata*, *Cyclopoida*
November	*Stephanodiscus* spp.	*B. berolinensis*, *Cyclopoida*

The data of Laugaste (1968) and Bessonov and Vasilyev (Бессонов and Васильев, 1975) were used as comparative material. Their results were recalculated with the method described by P. and T. Nõges (1990) and expressed in g $C \cdot m^{-2} \cdot day^{-1}$. In case water transparency was unknown, 1.6 m was used as the average for Lake Peipsi. The average PP_g and D measured by Bessonov and Vasilyev (2.37 and 4.90 g $C \cdot m^{-2} \cdot day^{-1}$, respectively) were quite similar to our results, but both remained twice smaller than the values obtained by Laugaste (2.37 and 4.90 g $C \cdot m^{-2} \cdot day^{-1}$, respectively; see Table 4). It is difficult to bring out the causes of this discrepancy because of the long time interval. The differences could be of methodological origin. Primary production in Lake Peipsi was measured by Yastremski for a long time (Ястремский, 1983; 1986); the average value for 1970—1984, 1 g $C \cdot m^{-2} \cdot day^{-1}$, is in good accordance with our average for 1985—1986, 0.95 g $C \cdot m^{-2} \cdot day^{-1}$.

Table 4

The average primary production per vegetative period measured by different authors in Lake Peipsi

Years	Method	PP_g	D	Author
		mg $C \cdot m^{-3} \cdot day^{-1}$		
1965—1966	O_2	2.37	4.90	Laugaste, 1968
1969—1973	O_2	0.63	2.20	Бессонов and Васильев, 1975
1970—1984	O_2	1.00	—	Ястремский, 1986
1986—1987	O_2	0.59	2.17	Present paper
1986—1987	^{14}C	0.99*		"
1985—1986	^{14}C	0.95	—	"

* — only the cases of simultaneous measurement of primary production and destruction were taken into account

The data of the other authors also revealed more than a twofold predominance of destructive processes over primary production (Table 4). This phenomenon could be explained by an intensive inflow of allochthonous organic matter; however, due to the huge water mass this factor can hardly be significant in the case of Lake Peipsi.

One has to take into account that the seasonal peaks of PP might be sharp and of short duration and can be missed as a result of the low frequency of measurements. Organic matter produced during these peaks can raise D for a longer period. Moreover, the early phytoplankton maximum during the under-ice or ice-break period is also often missed by investigators. The amount of organic matter produced during this period can be considerable because all nutrients released during winter are available.

5. Productivity and trophic relations in the plankton community

The average values of production per vegetation period for the years under study were as follows: phytoplankton 203.5 g $C \cdot m^{-2}$; bacterioplankton 37.9 g $C \cdot m^{-2}$; herbivorous zooplankton 20.6 g $C \cdot m^{-2}$ and predatory zooplankton 1.5 g $C \cdot m^{-2}$.

The mean value of the C_{filt} (0.55 ± 0.14 g $C \cdot m^{-2} \cdot day^{-1}$) constituted about 50% of the daily PP (1.1 ± 0.1 g $C \cdot m^{-2}$). The seasonal patterns of C_{filt} and PP_{int} were quite similar in both years (Fig. 6); their correlation coefficient was high and significant ($r = 0.66$, $P < 0.0001$). The average ratio of P_{filt} and PP_{int} during the vegetative period was 10.1%. The correlation analysis also revealed some significant reciprocal relationships between the biomass of filter-feeding zooplankton and Detr ($r = -0.62$, $P < 0.01$).

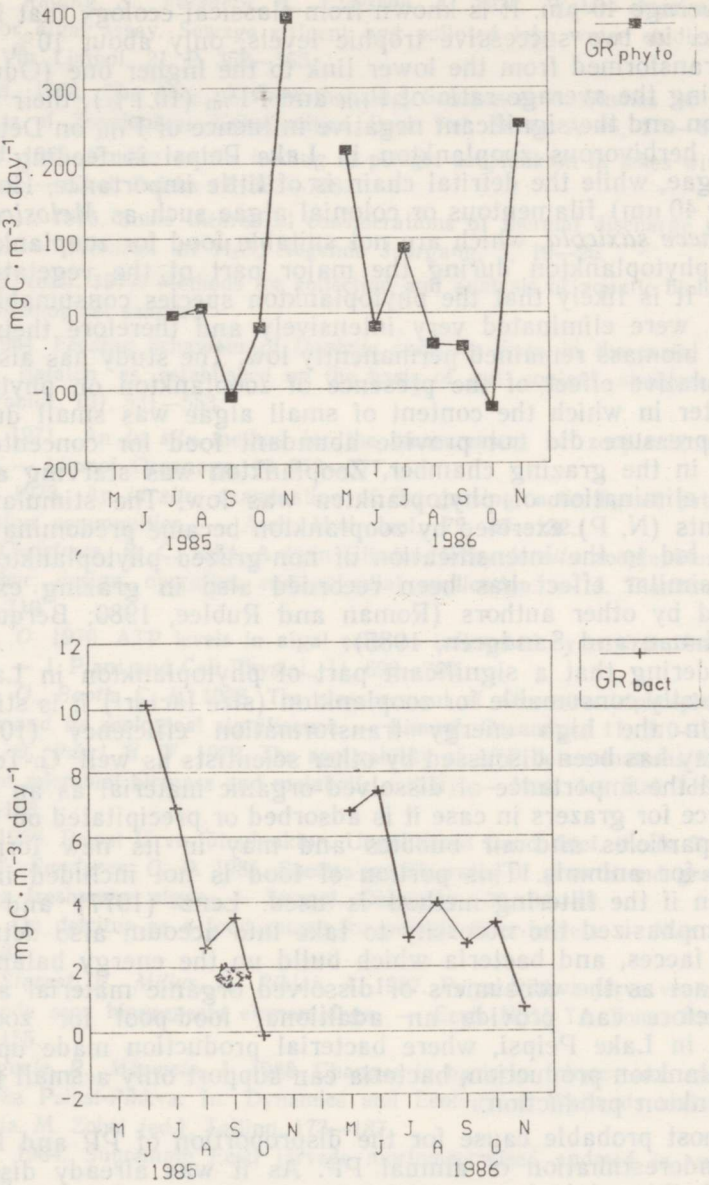

Fig. 7. The results of experimental measurements of zooplankton grazing on phytoplankton and bacterioplankton in the pelagial of Lake Peipsi in 1985 and 1986.

The measurements of zooplankton grazing revealed that the presence of zooplankton in the experimental vessel actually stimulated phytoplankton growth: in many cases negative grazing values were found (Fig. 7). From May to November bacterial food formed about 11% of the total food requirements of zooplankton. The correlation between GR_{phyto} and GR_{bact} was negative and highly significant ($r = -0.83$; $P < 0.01$). This indicates an increased bacterial consumption in the conditions where grazing on phytoplankton was somehow disturbed (e. g. due to an unsuitable species composition).

Our investigation was aimed at studying the relationship between zooplankton and phytoplankton in the food chain. The maximum size limit of the particle still consumable for zooplankton is considered to be on the average 40 μm. It is known from classical ecology that in the food chain, i. e. in two successive trophic levels, only about 10% of energy can be transformed from the lower link to the higher one (Odum, 1959). Considering the average ratio of P_{filt} and PP_{int} (10.1%), their significant correlation and the significant negative influence of P_{filt} on Detr, it seems that the herbivorous zooplankton in Lake Peipsi is feeding mostly on living algae, while the detrital chain is of little importance. However, the large (> 40 μm) filamentous or colonial algae such as *Melosira* spp. and *Aphanothece saxicola*, which are not suitable food for zooplankton, dominate in phytoplankton during the major part of the vegetation period (Fig. 3). It is likely that the phytoplankton species consumable for zooplankton were eliminated very intensively and therefore their share in the algal biomass remained permanently low. The study has also revealed the stimulative effect of the presence of zooplankton on phytoplankton. Lake water in which the content of small algae was small due to high grazing pressure did not provide abundant food for concentrated zooplankton in the grazing chamber. Zooplankton was starving and, therefore, the elimination of phytoplankton was low. The stimulative effect of nutrients (N, P) excreted by zooplankton became predominating there, and that led to the intensification of non-grazed phytoplankton production. A similar effect has been recorded also in grazing experiments performed by other authors (Roman and Rublee, 1980; Berquist et al., 1985; Lehman and Sandgren, 1985).

Considering that a significant part of phytoplankton in Lake Peipsi is not directly consumable for zooplankton (size factor!) it is still difficult to explain the high energy transformation efficiency (10%). This controversy has been discussed by other scientists as well. G.-Toth (1984) suggested the importance of dissolved organic material as an additional food source for grazers in case it is adsorbed or precipitated on suspended mineral particles and air bubbles and may in its new form become utilizable for animals. This portion of food is not included in primary production if the filtering method is used. Lenz (1977) and Williams (1981) emphasized the necessity to take into account also detritus, zooplankton faeces, and bacteria which build up the energy balance model. Bacteria act as the consumers of dissolved organic material and faeces and therefore can provide an additional food-pool for zooplankton. However, in Lake Peipsi, where bacterial production made up ca. 20% of phytoplankton production, bacteria can support only a small proportion of zooplankton production.

The most probable cause for the disproportion of PP and P_{filt} could be the underestimation of annual PP. As it was already discussed in Chapter 4, this might be caused by the sharp seasonal peaks of primary production, which can be missed due to the low frequency of measurements, and by the early phytoplankton maximum, which is also neglected by investigators.

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