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CYCLING OF ORGANIC MATTER DURING THE VERNAL GROWTH PERIOD IN THE OPEN NORTHERN BALTIC PROPER

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Page	Location	Error	Correction
24	Fig. 6	mg m^{-3}	µg m^{-3}
42	Fig. 5	mmol C $m^{-3}d^{-1}$	mmol C $m^{-3}h^{-1}$

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ABSTRACT

Water temperature, salinity, pH, oxygen, currents, wind and solar irradiance were measured in the open northern Baltic Proper during the vernal growth period in 1982 as physical back-ground material for a comprehensive ecosystem research project. The total irradiation at the sea surface during the observation period was 160 KJ cm^{-2}. The depth of 1 % relative irradiance varied from 12 to 28 m. The hydrographic conditions during the observation period represented typical spring conditions in the area, i.e. an almost continuous increase in the surface layer temperature and the development of the summer thermocline. The density profiles showed four different layers. The surface layer extending from the surface to a depth of ca. 30 m, the intermediate layer between 30 and 60 m, the halocline layer between 60 and 95 m, and the bottom layer below 100 m. The average current velocity at the depth of 30 m was ca. 10 cm s^{-1}. Due to the great variability in the current pattern, no distinct net water exchange could be detected. The oxygen concentrations were low in the water below the halocline, but no anoxia was observed.

Key words: Baltic Sea, vertical stratification, currents, pH, oxygen.

1. INTRODUCTION

The formation, decomposition and sinking of organic matter in the pelagic ecosystem is controlled by several biochemical, chemical and physical processes. The vernal phytoplankton bloom is a well-known example of the biological response to an aquatic ergocline (sensus Legendre & Demers 1985). The bloom is determined by the balance between vertical mixing of the surface layer (i.e. formation of the seasonal thermocline) and solar radiation (e.g. Svedrup 1953 and Riley 1957). In the Baltic Proper the permanent halocline is another physical structure that has a profound influence on the functioning of the system (e.g. Grasshoff & Voipio 1981, Jansson et al. 1984). Horizontal water movements play an important role in the transport of matter between sea areas, the generation of patchiness (e.g. Kahru et al. 1986), as well as the resuspension of particulate matter.

The present paper briefly describes the hydrographical and weather conditions, the main emphasis being placed on describing the vertical zonation and water transport as a physical background for a comprehensive ecosystem research project dealing mainly with the production, decomposition and sinking of organic matter during the vernal growth period in the open northern Baltic Proper (Lahdes et al. 1988, Lahdes & Leppänen 1988, Leppänen 1988, Leppänen & Bruun 1988, Leppänen & Kononen 1988).

2. STUDY AREA

The study area is located in the open northern Baltic Proper (59°26.1′ N; 21°31.4′ E, Fig. 1).

The bottom topography of the area is characterized by two troughs. The troughs are narrow (ca. 2.5 km wide at the depth of 120 m). The "Teili trough" (NW-SE direction) is connected at one end to the large, deep basin of the northern Baltic Proper, and at the other end to the Archipelago Sea and the Åland Sea. The sampling site was close to the node of the troughs. The depth of the sampling site is 158 m, the site being surrounded by shallower areas with depths of 80-100 m.

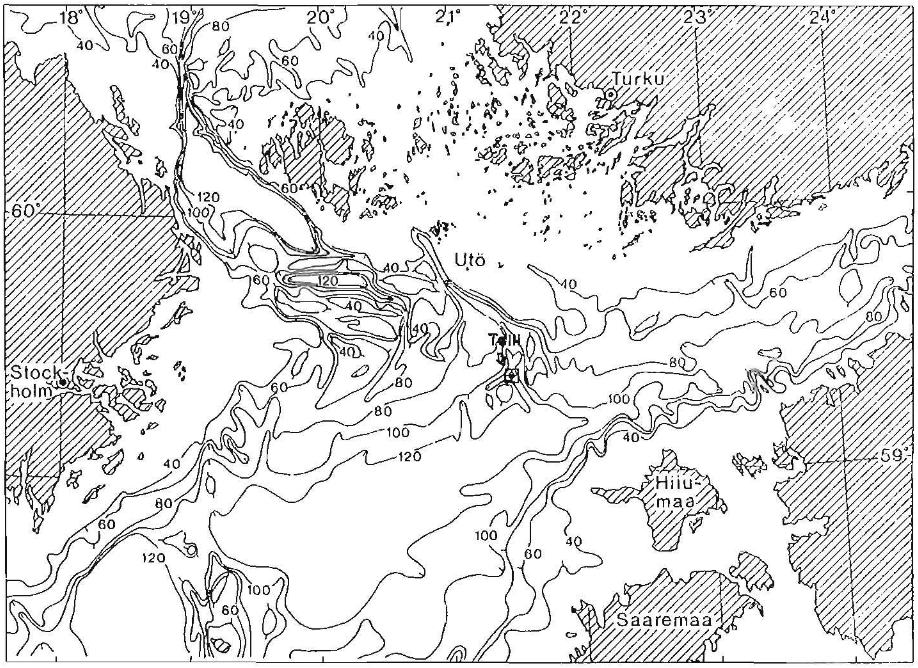


Fig. 1. Location of the sampling site in the open northern Baltic Proper.

3. MATERIAL AND METHODS

The temperature, salinity, pH and oxygen profiles were measured at one to two-week intervals from March 23 to June 17 in 1982. During the period April 14 - 29 daily sampling was performed. Currents were recorded from April 14 to June 17.

The vertical temperature and conductivity profiles were measured with a CTD-sonde (Plessey Environmental Co.). Salinity was computed from the data according to UNESCO (1981a), and density according to UNESCO (1981b).

Oxygen and pH were determined from water samples (0, 2, 5, 10, 15, 20, 30, 40, 50, 60, 80, 100, 130, 150 m and occasionally 70 m) according to Koroleff (1979).

Current (speed and direction) and continuous temperature measurements were recorded using Aanderaa RCM-4 current meters placed at five depths (30, 50, 80, 100 and 150 m, selected according to the sediment trap moorings, cf. Leppänen 1988). A single buoy subsurface mooring was used as the anchoring system. The recording interval was 10 min. Due to the time scales used in this study the data was filtered using simple, one-hour averaging. Only the current direction and temperature were obtained at the depth of 50 m due to the malfunctioning of the rotor of the current meter.

The surface irradiance was measured with a Kipp & Zonen solarimeter on board R/V Aranda. The vertical attenuation of irradiance in the water was measured with a Gossen lux-meter, equipped with a green filter.

The wind data was recorded at three-hour intervals at Utö Island by the Finnish Meteorological Institute.

The current meter and wind data have been compiled so as to match the periods corresponding to the successional stages of plankton and nutrients (cf. Lahdes & Leppänen 1988 and Leppänen & Kononen 1988).

4. RESULTS

4.1 Surface irradiance

The surface irradiance on the sampling dates is shown in Fig. 2. The average daily irradiance was 1700 J $cm^{-2}d^{-1}$ and the total irradiance during the whole observation period was ca. 160 KJ cm^{-2}. This is close to the long-term mean for the southern coast of Finland (Finnish Meteorological Institute 1982).

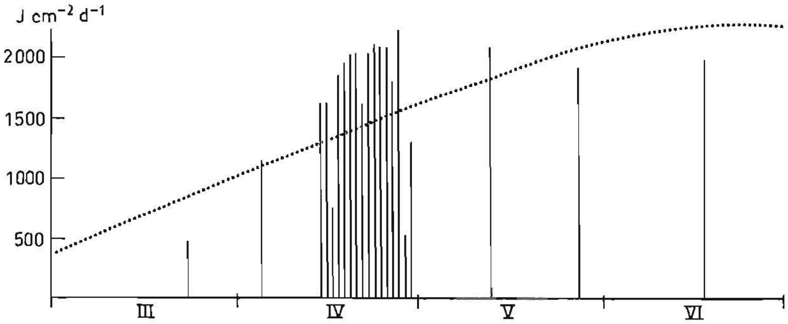


Fig. 2. Daily irradiance in the open northern Baltic Proper during the sampling period in 1982. The broken line represents the mean irradiance in Helsinki, on the N coast of the Gulf of Finland, in 1971-1980 (The Finnish Meteorological Institute 1982).

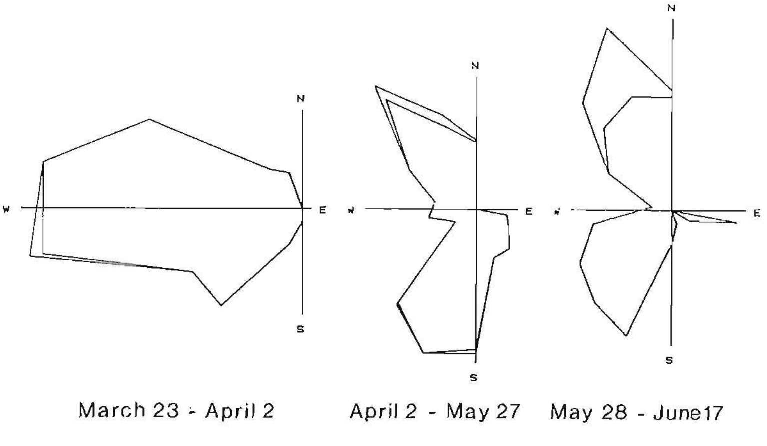
The vertical attenuation of irradiance in the water column is presented in Table 1. The depth of 1 % relative irradiance, which often corresponds to the depth of the euphotic zone (e.g. Niemi 1975, Bruun & Grönlund 1981 and Leppänen & Kononen 1988), varied between 12.4 and 28 m. The water was clearest on May 27 when the depth of 1 % relative irradiance was ca. 28 m.

Table 1. The depth (m) of 50, 10 and 1 % relative irradiance

% of surface light	March 23.	April 14.	15.	17.	19.	25.	29.	May 27.	June 17.
50 %	2.4	3.2	2.0	2.7	2.0	1.8	2.1	4.1	2.6
10 %	7.9	10.6	6.7	9.1	6.6	6.2	7.2	13.8	8.6
1 %	15.7	21.3	13.4	18.1	13.3	12.4	14.3	27.5	17.3

4.2 Winds

The mean wind speed of 5.7 m s^{-1} during the observation period was slightly higher than the corresponding 20 year long-term mean (4.8 m s^{-1}, Kolkki 1969). The maximum observed wind speed was 15 m s^{-1}. The net effect of the wind was from west during March 23 - April 2. During the rest of the study period the winds were predominantly either in the NW or SSW (Fig. 3).



March 23 - April 2 April 2 - May 27 May 28 - June17

Fig. 3. Wind roses according to the data from Utö Island (northern Baltic Proper) in 1982.

4.3 Currents

The low-pass filtered, current vectors from depths of 30 and 150 m are presented in Figs. 4 and 5 as an example. They show the variability of the current field. The current speed decreased toward the bottom; no high velocities were recorded (max. 25 cm s^{-1} at the depth of 30 m). The high variability in the current directions is indicated by the great difference between the mean current speed and the velocity components, as well as by the great standard deviation of the components (Table 2). The distribution of current speeds and directions (Fig. 6) was uniform at all depths, except at 150 m where the bottom topography influenced the direction of the currents. Thus, near the bottom, the flow was mostly back-and-forth movement along the Teili trough.

Table 2. Means and standard deviations of current velocity and its components U (due east) and V (due north) during the study periods. Units: cm s^{-1}

		April 15-29	April 15-May 27	May 28-June 17	Whole period
30 m	speed	10.6±3.1	10.7±3.0	11.1±3.1	10.8
	U	0.9±7.5	-0.9±7.8	-1.1±7.5	-0.97
	V	0.04±8.0	1.8±7.7	0.9±8.6	1.2
80 m	speed	5.9±1.8	5.5±1.7	5.5±1.7	5.47
	U	2.2±4.1	0.3±4.0	0.3±3.6	0.31
	V	-0.2±4.0	0.1±4.1	1.8±4.1	0.58
100 m	speed	5.0±1.6	5.1±1.4	5.1±1.6	5.07
	U	-0.02±4.2	-0.2±3.9	0.2±3.7	0.02
	V	-0.4±3.3	-0.2±3.5	0.4±3.8	-0.01
150 m	speed	3.3±1.3	3.5±1.1	3.4±1.7	3.44
	U	0.9±2.7	1.0±2.6	0.8±2.7	0.91
	V	-0.3±2.1	-1.0±2.3	-0.6±2.5	-0.80

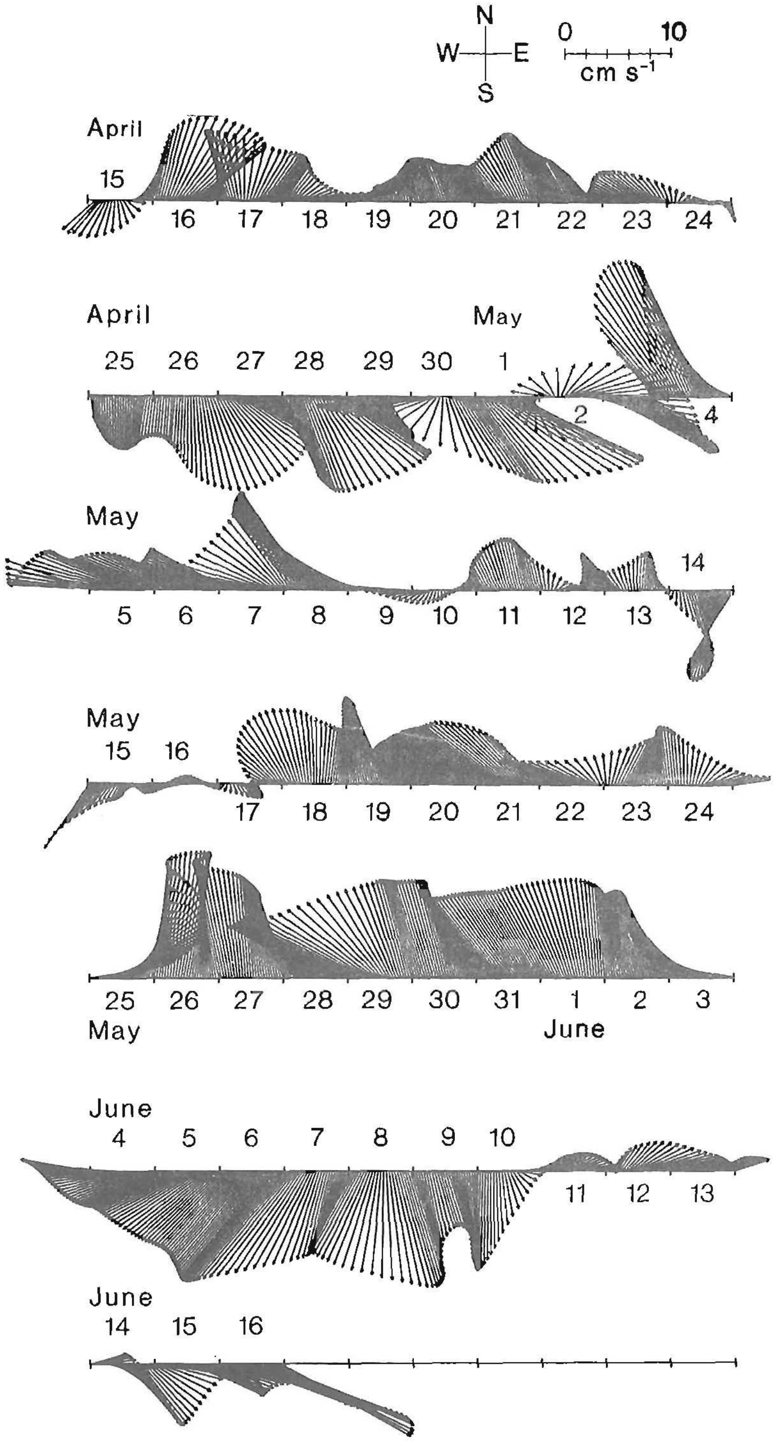


Fig. 4. Smoothed current vectors (direction, °, and speed, cm s^{-1}) at the depth of 30 m in April 15 - June 17 in 1982 in the open northern Baltic Proper.

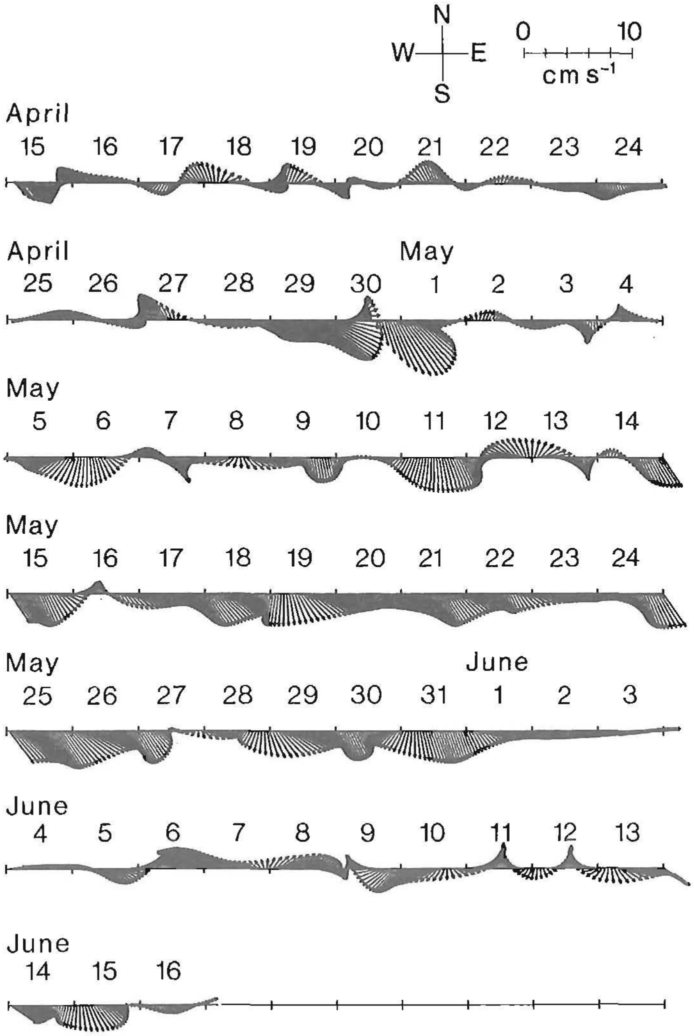


Fig. 5. Smoothed current vectors (direction, °, and speed, cm s^{-1}) at the depth of 150 m in April 15 - June 17 in 1982 in the open northern Baltic Proper.

4.4 Water temperature and salinity

Since the CTD-casts were performed once each sampling day, the diurnal variation in the upper layer hydrography could not be monitored.

During the whole study period the upper layer went through all the phases from the late winter condition to the developed summer thermocline (Fig. 7). The spring warming of the surface

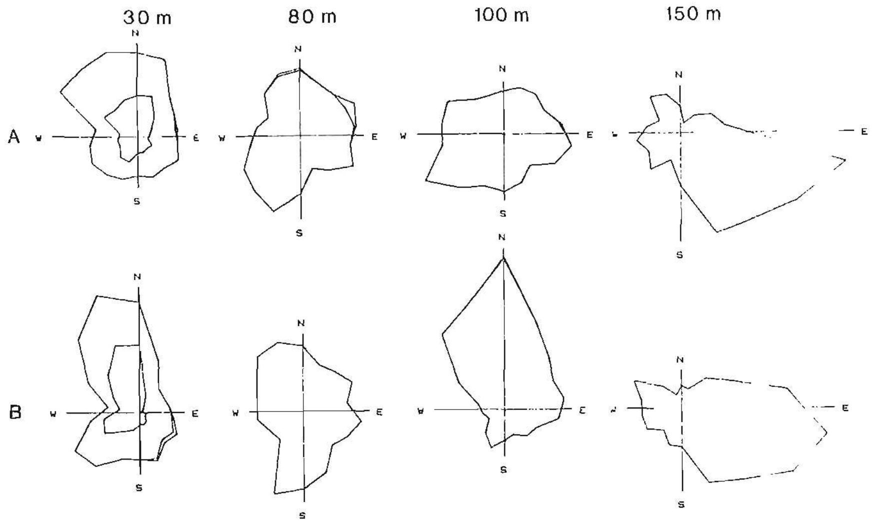


Fig. 6. Current roses for the different depths. A: April 15-May 27, B: May 28-June 17 in 1982.

layer resulted in thermal convection that kept the upper layer quite deep during April. The minimum temperature layer, from ca. 30 m to 60 m, represented the intermediate "winter water" layer.

Below the halocline, from the depth of ca. 95 m to the bottom, the water temperature remained almost stable and constant with depth.

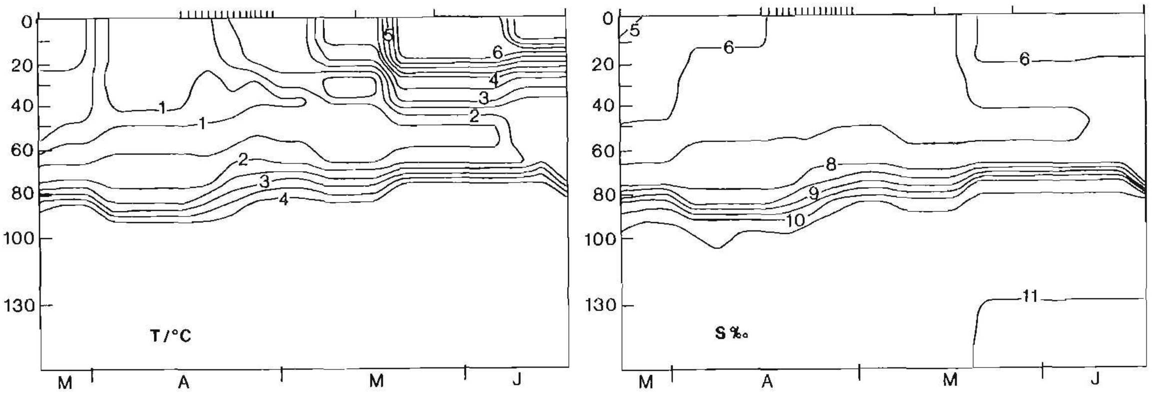


Fig. 7. Isolines of temperature (°C) and salinity (^{0}/oo) during the observation period March 23 - June 17 1982 in the open northern Baltic Proper. The sampling days are indicated by bars on the top of the figures.

The mean depth of the halocline was 84.5 m. The halocline rose from ca. 90 m to a depth of 60-70 m toward the end of the study period (Fig. 7). Some oscillations in the halocline were detected.

4.4.1 Temperature recordings made using the current meters

The temperature time series recorded by the current meters are presented in Fig. 8. The temperature at a depth of 30 m was ca. 1°C up until the end of April and then warmed up slowly with interruptions by distinct pulses. Corresponding pulses were not recorded at the depth of 50 m. The rise of the halocline was also seen in the evolution of the temperature at the depth of 80 m. The temperature was almost constant already at a depth of 100 m (4.47°C). The temperature sensor at the depth of 150 m malfunctioned and the recordings are questionable, especially in April. Oscillations close to the inertial period were recorded at all depths above the halocline.

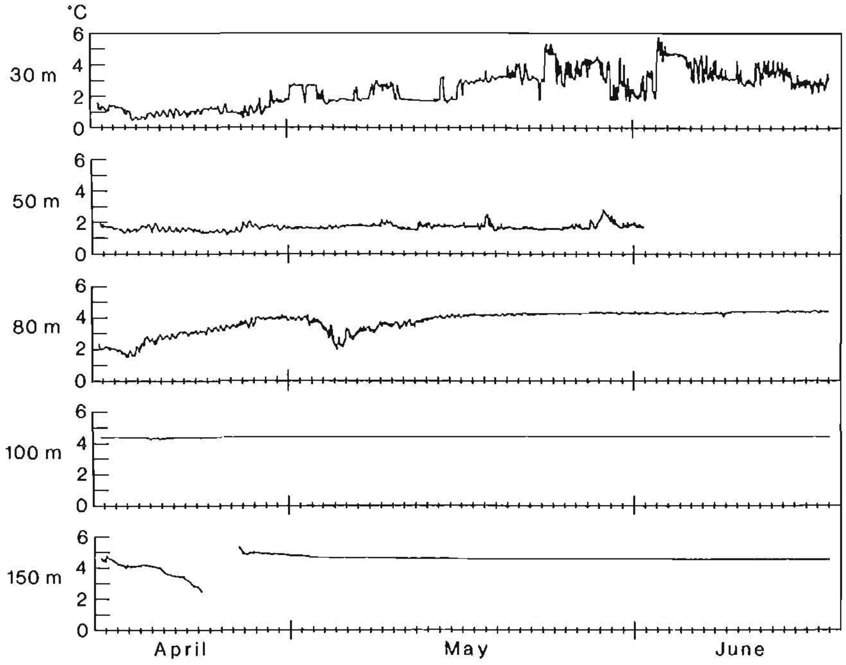
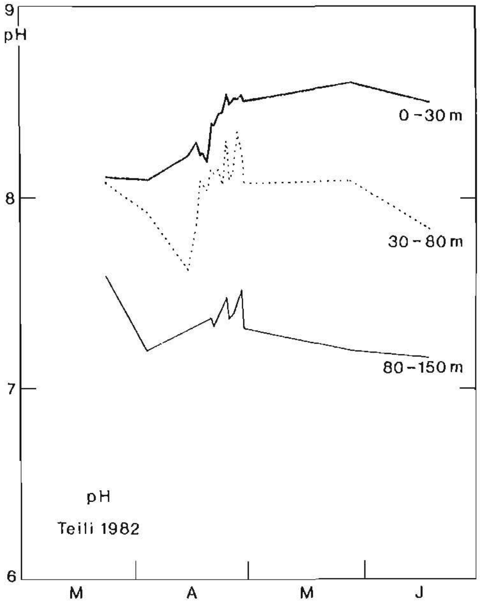


Fig. 8. Temperature time series from the current meter thermistors.

4.5 pH and oxygen

The pH values varied in the surface layer from 8.1 to 8.6, with a rapid increase in April (Fig. 9). The pH values were lowest in the water layer below the halocline.

The oxygen concentration in the water layer above the halocline varied between 8.5 and 10.5 mg^3 dm^{-3} (Fig. 10). The oxygen concentration decreased distinctly throughout the halocline, but no anoxia was observed. Frequent sampling in April revealed prominent fluctuations in the oxygen concentration, especially below the halocline (Fig. 11).



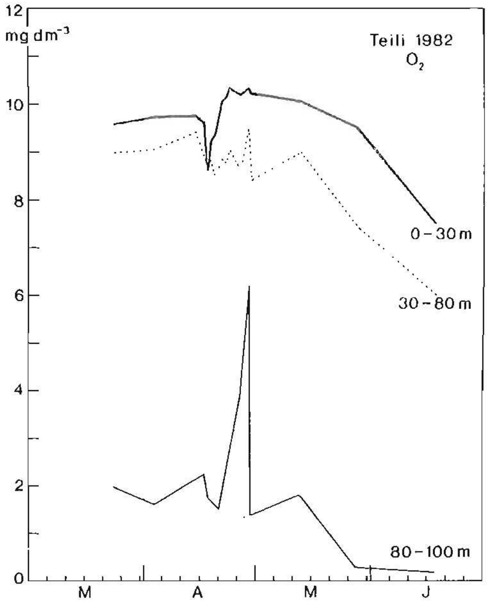


Fig. 9. Mean pH values in the different water layers (thick line 0-30 m, dotted line 30-80 m, thin line 80-150 m).

Fig. 10. Mean oxygen concentrations in the different water layers (thick line 0-30 m, dotted line 30-80 m, thin line 80-150 m.

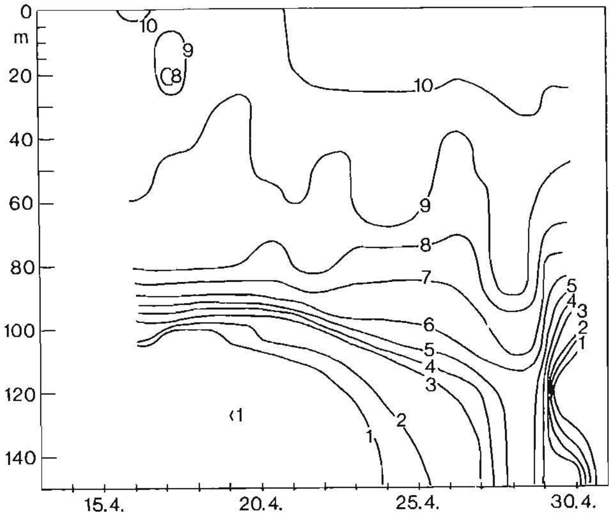


Fig. 11. Oxygen concentrations ($mg^3\ dm^{-3}$) during the period April 16-29 in 1982 in the open northern Baltic Proper.

5. DISCUSSION

The hydrographic conditions during the observation period represented the typical spring situation in the Baltic Sea area, i.e. an almost continuous warming up in the upper layer and development of the summer thermocline. The temperature and salinity profiles were typical for the area (Simojoki 1946, Alenius & Leppäranta 1982). The bottom of the mixed surface layer was close to the depth of 30 m. This was also supported by the pulsation in the continuous temperature recordings made at the depth of 30 m. The mixing surface layer was in most cases deeper than the euphotic layer (depth of 1 % relative irradiance). The vertical oscillations of the bottom of the surface layer, which were seen as a pulse-like temperature variation, is probably an important mechanism in the transport of nutrients from below a depth of 30 m to the euphotic layer (cf. Lahdes & Leppänen 1988). More frequent CTD casts or a thermistor chain in the layer above the halocline would have been needed in order to gain an accurate measure of thermal convection and turbulent mixing. This would have permitted the vertical convection velocities and the nutrient input to the euphotic layer to be estimated.

Hydrographically the layer below the halocline was homogeneous and stationary. The currents in this layer were, however, vertically variable in speed and direction. The same inhomogeneity was also seen in the oxygen and nutrient concentrations (Lahdes & Leppänen 1988). The prominent increase in oxygen concentrations near the bottom at the end of April seemed to be connected to NE currents. Although the oxygen measurements were sporadic compared to the current measurements, and we do not have both observations from other exactly similar situations, the rapid increase in oxygen seemed to be sporadic. Such short-term oxygen pulses near the bottom have probably only a minor effect on the bottom ecosystem; e.g. the benthic community is mainly controlled by the most unfavorable oxygen conditions (Andersin et al. 1978).

The currents were variable at all the observation depths, the rather low velocities being typical of open sea conditions. The great variability of the currents indicates small net water exchange in the study area during the vernal production period. This is somewhat contradictory to the rise of the halocline by ca. 20 m. No clear correlation was found between the movements of the halocline and currents. Thus the current measurements did not support the assumption that the rise of the halocline was caused by water masses flowing from the Baltic Proper. The complicated bottom topography may, however, cause eddy-like currents in the bottom layer near the edges of the troughs. The interpretation of the current field on the basis of observations made at only one mooring site situated in the node of the troughs may thus be misleading.

The physical regime is of major importance in determining the progression of phytoplankton communities. Surface mixing and irradiance are important in the initialization of the vernal phytoplankton bloom. Already Svedrup (1953) presented the idea of critical depth and its effect on the net photosynthesis of the plankton community. The effect of solar radiant energy and surface mixing on the initialization of the vernal phytoplankton bloom can be simplified by the following equation (Riley 1957):

$$I = (I_o/kZ)(1-e^{-kZ}) \qquad (1)$$

where I_o is the surface irradiance (J $cm^{-2}d^{-1}$), k is the attenuation coefficient of the water, and Z is the depth of the mixing surface layer (from the CTD casts). The value of ca. 170 J $cm^{-2}d^{-1}$ for I has been found to be the limit for effective net primary production (Gieskes & Kraay 1975, Horn & Paul 1984). In our study area, the value of I was below 50 J $cm^{-2}d^{-1}$ in March, but ca. 230 J $cm^{-2}d^{-1}$ in the beginning of April. This fits well with the observed initialization of the spring phytoplankton bloom (Leppänen & Kononen 1988).

The biochemical processes of the plankton community have, on the other hand, a clear effect on the development of pH and oxygen values. The observed high oxygen and pH values in the surface layer were caused by the active photosynthesis in April-May (cf. Leppänen & Kononen 1988). The decomposing phase of the bloom decreased oxygen saturation of the whole water body in June (Lahdes et al. 1988).

In conclusion, the surface layer during the vernal production period was being mixed down to the depth of ca. 30 m. The intermediate layer, which stayed relatively cool during the whole study period, was below this, between ca. 30 and 60 m. The halocline was situated between the depths of 60-95 m, and the subhalocline layer below ca. 100 m. The halocline rose by ca. 20 m during the observation period. The formation of the seasonal thermocline initiated the vernal phytoplankton bloom. The mixing surface layer was deeper than the euphotic layer. Vertical movements of the thermocline, observed as rapid pulses in the continuous temperature measurements at the depth of 30 m, might have been an important mechanism in the transport of nutrients from below the depth of 30 m to the euphotic layer. Despite of the rise of the halocline, the current measurements indicated only a small net exchange of water in the area.

Acknowledgements

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CYCLING OF ORGANIC MATTER DURING THE VERNAL GROWTH PERIOD IN THE OPEN NORTHERN BALTIC PROPER. II. NUTRIENT DEVELOPMENT AND CHEMICAL COMPOSITION OF PARTICULATE MATTER

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ABSTRACT

Nutrient dynamics and the chemical composition of particulate matter were followed during the vernal period in the open northern Baltic Proper in 1982. The hydrochemical and biological features corresponded well with earlier observations. During the growth stage of the phytoplankton dissolved, inorganic nitrogen and phosphorus decreased at the same rate in the surface layer as the particulate forms increased. Elemental ratios indicated that both nitrogen and phosphorus were removed faster than carbon from the seston during sinking. The processes affecting the changes in nutrient pools were different in the layers above and below the halocline. In the surface layer most of the processes were connected to the phytoplankton. Below the halocline, physico-chemical reactions of the nutrients, such as adsorption on particles and mobilization from sediments, hampered the quantification of the processes. The decrease in nitrate below the halocline is probably caused by bacterial denitrification under low oxygen conditions.

Key words: Baltic Sea, nitrogen, phosphorus, silicate, carbon, chlorophyll *a*, ATP.

1. INTRODUCTION

Nutrient dynamics in seawater are regulated by abiotic factors such as water circulation, stratification, light, and redox conditions, as well as by biotic factors, mainly the ability of plankton organisms to assimilate, excrete and mineralize nutrients. This creates complex interactions between the nutrient pools, different reaction rates and directions being involved. During the vernal period this complexity is less pronounced. At the end of the winter plankton community succession starts to develop. The growth of phytoplankton biomass is rapid, and its effects on the environment are distinct and easily measurable. Phytoplankton is the dominant group in the plankton biomass; the amount and activity of consumers and decomposers is small.

The aim of this study is to quantify the changes in the nutrient pools and to describe the chemical and biochemical composition of the particulate matter. The present paper is a part of a comprehensive ecosystem research project dealing with the cycling of organic matter in the pelagial of the open waters of the northern Baltic Proper.

2. MATERIAL AND METHODS

The sampling area is in the open northern Baltic Proper (59°26.1′ N; 21°31.4′ E). See Leppänen & Alenius (1988) for a detailed description of the area.

The water samples were taken at either one or two-week intervals, apart from the period April 14-29 when daily sampling was performed. The sampling depths were 0, 2, 5, 10, 15, 20, 30, 40, 50, 60, 80, 100, 130, and 150 m, and occasionally 70 m.

Total and inorganic nutrients were analyzed according to Koroleff (1979, 1983). Particulate phosphorus (PP) and nitrogen (PN) were analyzed as described by Laakkonen et al. (1981). Particulate silicate (PSi) was analyzed according to Paasche (1980), and particulate carbon (PC) according to Salonen (1979). The sample volume varied between 50 and 500 cm^3 according to the amount of particulate matter in the water. Whatman GF/C glass fiber filters (median retention size ca. 1 m) were used for the PP, PN and PC analyses, and Gelman GA-4 membrane filters (pore size 0.8 m) for the PSi analyses.

Dissolved inorganic nitrogen (DIN) is the sum of NO_2-N, NO_3-N and NH_4-N. Dissolved organic phosphorus (DOP) and nitrogen (DON) are calculated by substracting DIP and PP from total P, and DIN and PN from total N, respectively.

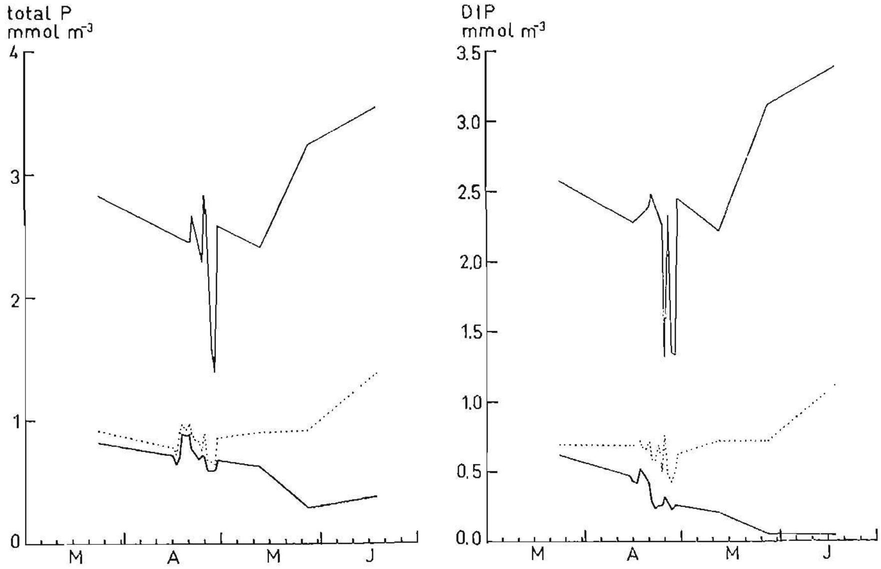

Fig. 1. Mean concentrations of total P and DIP in the different water layers during the study period (March 23-June 17) in the open northern Baltic Proper in 1982. (Thick line = 0-30 m, dotted line = 30-80 m, thin line = 80-150 m).

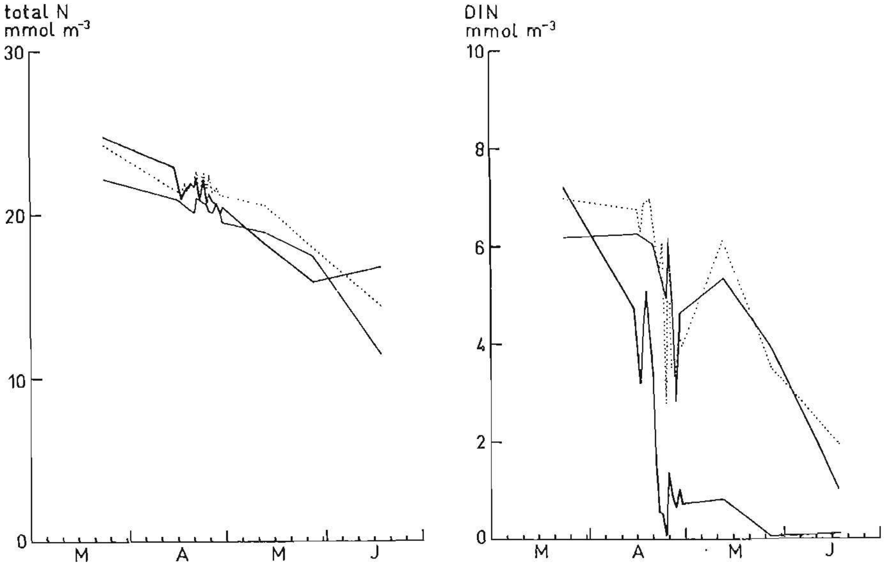

Fig. 2. Mean concentrations of total N and DIN in the different water layers during the study period (March 23-June 17) in the open northern Baltic Proper in 1982. (Thick line = 0-30 m, dotted line = 30-80 m, thin line = 80-150 m).

Adenosine triphosphate (ATP) was analyzed by the bioluminescence technique according to Myhrman et al. (1978). 50-100 cm^3 of sample were filtered on Whatman GF/C filter and extracted in 1 % trichloracetic acid (TCA). Purified luciferin-luciferase reagent (LKB-Wallac) was used for determining ATP via the luminescence reaction on a LKB-Wallac Luminometer 1250.

Chlorophyll a was analyzed fluorometrically using 90 % acetone as solvent (Edler 1979).

3. RESULTS

As described by Leppänen & Alenius (1988), the water column was divided by the permanent halocline at a depth of 60-95 m. A weak thermocline was formed in the beginning of April, developing more distinct towards the end of the study period. During the bloom phase the surface layer was occasionally mixed down to a depth of 20-30 m at least (Leppänen & Alenius 1988).

The data was divided, on the basis of the physical, chemical and biological features to correspond to the following three layers: surface layer (0-30 m), intermediate layer (30-80 m) and bottom layer (i.e. subhalocline layer, 80-150 m).

There was a clear seasonal pattern in the change in nutrient (Figs. 1-5) and ATP and chlorophyll a concentrations (Fig. 6) in the surface layer where most of the biological activity took place (Leppänen & Kononen 1988, Leppänen & Bruun 1988, Lahdes et al. 1988). The

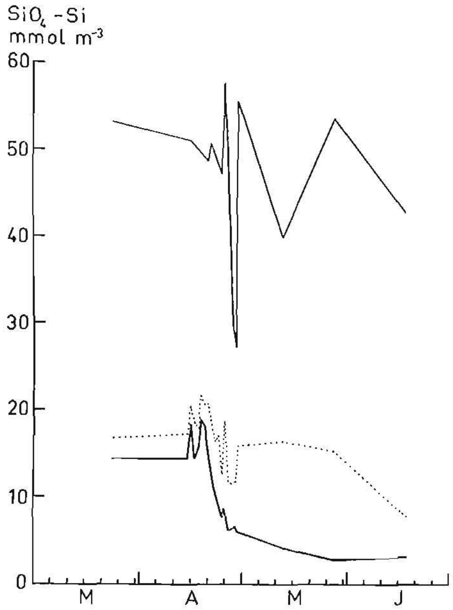

Fig. 3. Mean concentration of SiO_4-Si in the different water layers during the study period (March 23-June 17) in the open northern Baltic Proper in 1982. (Thick line = 0-30 m, dotted line = 30-80 m, thin line = 80-150 m).

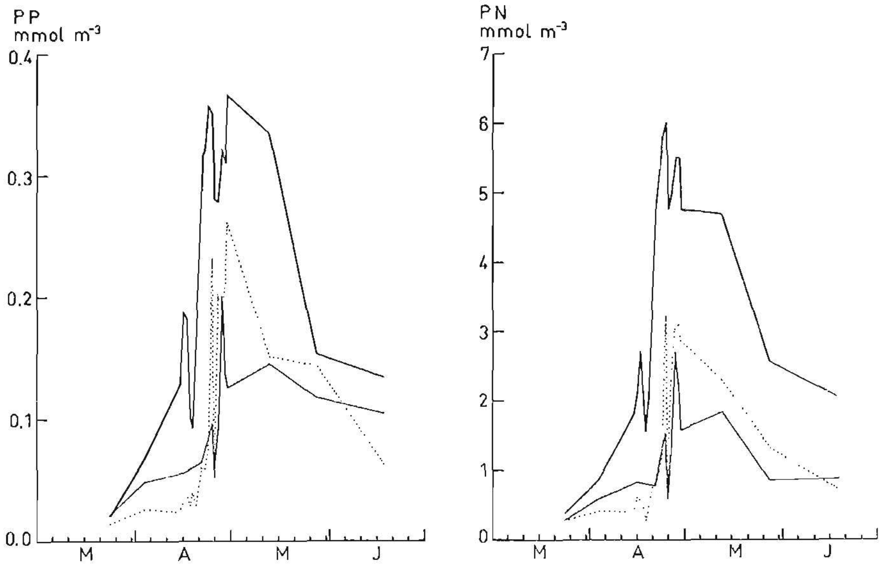

Fig. 4. Mean concentrations of PP and PN in the different water layers during the study period (March 23-June 17) in the open northern Baltic Proper in 1982. (Thick line = 0-30 m, dotted line = 30-80 m, thin line = 80-150 m).

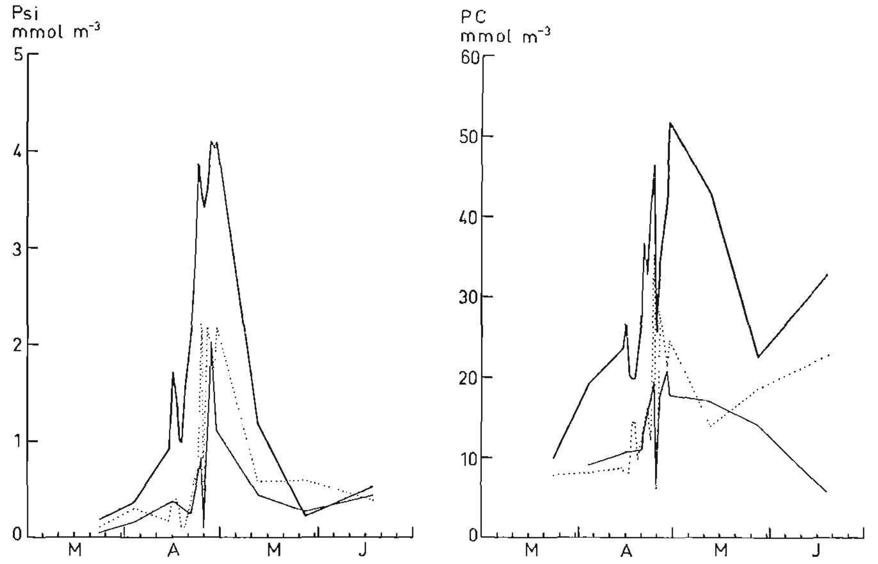

Fig. 5. Mean concentrations of total PSi and PC in the different water layers during the study period (March 23-June 17) in the open northern Baltic Proper in 1982. (Thick line = 0-30 m, dotted line = 30-80 m, thin line = 80-150 m).

prominent short-term fluctuation in the nutrient concentrations, in the bottom layer especially, observed during the period April 14-29 with frequent sampling, is caused by both hydrodynamic and biological processes, and resulted in a patchy distribution of the determinants. This is commonly observed in open systems (Eberlein et al. 1980, Sambrotto 1983, Kahru et al. 1984, McCarthy et al. 1984).

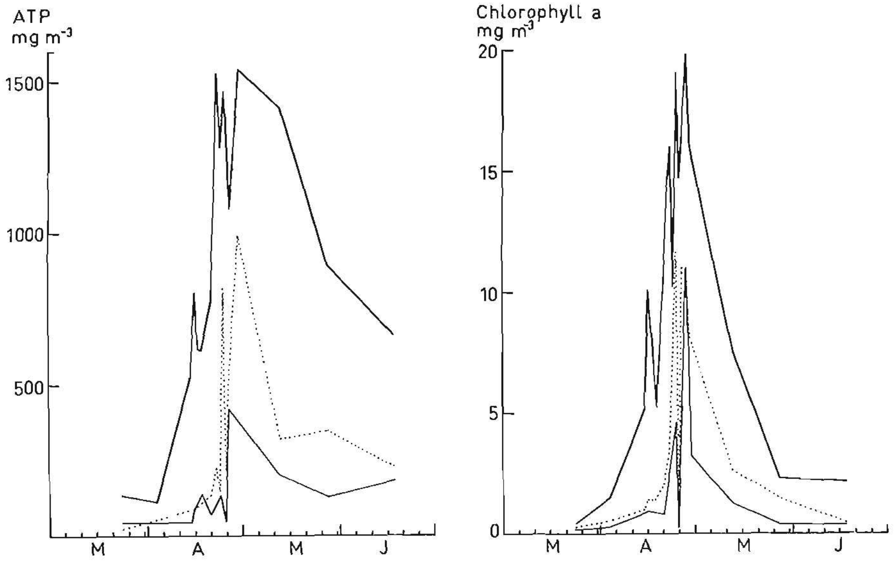

Fig. 6. Mean concentrations of ATP and chlorophyll *a* in the different water layers during the study period (March 23-June 17) in the open northern Baltic Proper in 1982. (Thick line = 0-30 m, dotted line = 30-80 m, thin line = 80-150 m).

During the phytoplankton bloom the inorganic nutrients were rapidly bound to particles in the euphotic layer (Figs. 4 and 5). During the bloom peak in April 22-24, DIN was almost depleted in the surface layer, but ca. 30 % of the phosphorus was still in the form of DIP (Fig. 7). In the layers below 30 m the contribution of PP and PN increased immediately after the bloom peak, indicating the sinking of organic matter from the euphotic zone (Fig. 7).

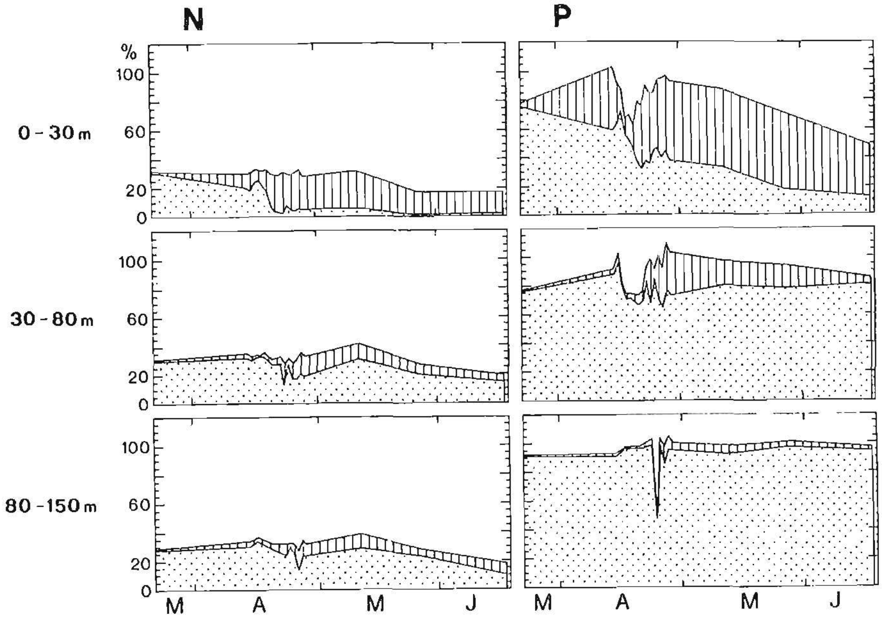

Fig. 7. The percentage contribution of the nutrient pools in the different water layers during the whole study period (March 23-June 17) in the open northern Baltic Proper in 1982. N refers to nitrogen and P to phosphorus. (Blank = dissolved organic compounds, vertical lines = particulate compounds, dots = dissolved inorganic compounds).

During the whole study period the bulk of the nitrogen was in the form of dissolved organic compounds. The ammonium concentration remained low in all layers - only at the last sampling occasion, June 17, was ca. 30 % of the DIN in the form of ammonium in the subhalocline layer. The values for DOP are probably too low, especially below the surface layer, due to the analytical methods used: part of the inorganic phosphorus adsorbed onto the particles was analyzed twice, first as DIP when it dissolves and reacts with molybdenum in the acidic solution, and secondly as PP (Folke Koroleff, pers. com. 1985).

The inrease in the C:N and C:P ratios (Table 1) indicates that the relative amount of carbon in the particulate matter increased toward the bottom. The contribution of PSi to particulate matter was quite stable during the bloom phase, but decreased markedly thereafter. This was caused by the change from a diatom-dominated phytoplankton population to a population containing more dinoflagellates, monads and blue-green algae as described by Leppänen & Kononen (1988).

Table 1. Mean elemental ratios of the particulate matter in the different water layers during March 23-June 17 in the open northern Baltic Proper in 1982.

		0-30 m			30-80 m			80-150 m		
		C : N : Si : P	C:N	N:Si	C : N : Si : P	C:N	N:Si	C : N : Si : P	C:N	N:Si
March	23	497 : 18 : 9 : 1	28	2.0	561 : 19 : 7 : 1	30	2.7	452 : 12 : 2 : 1	38	6.0
April	3	278 : 13 : 6 : 1	21	2.2	309 : 15 : 11 : 1	21	1.4	184 : 11 : 3 : 1	17	3.7
	14	183 : 14 : 7 : 1	14	2.0	366 : 16 : 7 : 1	23	2.3			
	15	141 : 11 : 9 : 1	13	1.2	252 : 19 : 12 : 1	13	1.6	195 : 15 : 6 : 1	13	2.5
	16	111 : 14 : 8 : 1	8	1.8	214 : 14 : 10 : 1	17	1.4			
	17	193 : 19 : 10 : 1	10	1.9	476 : 14 : 9 : 1	34	1.6	436 : 18 : 7 : 1	24	2.6
	18	187 : 16 : 10 : 1	12	1.6	264 : 7 : 2 : 1	38	3.5			
	19	155 : 14 : 10 : 1	11	1.4	337 : 19 : 3 : 1	18	6.3			
	20	197 : 22 : : 1	9							
	21	115 : 14 : 7 : 1	8	2.0	234 : 14 : 6 : 1	17	2.3	209 : 11 : 3 : 1	19	3.7
	22	101 : 16 : 9 : 1	6	1.8	274 : 16 : 10 : 1	17	1.6			
	23	115 : 16 : 11 : 1	7	1.4	161 : 15 : 8 : 1	11	1.9			
	24	132 : 17 : 10 : 1	8	1.7	152 : 13 : 9 : 1	12	1.4	203 : 15 : 8 : 1	14	1.9
	25	91 : 16 : 12 : 1	6	1.3	120 : 16 : 10 : 1	8	1.6	113 : 11 : 1 : 1	10	1.3
	26	123 : 18 : 13 : 1	7	1.4	139 : 11 : 11 : 1	13	1.0	190 : 14 : 11 : 1	14	1.3
	27	17 : 13 : 1		1.3	120 : 16 : 10 : 1	8	1.6	137 : 13 : 9 : 1	10	1.4
	28	137 : 17 : 13 : 1	8	1.3	101 : 14 : 8 : 1	7	1.8	151 : 15 : 10 : 1	10	1.5
	29	141 : 12 : 11 : 1	12	1.1	94 : 10 : 8 : 1	9	1.2	141 : 12 : 8 : 1	12	1.5
May	12	128 : 13 : 3 : 1	10	4.3	92 : 15 : 3 : 1	6	3.9	117 : 12 : 3 : 1	10	4.0
	27	146 : 16 : 1 : 1	9	11.3	128 : 9 : 4 : 1	14	2.2	120 : 7 : 2 : 1	17	3.5
June	17	15 : 4 : 1		3.8	362 : 11 : 6 : 1	33	1.8	154 : 8 : 4 : 1	19	2.0

4. DISCUSSION

The hydrochemical and biological features during the study period corresponded well with earlier observations made in the northern Baltic Proper and the western Gulf of Finland (Niemi 1973, 1975, Laakkonen et al. 1981, Leppänen & Tamelander 1981, Forsskåhl et al. 1982, Lassig et al. 1984, Kuparinen et al. 1984, Larsson et al. 1986).

Three successive stages can be distinguished on the basis of the nutrient development and the succession of the plankton community (see Leppänen & Bruun 1988, Leppänen & Kononen 1988). The sampling in March represented the winter stage, with low biological production and high concentrations of dissolved nutrients in the whole water body. The vernal phytoplankton production stage, from its initiation to the sinking from the euphotic zone (Leppänen 1988), took place in April-May. The last sampling in June represented the early summer phase.

4.1 Composition of the particulate matter

The biochemical composition of the particulate matter (seston) determines its energy content, nutritional value, and rate of decomposition in the subsequent biological and chemical processes in the food web. Although adenosine triphosphate (ATP) and chlorophyll *a* were the only organic compounds analyzed in this study, these compounds together with the elemental composition give a rough estimate of the structure and "status" of the seston.

The range of elemental ratios in this study (Table 1) agree well with earlier observations from the Baltic Sea (Voipio 1969, Sen Gupta & Koroleff 1973, Smetacek & Hendrikson 1979, Laakkonen et al. 1981).

The determination of particulate elements does not differentiate between living and detrital material. ATP, and to a lesser extent, chlorophyll *a* indicate the relative amount of living matter in the seston. According to the results, the living matter was concentrated in the surface layer (Fig. 6). The PC:ATP and PC:chlorophyll *a* ratios (Table 2) indicate that the contribution of detritus was highest in the beginning of the study period (i.e. before the bloom) and again in early summer. Below the surface layer the ratios remained high, except just after the peak of the diatom bloom, indicating the sinking of large amounts of living phytoplankton (Table 2). The variation

Table 2. Mean ratios of PC to ATP and chlorophyll *a* (chl-a) in the different water layers during the study period in the open northern Baltic Proper in 1982.

	0-30 m		30-80 m		80-150 m	
	PC/ATP	PC/chl-a	PC/ATP	PC/chl-a	PC/ATP	PC/chl-a
March 3	888	274	4090	334	2590	791
April 3	2091	156	1796	183	-	389
14	526	54	1208	104	2477	342
15	397	32	1067	67	1433	142
16	395	28	980	55	-	-
17	391	38	1573	125	1092	194
18	-	40	-	194	-	-
19	-	35	-	99	-	-
20	434	32	1102	72	1913	164
21	-	31	-	63	-	117
22	258	25	870	59	-	-
23	388	49	980	29	1052	-
24	381	29	517	36	-	51
25	226	21	339	38	1729	313
26	382	25	527	31	508	42
27	-	26	-	-	-	30
28	-	32	-	33	-	34
29	405	40	298	38	563	66
May 12	364	68	520	64	1025	163
27	301	118	640	153	1336	458
June 17	601	186	1195	626	1070	565

in the PC:chlorophyll a and PC:ATP ratios in the surface layer is feasible considering the large intra- and interspecific variation described, for instance by Sakshaug (1978) and Knoppers (1982). The values corresponded to those measured in the southern Baltic Sea (Smetacek & Hendrikson 1979).

Table 3 shows that PSi in the surface layer was closely associated with the phytoplankton biomass during the vernal growth period. According to the correlation with ATP detrital interference seems to be small for PN and PP, but more distinct for PC.

Table 3. Correlation matrix for the linear correlations between the elemental and living components of the particulate matter in the 0-30 m layer during the vernal period (3 April - 27 May 1982) in the open northern Baltic Proper.

	Sample Correlations Coefficient, (sample size), significance level					
	PP	PN	Psi	PC	ATP	chlorophyll *a*
PN	.9482 (19) .0000					
Psi	.8080 (19) .0000	.8606 (19) .0000				
PC	.9104 (19) .0000	.8539 (19) .0000	.7731 (19) .0001			
ATP	.9237 (14) .0000	.9327 (14) .0000	.7336 (14) .0028	.8007 (14) .0006		
chlorophyll *a*	.7852 (19) .0001	.8477 (19) .0000	.9046 (19) .0000	.7289 (19) .0004	.7318 (14) .0029	
phytoplankton	.5669 (8) .1428	.7245 (8) .0421	.9465 (8) .0004	.4104 (8) .3125	.6538 (8) .0787	.9416 (8) .0005
ciliate biom.	.7636 (9) .0166	.7782 (9) .0135	.3591 (9) .3425	.7008 (9) .0355	.7970 (9) .0101	.4132 (9) .2690
bact. biom.	.7383 (9) .0231	.7102 (9) .0321	.3064 (9) .4227	.6567 (9) .0547	.8264 (7) .0219	.2414 (9) .5316
mesozoopl. biom.	-.2909 (9) .4475	-.3034 (9) .4274	-.4877 (9) .1830	-.3124 (9) .4131	-.1293 (8) .7602	-.5675 (9) .1110

4.2 Changes in the nutrient pools

The observed changes in the nutrient pools (Table 4) represent the net results of different pathways: biological carbon and nutrient uptake, assimilation, remineralization and excretion, as well as chemical reactions, lysis, sinking and resuspension of particles.

Table 4. The initial reserves (situation on March 23) and changes in the nutrient pools in different layers during the vernal production period (April 3-May 27) expressed as mmol m^{-2}.

	Surface layer			Intermediate l.		Bottom layer	
	reserve	change	production*	reserve	change	reserve	change
DIN	216	-215		348	-173	433	-157
PN	11	+ 66	481	14	+ 53	19	+ 42
tot-N	743	-226		1211	-183	1550	-328
DIP	19	- 17		35	+ 1	180	+ 38
PP	6	+ 4	27	1	+ 6	1	+ 7
tot-P	25	- 16		46	+ 15	198	+ 29
SiO_4	435	-350		864	- 77	3569	+ 39
PSi	6	+ 1	280	5	+ 24	3	+ 15
PC	575	+100	3000				

* Calculated on the basis of total particulate primary production (phytoplankton + *Mesodinium rubrum*, Leppänen & Bruun 1988) and the measured ratio of phytoplankton C:PN:PSi:PP of the surface layer during the increase phase of the vernal bloom. The phytoplankton C is adopted from Leppänen & Kononen (1988).

During the intensive sampling period in April 14 - 29, representing the growth stage of the diatom bloom, the decrease in inorganic nutrients in the surface layer corresponded to the increase in the particulate forms of N and P but not of silicon (Fig. 8). The concentrations of the particulate elements

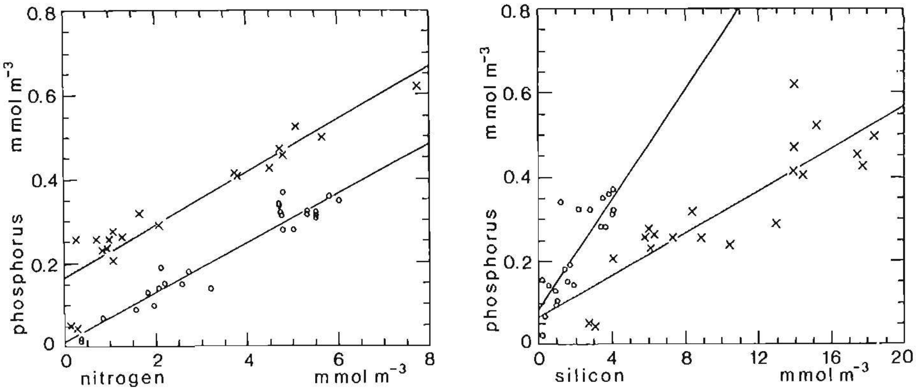

Fig. 8. Correlations between phosphorus, nitrogen and silicon in the surface layer (0-30 m) during the whole study period (March 23-June 17) in the open northern Baltic Proper in 1982 (x - particulate forms, o - dissolved inorganic forms).

increased in the ratio of 98 C: 18 N: 14 Si: 1 P and the inorganic forms decreased in the ratio of 95 C: 18 N: 49 Si: 1 P (the decrease in CO_2 is calculated using primary production data from Leppänen & Kononen 1988). The increase ratio of particulate elements corresponded well with those reported elsewhere for the same phase of succession (Weichart 1980, Leppänen & Tamelander 1981).

The decrease in dissolved silicon was, on the average, 3.5 times higher than the increase in PSi. The reason for this discrepancy appears to be the sporulation of the dominant diatoms, and their rapid sinking down the water column (Leppänen 1988).

The elemental ratios of the particulate matter in the different layers indicate that both nitrogen and phosphorus were removed from seston faster than carbon during the sinking. This was clear in the layer above the halocline. In the subhalocline layer, processes such as adsorption of dissolved inorganic nutrients on the particles (cf. Voipio 1969) obscure the decomposition process and make estimation of the proportional release rates of the elements difficult.

The processes affecting the changes in the nutrient pools differ in the layers above and below the halocline:

- The trend for phosphorus is caused by the uptake and assimilation processes of the phytoplankton in the surface layer, followed by the sinking of POM and dissolution in the bottom layer. Most of the increase in phosphorus in the bottom layer can be attributed to mobilization from the sediment under low oxygen conditions.
- The decrease in total N was connected to the decrease in NO_3-N in all layers. Above the halocline the decrease in DIN was mostly caused by phytoplankton assimilation. Below the halocline, where the oxygen concentration was low, especially in May-June, the decrease can be associated with the bacterial denitrification. Rönner (1983, 1985) reports denitrification rates of from 0.5 to 9.8 N/mg m^{-3} d^{-1} (depending on the determination method) in the Baltic Proper when the oxygen concentration is <0.2 cm^3 dm^{-3}.

Table 4 shows that only about half of the primary formation of PN and 70 % of PP during the vernal period could be based on the initial reserves of the corresponding inorganic forms in the surface layer. The low biomass and total activity of the consumers (Leppänen & Bruun 1988, Lahdes et al. 1988) suggest small recycling of nutrients. The most important mechanism in supporting the primary production seems to be the vertical transport of nutrients from the intermediate layer. This is illustrated, for instance, by the concentration profiles of DIN (Fig. 9) and the observations of Leppänen & Alenius (1988). The same mechanism was suggested by Holligan et al. (1984) and Rönner (1985). The decrease in the silicon reserves fits the sedimentation values measured by Leppänen (1988), but not the primary formation of PSi calculated on the basis of the measured C:N:Si:P ratio (Table 4).

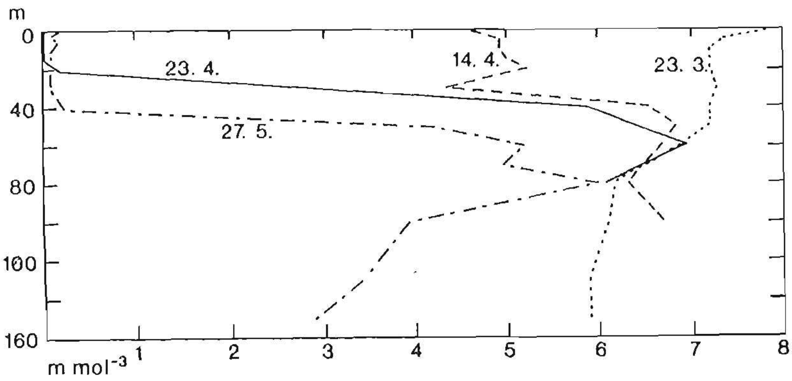

Fig. 9. Vertical distribution of NO_3-N on some sampling occasions in the open northern Baltic Proper in 1982. Adopted from Leppänen et al. 1986.

5. CONCLUSIONS

In the layer above the halocline, most of the nutrient dynamics during the study period (from March 23 to June 17) were associated with biochemical reactions, lysis and sedimentation of phytoplankton cells. The living biomass was concentrated in the surface layer. Detritus was predominating in the seston below the depth of 30 m. The particulate matter was predominantly autochtonous, originating from plankton organisms. The initial reserves of dissolved inorganic nutrients in the surface layer, together with the vertical transport from the intermediate layer, supported most of the primary formation of POM. During the growth of the phytoplankton bloom dissolved inorganic nitrogen and phosphorus decreased at the same rate as the particulate forms increased in the surface layer. During the whole study period the accumulation of POM in the water column was, however, of minor importance. Below the halocline, the decrease in total nitrogen values could be partly explained by biological denitrification, and the increase in total phosphorus by the mobilization of DIP from the sediment.

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CYCLING OF ORGANIC MATTER DURING THE VERNAL GROWTH PERIOD IN THE OPEN NORTHERN BALTIC PROPER. III. PHYTOPLANKTON COMPOSITION AND ESTIMATION OF LOSS RATES OF PHYTOPLANKTON PRODUCTION

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ABSTRACT

Phytoplankton primary production, biomass and species composition were followed during the vernal production period in the open northern Baltic Proper in 1982. The peak of the vernal phytoplankton bloom occurred at the end of April, with a mean biomass of ca. 0.4 mol C m^{-3} in the layer 0-30 m and a gross production of ca. 0.22 mol C $m^{-2}d^{-1}$. During the 50-day vernal bloom period the gross production of phytoplankton was 6.58 mol C m^{-2}. Almost half of this was remineralized through algal respiration in the mixing surface layer. About 20 % of the remaining net production was estimated to be in the form of exudates.

Key words: Baltic Sea, phytoplankton species composition, primary production.

1. INTRODUCTION

The results presented by Elmgren (1984) and Poutanen (1985) indicate that the organic matter in the open Baltic Proper is predominantly autochthonous. This implies that planktonic primary production is an important process in the regulation of the ecosystem, and its quantification is essential when estimating the cycling of organic matter in the food web.

This work is part of a comprehensive ecosystem study dealing with the production, decomposition and sinking of organic matter in the northern Baltic Proper. The aim of this paper is to describe the species and biomass composition of phytoplankton, to quantify the amount of organic carbon fixed by phytoplankton, and to estimate the mineralization by phytoplankton respiration and the production of dissolved organic material by exudation.

2. MATERIAL AND METHODS

The samples were taken in the open northern Baltic Proper at a site (59°26.1' N; 21°31.4' E) where the water depth is ca. 160 m. For detailed description of the area, hydrography and nutrient dynamics see Leppänen & Alenius (1988) and Lahdes & Leppänen (1988).

Water samples were taken once a week or every second week from March 23 to June 17, 1982, except during the period April 14-29, when daily sampling was carried out. A plastic sampler of either 50 dm^3 or 5 dm^3 was used. When the smaller sampler was used three subsamples were taken from every depth and combined. The sampling depths for chlorophyll *a* and primary production capacity were 0, 2, 5, 10, 15, 20, 30, 40, 50, 60, 80, 100, 130 and 150 m, and occasionally also 70 m. Additional samples for *in situ* primary production measurements were taken from depths of 1, 3, 5 and 7 m. The phytoplankton samples were preserved with Lugol+Aa solution. The species composition was determined on integrated samples (0-10 m, 15-30 m and 40-50 m), and below the halocline on single samples, using the inverted microscope technique (Utermöhl 1958). Biomass values were calculated according to Edler (1979) with modifications presented by Kononen et al. (1984).

The water samples for chlorophyll *a* analysis were filtered through Whatman GF/C glass fiber filters (Ø 25 mm, median retention size ca. 1 µm), 90 % acetone being used as solvent (Edler 1979). The amount of chlorophyll *a* in the extract was measured fluorometrically according to Edler (1979) on a Turner 110 fluorometer.

Particulate primary production was measured using the ^{14}C technique (Steemann Nielsen 1952). The primary production capacity was determined *in vitro* using a constant light incubator. Philips TLD 38/33 fluorescence tubes were used as the light source with a total radiant energy of 52 J cm^{-2} h^{-1}. The incubation time was 2 h and the temperature of the incubator was adjusted to correspond to the mean temperature of the euphotic layer. The sample volume was ca. 30 cm^3, and 2 µCi $Na_2{}^{14}CO_3$ was added to each sample. Daily production was calculated from the production capacity values as described by Gargas & Hare (1976).

Two measurements of daily primary production were carried out *in situ* according to Lassig & Niemi (1972) in order to compare the results to the calculated daily production. The samples were incubated at the sampling depths (0, 1, 2, 3, 5, 7, 10, 15, and 20 m) for 24 h. Bottles with a volume of 130 cm^3 were used, and 2 µCi of $Na_2{}^{14}CO_3$ was added to each sample.

All the incubations were usually started between 9-11 a.m. The samples were filtered immediately after the incubation on membrane filters (Sartorius, Ø 25 mm, pore size 0.45 µm). The wet filters were transferred to scintillation vials and 0.15 cm^3 of 0.5 N HCl added to the filters in order to remove the residual $^{14}CO_2$. The filters were then dried and dissolved in 1 cm^3 of ethylacetate. 10 cm^3 of scintillation liquid (PCS, Amersham Co.) was used and the activity measured with a LKB/Wallac 1217-Rackbeta liquid scintillator.

The total CO_2 concentration of the water was calculated according to Buch (1945).

The loss rates of phytoplankton production were estimated using the method described by Tilzer (1983) by comparing observed changes and potential growth of the phytoplankton biomass.

3. RESULTS AND DISCUSSION

3.1 Phytoplankton composition

At the two first sampling occasions in March 23 and April 3 the phytoplankton biomass was at the low winter level (Fig. 1). It consisted of unidentified small flagellates (70-50 % of the total biomass) and dinoflagellates (*Gymnodinium* spp. and unidentified naked species) (Fig. 2).

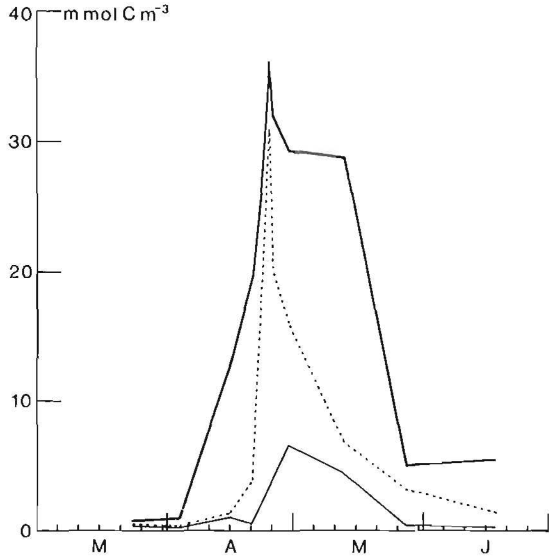

Fig. 1. Total amount of phytoplankton biomass in the different water layers in the open northern Baltic Proper from March 23 to June 17, 1982. Thick line = 0-30 m; dotted line=30-80 m, thin line = 80-150 m. (Adopted from Leppänen & Bruun 1986).

On April 15 diatoms were the main phytoplankton group, forming 70-80 % of the total biomass up until the end of April.

Chaetoceros holsaticus and *Achnanthes taeniata* were the dominant species. The peak of the diatom bloom coincided with the depletion of nitrate nitrogen near the surface (cf. Lahdes & Leppänen 1988).

During April 24-29 most of the *Chaetoceros* cells had sporulated. On May 12 the biomass consisted primarily of naked dinoflagellates and the diatom *Skeletonema costatum*. At the end of May the dinoflagellate *Gonyaulax catenata* and unidentified small flagellates dominated. In June the phytoplankton community typical of the summer season prevailed: small flagellates, blue-green algae (*Microcystis reinboldii*) and dinoflagellates made up the bulk of the biomass.

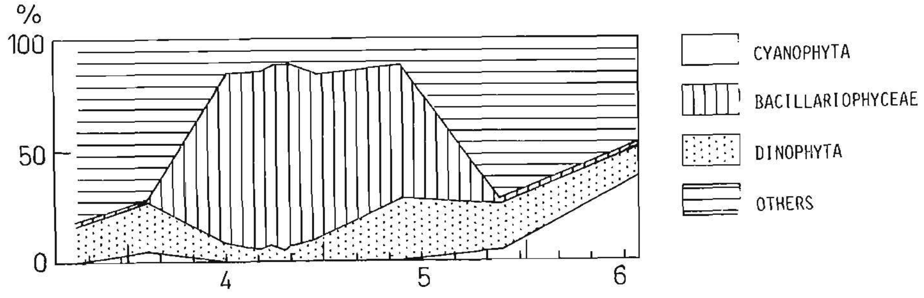

Fig. 2. The contribution (%) of different phytoplankton groups to the total phytoplankton biomass in the 0-30 m layer in the open northern Baltic Proper from March 23 to June 17, 1982.

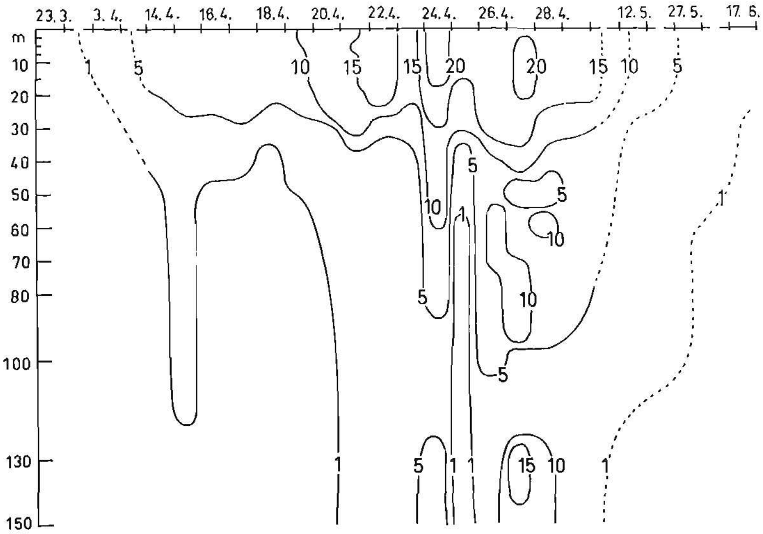

Fig. 3. Concentrations of chlorophyll *a* (mg m^{-3}) in the open northern Baltic Proper from March 23 to June 17, 1982.

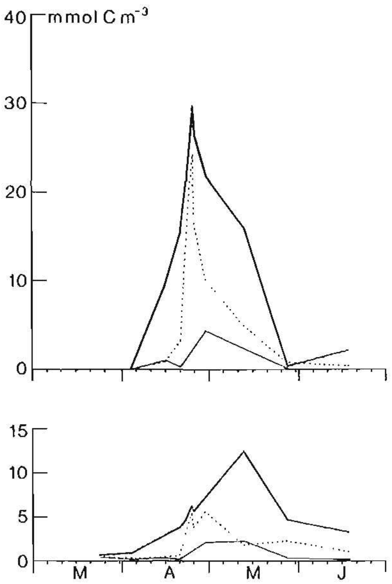

Fig. 4. Mean biomass of non-motile (upper figure) and motile phytoplankton species in the different water layers in the open northern Baltic Proper from March 23 to June 17, 1982. (Thick line = 0-30 m; dotted line = 30-80 m; thin line = 80-150 m).

According to the chlorophyll *a* values, the phytoplankton biomass was concentrated in the mixing surface layer during the growth phase of the bloom, the highest concentrations occurring above a depth of 10 m. High chlorophyll values were measured in the water above the halocline after April 24, and at all depths at the end of the month (Fig. 3), thus indicating the sinking of the bloom.

There was no distinct difference in the vertical distribution between the flagellated and non-flagellated species, except at the end of May (Fig. 4).

3.2 Primary production

The values for particulate primary production capacity followed the pattern of phytoplankton biomass (Fig. 5). High values below the euphotic layer indicated that phytoplankton cells sinking out of the mixing surface layer were still active.

The temporal pattern of the daily primary production, calculated on the basis of the capacity values, was similar to the primary production capacity (Fig. 6.). The sum was 7.58 mol C m^{-2} for the whole study period. The ratio of daily production to biomass (P/B ratio) varied between 0.32 and 0.06, the lowest value being recorded on May 12 (Fig. 7).

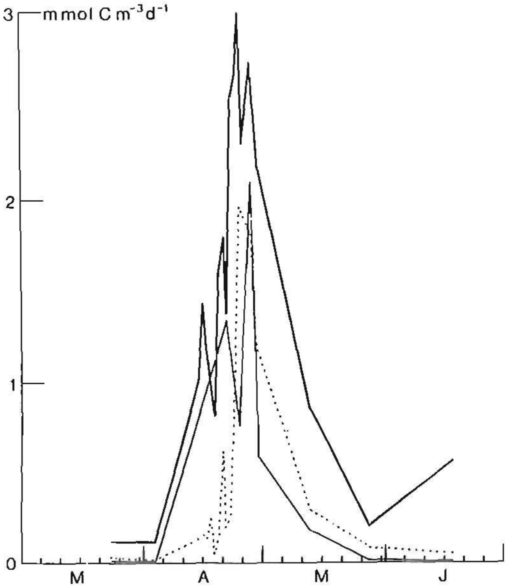

Fig. 5. Mean primary production capacity in the different water layers in the open northern Baltic Proper from March 23 to June 17, 1982. (Thick line = 0-30 m; dotted line = 30-80 m; thin line = 80-150 m).

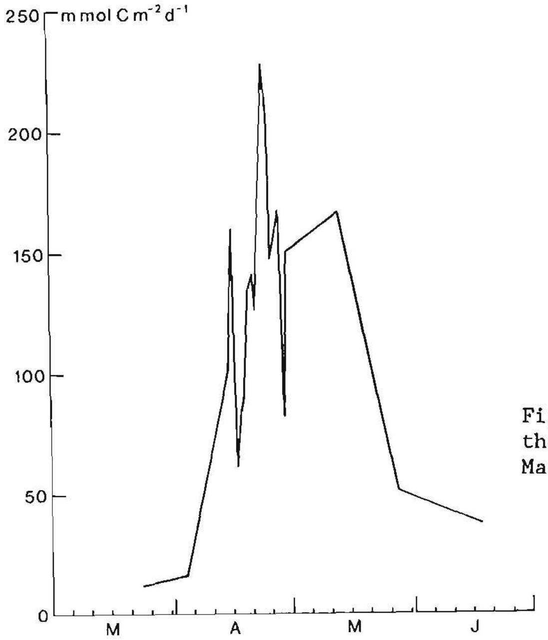

Fig. 6. Daily primary production in the open northern Baltic Proper from March 23 to June 17, 1982.

3.3 The fate of the incorporated carbon

3.3.1 Gross production

Despite the fact that the ^{14}C method has been in use for about 30 years, it is not completely clear what it really measures (Peterson 1980). When short incubation times (usually <4 h) are used the production values are supposed to approximate gross production, and with long incubation times (usually >24 h) the production values should be close to the net production (Peterson 1980, Dring & Jewson 1982, Li & Harrison 1982). It can thus be assumed that the daily particulate production values which were calculated using the 2 h production capacity values, represent daily gross production, especially since only the period between sunrise and sunset was taken into account.

3.3.2 Processes associated with the loss of phytoplankton production from the surface layer

Part of the inorganic carbon fixed in the phytoplankton biomass passes directly back to the inorganic pool through the phytoplankton respiration. Net primary production is lost through exudation of organic soluble compounds, through mortality and subsequent lysis of cells, through grazing of consumers, and through the sinking of cells down out of the euphotic layer. In the next three paragraphs we will estimate the total loss of phytoplankton from the 0-30 m layer (in comparison to the sedimentation studies by Leppänen 1988), and the contribution of algal respiration and exudation to this total loss.

3.3.2.1 Total loss of phytoplankton

Total loss of phytoplankton production from a water column can be estimated on the basis of primary production and subsequent biomass change (e.g. Jassby & Goldman 1974, Peterson 1978, Jewson et al. 1981, Leppänen & Tamelander 1981a). The loss rates calculated according to the method described by Tilzer (1984) were low up until the end of the diatom bloom, after which they increased and remained at a high level up until the end of April (Fig. 8). The estimated total loss of phytoplankton production for the whole study period was 5.92 mol C m^{-2}.

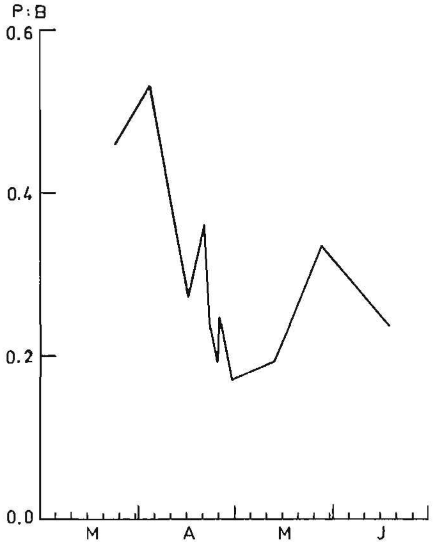

Fig. 7. The ratio of daily primary production to phytoplankton biomass (P:B ratio) in the 0-30 m layer in the open northern Baltic Proper from March 23 to June 17, 1982.

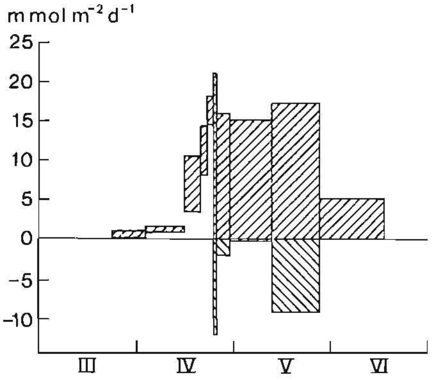

Fig. 8. Potential growth, observed changes, and loss of phytoplankton biomass in the 0-30 m layer in the open northern Baltic Proper from March 23 to June 17, 1982. The upper edges of the columns represent production rates ($P=B_t(e^{\mu *}-1)$), the lower edges the rates of biomass changes ($B=B_t(e^{k}-1)$, and the whole columns represent the daily loss rates.

3.3.2.2 Respiration of phytoplankton

As can be seen from the P:B values presented in Fig. 7, the growth rate of phytoplankton was high enough to bring the ratio of ^{14}C to ^{12}C between the cells and the sample water into balance during 24-hour incubations (cf. Dring & Jewson 1982). The two *in situ* incubations, carried out on April 22 and 25, thus represent apparent net particulate production in the 0-20 m layer (Fig. 9). The difference between the daily production values obtained by the incubator technique and the *in situ* technique can be used to estimate phytoplankton respiration. According to these results, respiration accounts for almost one third of the gross production in the 0-20 m layer, which is in accordance with the observations of Eppley & Sharp (1975) and Mague et al. (1980). As a result of the different light

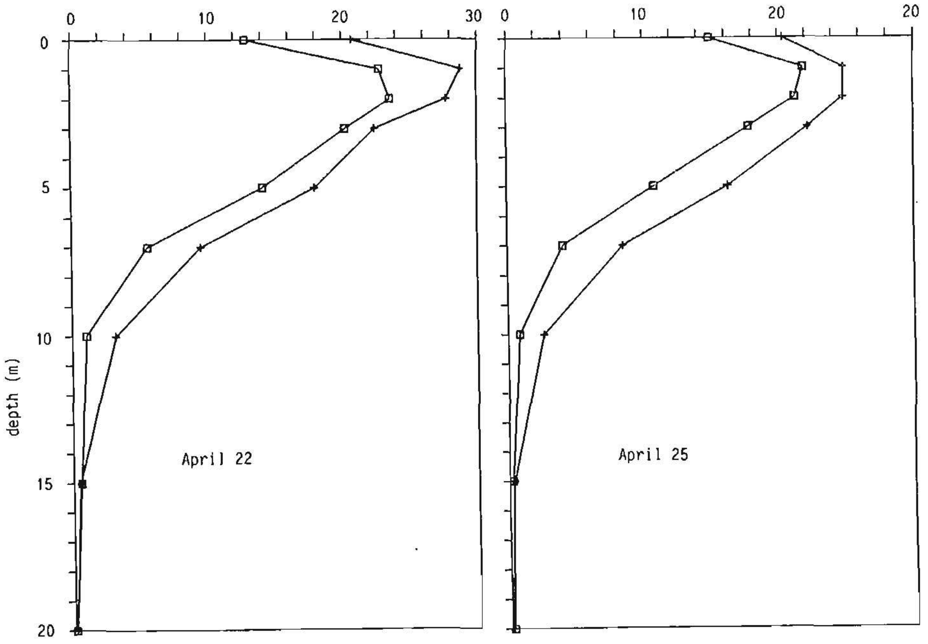

Fig. 9. Vertical distribution of daily primary production (mmol C m^{-3} d^{-1}) based on the incubator measurements (-x-) and *in situ* measurements (-[]-) in the open northern Baltic Proper on April 22 and 25, 1982.

intensities, the ratio of respiration to apparent net photosynthesis varied at different depths: the difference between daily gross and apparent net production was 27-48 % near the surface, 12-17 % at the depths of maximum production, and 41- 68 % at depths of 10-20 m. Mean respiration in the 0-10 m layer corresponded to the values reported by Kuparinen (1984) for the Tvärminne sea area at the entrance to the Gulf of Finland.

In order to compare primary production to the sedimentation values measured at 30 m depth (Leppänen 1988) algal respiration for the 0-30 m layer has to be quantified. The depth of the euphotic layer varied between 12 and 28 m (Leppänen & Alenius 1988). Since algal respiration exceeds production in the aphotic layer, the ratio of production to respiration is smaller for the 0-30 m layer than for the 0-20 m layer.

Since the maximum photosynthetic rate (P_{max}) depends on the physiological state, growth history and environmental conditions of the algae, the algal respiration (R) can be assumed to be proportional to P_{max} as follows (Parsons et al. 1977):

$$R = rP_{max}, \tag{1}$$

if P_{max} is measured under the same conditions as estimated respiration (e.g. temperature). The algal respiration can thus be calculated using the two-hour production capacity values which represent P_{max} (cf. Bruun & Grönlund 1981) with $r = 0.06$ (e.g. Gargas & Hare 1976, Holligan et al. 1984). The values presented in Table 1 were calculated with the assumption that respiration remains constant throughout the night and day. On average almost half of the gross production was remineralized by the phytoplankton in the 0-30 m layer, and the algal respiration contributed ca. 63 % of the calculated total loss from the gross primary production.

Table 1. Primary gross production (P, mmol C m^{-2} d^{-1}), phytoplankton respiration (R, mmol C m^{-2} d^{-1}), and the percentage of respiration out of gross production (R %) in the 0-30 m water layer in the open northern Baltic Proper in 1982.

date		P	R	R %
March	3	10.0	5.1	50
April	4	16.3	4.8	30
	14	101.2	43.8	43
	15	158.9	61.6	39
	16	62.2	48.8	78
	17	84.6	41.4	49
	18	91.3	34.9	38
	19	136.0	69.3	51
	20	142.5	77.4	54
	21	127.2	59.3	47
	22	182.0	109.6	60
	23	231.3	115.6	50
	24	210.8	130.3	62
	25	160.3	99.5	62
	27	170.9	118.4	69
	28	80.2	103.0	128
	29	151.3	93.6	62
May	12	14.0	90.8	54
	27	51.2	8.7	17
June	17	39.5	23.8	61

When the ^{14}C method is used with short incubation times the estimated amount of phytoplankton respiration is a critical factor in calculating the amount of organic carbon available to the other trophic levels. The respiration values calculated on the basis of P_{max} for the 0-30 m layer are higher than the community respiration values measured simultaneously with the dark oxygen bottle method (Lahdes et al. 1988, Table 3). The respiration values obtained in this study, however, fit well with the overall picture of the cycling of organic carbon in the food web (Leppänen 1988), and are of the same order of magnitude as those reported for many pelagic systems (e.g. McKellar & Hobro 1976, Smith 1977, Joiris et al. 1979, Kuparinen et al. 1984).

3.3.2.3 Algal exudation

The literature gives variable and somewhat contradictory values for the amount of algal exudation, which is dependent on the species composition, nutrient and light conditions, incubation time etc. (Choi 1972, Saunders 1972, Fogg 1977, Lancelot 1979, Larsson & Hagström 1979, Mague et al. 1980). The preservation and filtration procedures may also lead to erroneous exudation values (e.g. Leppänen & Tamelander 1981b). The exudation of fast-growing populations has been shown to be close to 10 % of gross production (Wolter 1982, Iturriaga & Zsolnay 1983, Jensen 1983, Smith & Platt 1984, Joint et al. 1986). When this value is applied, the amount of dissolved production during the study period can be estimated to be ca. 0.75 mol C m^{-2}, representing ca. 13 % of the calculated total loss of gross primary production. Exudation values measured by Kuparinen (1984) in the western Gulf of Finland have ranged from 15- 36 % of the phytoplankton gross production.

4. EVALUATION

The results for species composition and production level were in accordance with earlier observations from the western Gulf of Finland (e.g. Niemi 1973, 1975, Forsskåhl et al. 1982, Lassig et al. 1984, Kononen & Niemi 1984) and from the Askö area (Larsson et al. 1986). This being the case, it might be possible to generalize the results to concern a "typical vernal period" in the Baltic Proper.

The pattern of phytoplankton composition shows that the sampling dates from April 3 to May 27 represent the actual vernal phytoplankton bloom period. This is also supported by the observations made by Lahdes & Leppänen (1988). The onset of the bloom was clearly related to the amount of irradiation and to the depth of the mixing layer (cf. Leppänen & Alenius 1988). During the growth phase of the bloom, sinking of phytoplankton was small and the biomass was concentrated in the surface layer. The diatom bloom ended when inorganic nitrogen was depleted in the euphotic layer. The loss of phytoplankton production reached a maximum after the bloom peak. The chlorophyll a and production capacity values reached their maxima below the surface layer at the same time, thus indicating rapid sinking of living phytoplankton cells.

The net increase in the phytoplankton biomass in the 0-30 m layer was 0.13 and 0.14 mol C m^{-2} during the bloom period and the whole study period, respectively. About 0.17 mol C m^{-2} was left in this water layer. The values related to the phytoplankton are presented in Table 2.

Table 2. Phytoplankton production, respiration and calculated total loss of gross production in the layer 0-30 m during the whole study period (March 23 - June 17), and during the bloom period (April 3 - May 27) in the open northern Baltic Proper in 1982.

	whole study period mol C m^{-2}	vernal bloom period mol C m^{-2}
gross production	7.58	6.58
respiration	3.75	3.17
net production	3.83	3.42
-particulate	3.08	2.75
-dissolved	0.75	0.67
total loss of phytoplankton	5.92	5.00

Extrapolating from measured rates of carbon assimilation to growth of the algae is not unambiguous (e.g. Eppley 1981), especially when short incubation times are used (Morris 1981). This obviously explains the discrepancy between calculated total loss, respiration, exudation and reserves. The main pathways and amount of carbon cycled through phytoplankton during the vernal bloom period in the 0-30 m layer are, however, clear: almost half of the inorganic carbon fixed was directly remineralized by the primary producers, ca. 20 % of the net production of carbon being in the form of dissolved exudates and only 3 % in the form of living cells of primary producers at the end of the bloom.

The net primary production serves as the potential energy source for consumers and decomposers. Low molecular weight compounds are shown to predominate in exudates (Mague et al. 1980, Chrost 1981, Jensen 1983), and a considerable proportion of this component has been shown to flow directly from phytoplankton to bacteria (Hoppe 1978, Larsson & Hagström 1982, Riemann et al. 1982). If a 60 % gross growth efficiency is assumed for bacteria, then exudates alone could support a bacterial production of ca. 0.5 mol C m^{-2} during the vernal period. The bacterial incorporation of exudates has been shown, however, to vary considerably, possibly depending on algal species composition (Wolter 1982). According to Wolter's (1982) observations, exudate levels are low when diatoms are present in the sample. This may be one explanation for the measured low bacterial production during the vernal period in the northern Baltic Sea (Kuparinen 1984, Lahdes et al. 1988).

The particulate primary production could support a herbivore zooplankton production of ca. 1.67 mol C m^{-2} if gross growth efficiency is assumed to be 50 %. This is plausible for copepodites and for ciliates (Daro & Gijsegem 1984, Jones 1984, Verity 1985), which were the dominant group of consumers during the study period (Leppänen & Bruun 1988). However, as observed in many areas of the Baltic Sea (Jansson 1972, Forsskåhl et al. 1982, Kuparinen et al. 1984, Smetacek et al. 1984) most of the net primary production during the vernal period sinks down out of the euphotic layer and is also retained as a reserve in the water column. The rapid sinking of the living phytoplankton biomass after the bloom peak was apparent also in this study. Since the vernal primary production contributes for ca. 1/3 to the annual primary production (Lassig et al. 1984), the reserves form an essential energy input for the ecosystem, especially the sinking portion for the benthos (e.g. Graf et al. 1984).

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CYCLING OF ORGANIC MATTER DURING THE VERNAL GROWTH PERIOD IN THE OPEN NORTHERN BALTIC PROPER. IV. CILIATE AND MESOZOOPLANKTON SPECIES COMPOSITION, BIOMASS, FOOD INTAKE, RESPIRATION, AND PRODUCTION

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ABSTRACT

The dynamics of the ciliate and mesozooplankton communities were followed and their quantitative role in the organic carbon cycle estimated during the vernal growth period in the open northern Baltic Proper in 1982. The biomass of zooplankton was concentrated in the surface layer. The autotrophic ciliate *Mesodinium rubrum* was the dominant ciliate species. Most of the heterotrophic ciliates were non-loricated. Calanoid copepods predominated in the mesozooplankton biomass. During the vernal phytoplankton bloom period (April-May) the contribution of *Mesodinium* to total particulate primary production was ca. 7 %. About one third of the particulate primary production was cycled through zooplankton, mostly ciliates.

Key words: Baltic Sea, zooplankton, *Mesodinium rubrum*, ciliates, copepods.

1. INTRODUCTION

Herbivorous zooplankton regulates the composition of phytoplankton, and stimulates its production by recycling nutrients. Together with bacterivorous, omnivorous and carnivorous zooplankton they process the material originally produced by phytoplankton; the vertical migration of certain species and the formation of fecal pellets can also be important in the vertical transport of organic matter (Paffenhöfer & Knowles 1979, Fowler

& Fisher 1983). A wide variety of organisms are included in this group if it is assumed to comprise all eucaryotic heterotrophs. The most important groups in the Baltic Sea are heterotrophic flagellates, ciliates, rotifers, copepods, cladocerans, mysids and coelenterates.

The aim of this paper is to describe the dynamics of the zooplankton community and to quantify its role in the organic carbon cycle during the vernal phytoplankton bloom period. The heterotrophic flagellates are not included in this study. This study is part of a comprehensive ecosystem research project carried out in the open northern Baltic Proper in 1982 (Leppänen & Alenius 1988, Lahdes & Leppänen 1988, Leppänen 1988, Leppänen & Kononen 1988), and summarizes the results presented by Leppänen (1985), Bruun (1985), and Leppänen & Bruun (1986).

2. MATERIAL AND METHODS

The samples were collected in the open northern Baltic Proper (59° 26.1' N; 21° 31.4' E) at a point were the water depth is ca. 160 m (for a more detailed description of the area and its chemical and biological characteristics see Leppänen & Alenius 1988, Lahdes & Leppänen 1988, Leppänen & Kononen 1988).

The sampling period was from 23 March to 17 June 1982 . The sampling frequency was 1-2 times a week, except during the period 14-29 April when sampling was more frequent. The samples were collected usually before noon. Water samples for determining microzooplankton were collected with a plastic sampler of either 40 or 5 dm^3. The sampling depths were 0, 2, 5, 10, 15, 20, 30, 40, 50, 80, 100, 150 m, and occasionally 70 m. Mesozooplankton samples were collected with a standard WP-2 net with mesh size of 100 µm (Fraser 1968). The depth intervals for the vertical hauls were 0-30 m, 30-80 m, and 80-150 m.

The microzooplankton samples were preserved with Lugol AA solution. The species composition was determined on integrated samples (0-10 m, 15-30 m and 40-50 m), and below the halocline on single samples, using the inverted microscope technique (Utermöhl 1958). The biomass was calculated on the basis of average individual volumes, using 0.11 as the ratio of carbon to volume (Edler 1979) and 0.2 as the ratio of dry weight to volume (Capriulo & Carpenter 1983).

The mesozooplankton samples were preserved in 4 % buffered formalin, subsampled with the Folsom plankton sample splitter (McEven et al. 1954), and analyzed to species level as well as counted microscopically. The biomass of copepods and of the cladoceran *Eubosmina longispina maritima* were calculated using the correlation between animal length and carbon content (Hernroth 1985). The carbon to volume ratio (%) for *Fritillaria borealis* was supposed to be 0.6, for *Pleurobrachia pileus* 0.25, for Bivalvia larvae 0.05, and for Polychaeta larvae 5.8 (Parsons et al. 1977). A carbon content of 5.2 % was used for other taxa (Mullin 1969). The dry weight of the animals was calculated from the wet weight using a conversion factor of 0.5 (Heinbokel 1978, Capriulo & Carpenter 1983).

No direct measurements on food intake, respiration and production were performed. All the processes were estimated using equations obtained from the literature. The food intake of ciliates was calculated using empirical equations presented by Spittler (1973) and Heinbokel & Beers (1979). The minimum and maximum ranges of rotifer food intake were calculated according to Starkweather (1980). The food intake of copepods and cladocerans was calculated using the equations of Peters & Downing (1984).

The amount of food potentially available for zooplankton was estimated using particulate organic carbon (POC) values measured simultaneously by Lahdes & Leppänen (1988). The size fraction suitable for different animals (POC_f) was calculated from POC values using particle measurements performed with a Coulter Counter TA-II counter as follows:

$$POC_f = POC\ (V_f/V_{tot}), \qquad (1)$$

where POC_f is the amount of particulate carbon in the size fraction suitable for the animal, V_f the particle volume of the same size fraction and V_{tot} the total particle volume in the water. The particle size for the food items for ciliates was assumed to be 43 % of the oral diameter (Heinbokel 1978). A medium particle diamater of 5 µm was used for *Eubosmina longispina maritima* (Peters & Downing 1984). The medium particle size for copepods was 28 µm, determined through grazing experiments (unpublished results of the Finnish Institute of Marine Research).

Respiration was calculated using the equations of Ikeda (1970), Dagg et al. (1982), and Vidal & Whitledge (1982). 50 % of the dry weight was assumed to be carbon (Omori & Ikeda 1984). The respiration of microzooplankton was also calculated with the equation of Laybourn & Finlay (1976). The oxygen consumption was converted to carbon respiration according to McKellar & Hobro (1976). An RQ of 0.85 was used for heterotrophes, and of 1.0 for the autotrophic *Mesodinium rubrum*.

The production of ciliates and rotifers was calculated using the equation of Galkowskaya (1965). The production of copepods was calculated using the equation of Edmondson & Winberg (1971). The production of cladocerans was calculated using the P:B ratios obtained by Eerola (1979) in the Gulf of Finland.

3. RESULTS

3.1 Biomass and species composition

The biomass of ciliates was concentrated in the surface layer (0-30 m, Fig. 1), where the autotrophic ciliate *Mesodinium rubrum* was the dominant species (Table 1). *Mesodinium* was also found in the intermediate (30-80 m) and bottom (80-150 m) layers, although to a less dominant degree than in the surface layer. Non-loricated species of the genera *Lohmanniella*, *Lacrymaria* and *Didinium* were the most abundant heterotrophic ciliates (Table 1).

The genus *Synchaeta* was the only representative of rotifers with a low and fairly constant biomass (Table 2). A small maximum was observed on 12 May, contributing ca. 5 % to the total zooplankton biomass. During the whole observation period the biomass of mesozooplankton was low, increasing toward the

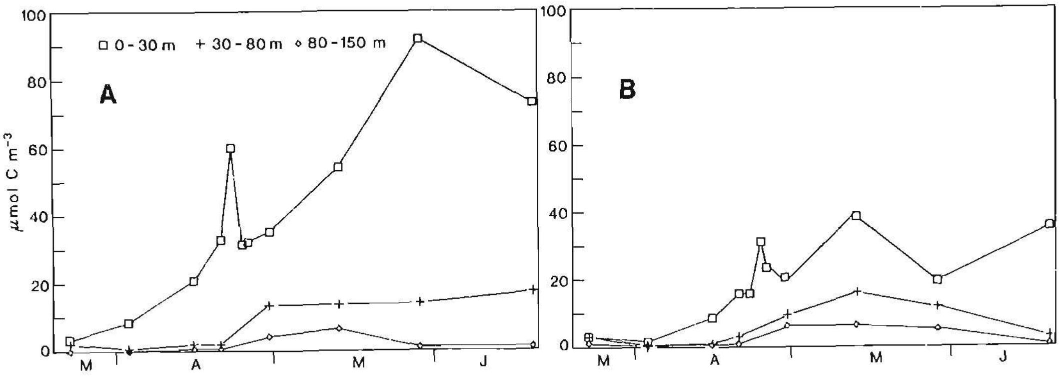

Fig. 1. Mean biomass of *Mesodinium rubrum* (A) and heterotrophic ciliates (B) in the different water layers during the observation period in 1982 in the open northern Baltic Proper.

Table 1. Percentage composition of the biomass of ciliates in the surface layer (0-30 m) of the open northern Baltic Proper during the study period in 1982 (Adopted from Leppänen & Bruun 1986).

	23 Mar.	3 Apr.	15 Apr.	20 Apr.	29 Apr.	12 May	27 May	17 June
CILIATA								
Vorticellidae								
Vorticella sp.					0.1			
Enchelyidae								
Lacrymaria sp.	2.0	0.8	3.0	2.2	7.3	5.9	2.2	
Didiniidae								
Askenasia sp.							0.2	
Didinium sp.					13.7	11.3	6.6	
Mesodinium rubrum	51.3	84.2	70.0	68.2	60.9	56.3	72.6	70.0
Strombididae								
Strombidium conicum				0.2		0.4		
Strombidium sp.	12.7	4.0	2.5	3.2	3.3	4.0	3.7	9.0
Strobilididae								
Strobilidium sp.	0.2		1.5	1.8	0.6	0.6	1.7	15.7
Lohmanniella oviformis	24.2	7.7	16.1	18.3	8.5	6.8	4.8	1.2
L. spiralis	2.7		5.0	4.8	3.6	5.0	4.0	3.5
Lohmanniella sp.						2.3		
Codonellidae								
Tintinnopsis tubulosa	2.4			0.4	0.4	0.2	0.7	
T. beroidea		0.4	0.5	0.4		0.1	0.04	
T. parvula	0.1		0.1	0.1	0.04	0.1	0.06	0.1
Tintinnopsis sp.	1.3				0.1			
Matecylidinae								
Coxliella helix					0.2	0.2	1.5	
Helicostomella subulata	0.3							
Ciliata spp. (<50 µm)	0.8	0.1	0.5	0.5	1.1	6.8	0.6	0.1
Ciliata spp. (50-150 µm)	2.7	2.8	1.2		0.3	0.2	0.7	0.2

end of the study period (Fig. 2). Copepods were the dominant group, consisting almost totally of calanoids (Table 2). *Pseudocalanus elongatus* predominated in all the mesozooplankton samples, juvenile stages making up most of the biomass. The contribution of nauplii increased toward the end of the observation period. Variable amounts of other taxa were also present (grouped as "others" in Table 2). The appendicularian *Fritillaria borealis* and metatrochophora-larvae of a polychaet, *Harmothoe sarsi*, were the most predominating representatives of this group.

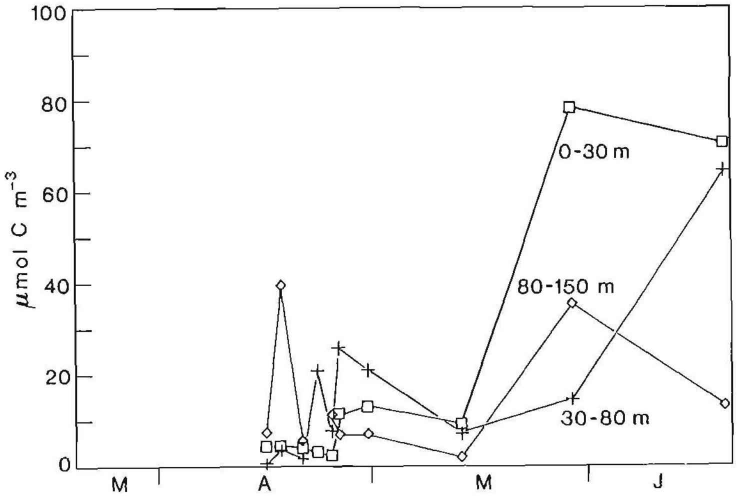

Fig. 2. Mean biomass of mesozooplankton in the different water layers during the observation period in 1982 in the open northern Baltic Proper.

3.2 Processes

The total zooplankton food intake in the whole water column during the observation period was 1.5-2.0 mol C m^{-2}, of which 85 % was concentrated in the surface layer. The food intake of heterotrophic ciliates varied from 1.1-1.6 mol C m^{-2} in the whole water column depending on the calculation method used (Fig. 3). The food intake of rotifers was of minor importance, only ca. 0.01 µmol C m^{-2} during the observation period (Fig. 4). The food intake of herbivorous copepods and cladocerans was almost 0.4 mol C m^{-2} (Fig. 5).

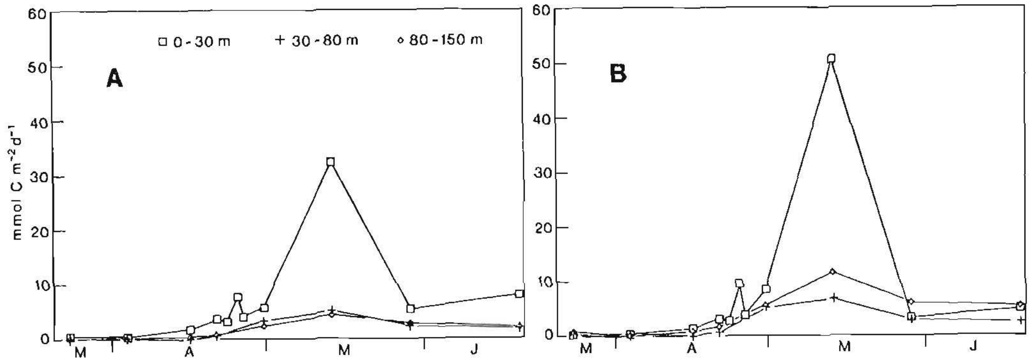

Fig. 3. Food intake of ciliates in the different water layers during the observation period in 1982 in the open northern Baltic Proper, calculated according to A: Heinbokel & Beers (1979) and B: Spittler (1973)

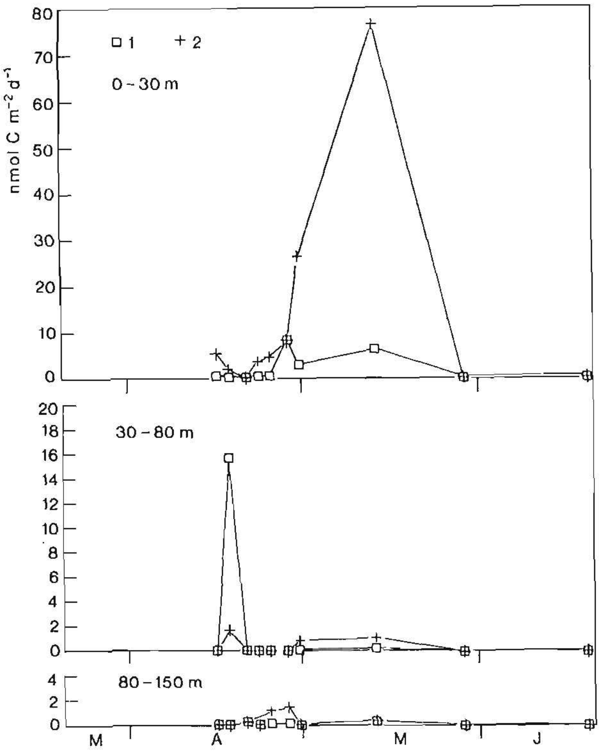

Fig. 4. Food intake of rotifers in the different water layers during the observation period in 1982 in the open northern Baltic Proper.

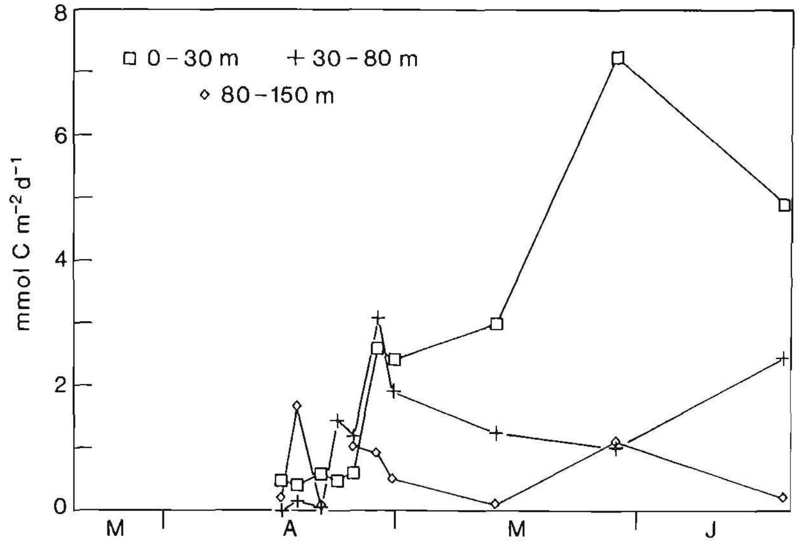

Fig. 5. Food intake of copepods and cladocerans in the different water layers during the observation period in 1982 in the open northern Baltic Proper.

Almost all the heterotrophic ciliates were herbi- or bacterivorous. The few representatives in the genus *Didinium* were predators. The bulk of mesozooplankton was herbi- or omnivorous. The amount of predators (*Evadne nordmanni* and *Podon spp.*) did not increase until the end of the study period. The larvae of *Harmothoe sarsi* were all in the metatrochophora stage, using energy from their yolk reserve. The Bivalvia larvae are bacterivorous, but their food intake could not be calculated. *Fritillaria borealis* feeds on very small particles, but no suitable equations for its food intake were available.

The respiration of ciliates and mesozooplankton was calculated using five and four different equations, respectively. The results from the 0-30 m layer are presented in Figs. 6-9 as an example. Equations 1-4 are based mostly on copepods, and gave very similar values. Equation 5 of Laybourn & Finlay (1976) resulted in respiration values for microzooplankton which were approximately half those calculated with equations 1-4 (Fig. 6 and 7). The respiration of ciliates, in the whole water column during the observation period, was 0.17-0.46 mol C m^{-2}, of copepods 0.14-0.22 and of other groups ca. 0.004 mol C m^{-2}.

The net production of heterotrophic ciliates of 1.1 mol C m^{-2} was obtained when a doubling time of 1 d was used (Fig. 10); the production of *Mesodinium rubrum* in the whole water column was

Table 2. Percentage composition of the biomass of the mesozooplankton in the surface layer (0-30 m) of the open northern Baltic Proper during the study period in 1982.
M = male, F = female, J = juvenile, N = nauplius.

	15 Apr.	17 Apr.	20 Apr.	22 Apr.	24 Apr.	27 Apr.	29 Apr.	12 May	27 May	17 June
Rotatoria										
Synchaeta monopus		0.01								
Synchaeta spp.	0.5	0.2	0.03	0.4	0.5	2.1	0.5	5.5		
Copepoda										
Acartia longiremis M		0.2								0.4
A. longiremis F	6.8	6.9	12.7	16.7	6.3	6.7	4.4	1.2	1.5	2.0
A. longiremis J 4-5	2.2	0.9	0.4	1.0	0.5	0.6	1.0	0.6		4.3
A. longiremis N										28.5
Acartia sp. M								0.6	3.6	2.4
Acartia sp. F			0.9				0.6	0.6	2.2	0.8
Acartia sp. J 4-5	1.1		0.8	0.7			1.0	4.8	2.0	
Acartia sp. J 1-3	1.4		2.2	3.6	2.5	10.0	5.4	6.0	1.5	1.4
Acartia sp. N	20.6	10.1	20.6	15.2	10.5	11.2	8.1	4.4	3.3	1.2
Pseudocalanus elongatus M		0.5	1.0			2.9	2.5			
P. elongatus F	15.1	23.2	12.1	17.3			20.9			
P. elongatus J 4-5	17.2	24.6	5.7	13.7	1.2	3.4	3.9	6.4		
P. elongatus J 1-3		0.1		0.2	0.9				25.8	
P. elongatus N	17.3	24.8	28.7	23.7	64.0	44.4	45.5	61.3	52.2	32.0
Temora longicornis M	3.4				4.0		1.5	1.6		
T. longocornis F	7.4	2.3	1.7	4.1	2.6	13.8	2.0	2.2		
T. longicornis J 4-5	0.4		0.4			1.1				
T. longicornis J 1-4							0.5			
T. longicornis N	0.1	0.4	0.1			0.1		0.5		1.5
Eurytemora sp. N				0.1					2.8	
Centropages hamatus J 4-5	0.2	0.8	0.3			0.5				
Cladocera										
Eubosmina longispina maritima F	0.3		0.2		0.1			0.4	0.4	0.1
E. longispina maritima J			0.01		0.03	0.1				0.02
Evadne nordmanni F	0.7	0.2	1.4			0.4		0.6	2.2	23.3
Podon polyhemoides		0.1	0.2	0.1					0.3	
P. leucarti F										1.7
Others										
Harmothoe sarsi larvae	3.4	1.0	5.8	2.0	2.1		1.6			0.04
Lamellibranchiata sp. larvae				0.01						
Fritillaria borealis	2.1	4.0	4.5		5.0	2.2	1.7	4.3	1.7	0.1
Pleurobrachia pileus 1 mm		0.8				0.8				
Pygospio elegans		0.02							0.1	0.1
Radiosperma corbiferum									0.9	

1.7 mol C m^{-2} (Fig. 10). The net production of rotifers (Fig. 11), as well as copepods and cladocerans (Fig. 12), was 0.001 and 0.12 mol C m^{-2}, respectively.

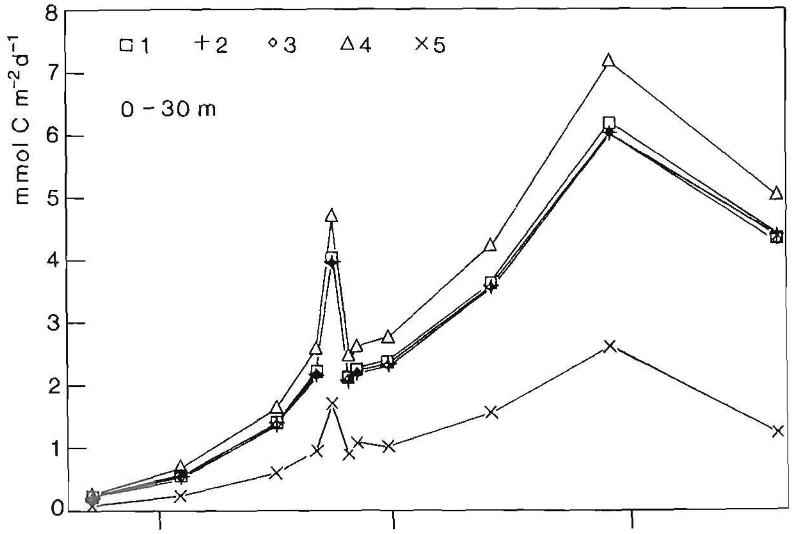

Fig. 6. Respiration of *Mesodinium rubrum* in the 0-30 m water layer during the observation period in 1982 in the open northern Baltic Proper, calculated according to 1. Ikeda (1970), 2. Dagg et al. (1982), 3. Vidal & Whitledge (1982, least-square linear regression), 4. Vidal & Whitledge (1982, geometric mean regression), and 5. Laybourn & Finlay (1976).

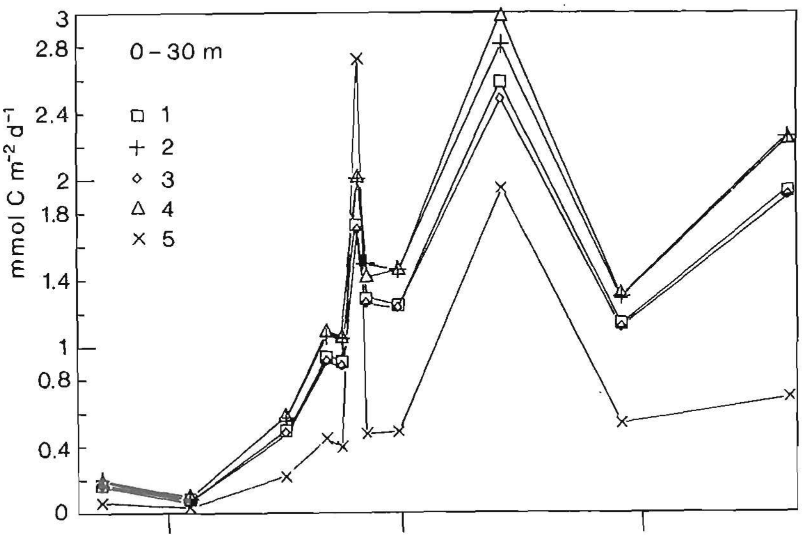

Fig. 7. Respiration of heterotrophic ciliates in the 0-30 m water layer during the observation period in 1982 in the open northern Baltic Proper, calculated according to 1. Ikeda (1970), 2. Dagg et al. (1982), 3. Vidal & Whitledge (1982, least-square linear regression), 4. Vidal & Whitledge (1982, geometric mean regression), and 5. Laybourn & Finlay (1976).

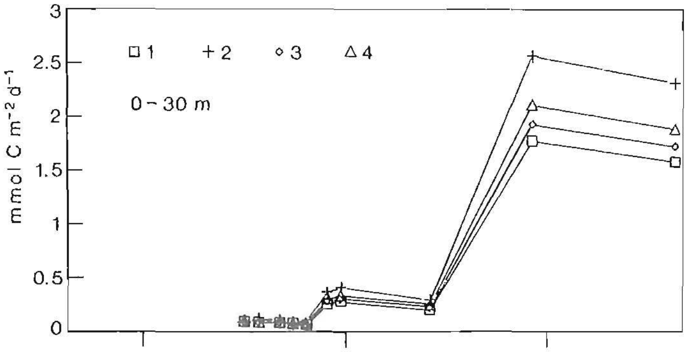

Fig. 8. Respiration of copepods and cladocerans in the 0-30 m water layer during the observation period in 1982 in the open northern Baltic Proper, calculated according to 1. Ikeda (1970), 2. Dagg et al. (1982), 3. Vidal & Whitledge (1982, least-square linear regression), and 4. Vidal & Whitledge (1982, geometric mean regression).

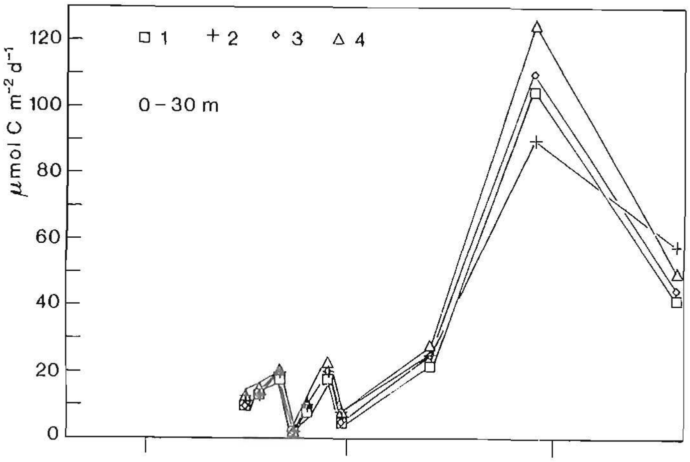

Fig. 9. Respiration of "others" in the 0-30 m water layer during the observation period in 1982 in the open northern Baltic Proper, calculated according to 1. Ikeda (1970), 2. Dagg et al. (1982), 3. Cidal & Whitledge (1982, least-square linear regression), and 4. Vidal & Whitledge (1982, geometric mean regression).

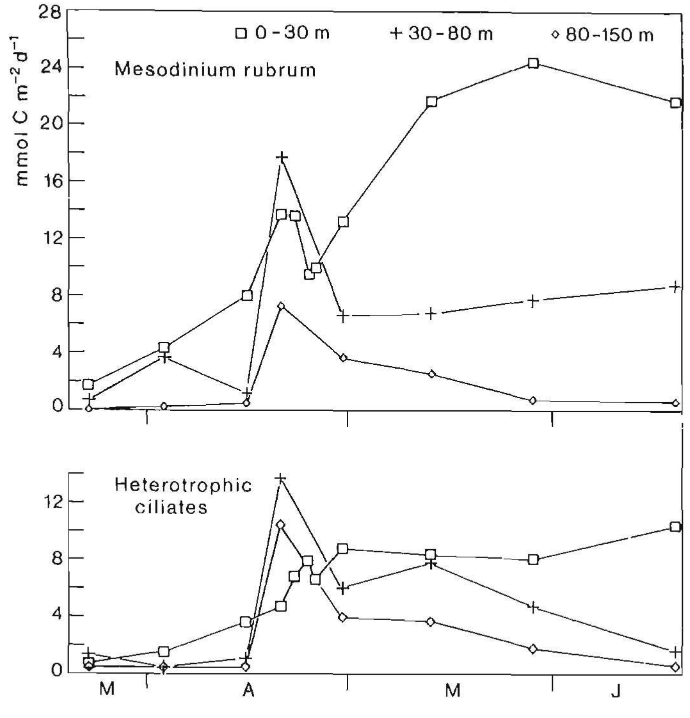

Fig. 10. Production of *Mesodinium rubrum* and heterotrophic ciliates in the different water layers during the observation period in 1982 in the open northern Baltic Proper.

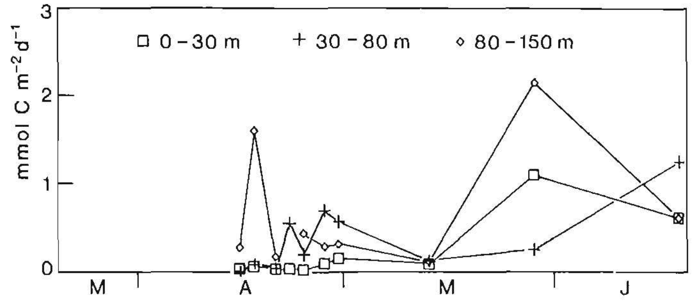

Fig. 11. Production of rotifers in the different water layers during the observation period in 1982 in the open northern Baltic Proper.

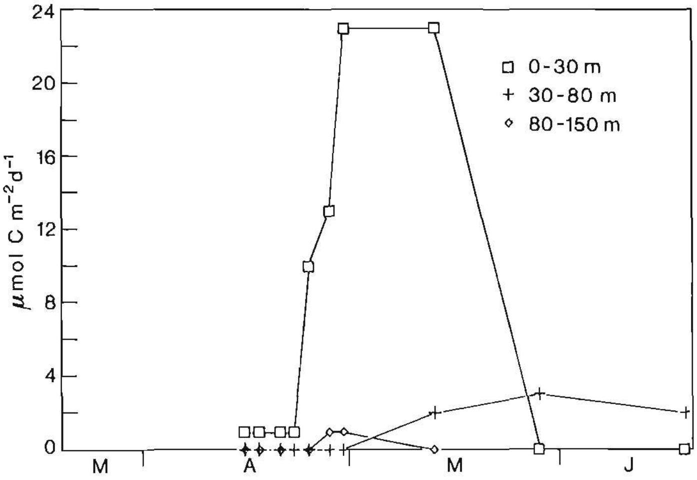

Fig. 12. Production of copepods and cladocerans, in the different water layers during the observation period in 1982 in the open northern Baltic Proper.

4. DISCUSSION

Although a number of studies on the quantitative role of zooplankton in the Baltic Sea food web have been published, they mainly concern the coastal areas (McKellar & Hobro 1976, Wulff & Jansson 1976, Wulff et al. 1977, Jansson 1978, Smetacek 1981, Jansson et al. 1984, Kuparinen et al. 1984). Our knowledge of microzooplankton species composition and biomass variation in the open Baltic Sea even is limited (McKellar & Hobro 1976, Boikova 1984).

Ciliates are known to respond very rapidly to the increase in the food source and can form rapid blooms (e.g. Margalef 1963, Turley et al. 1986). The annual pattern of the mesozooplankton biomass is more related to the development of temperature (Ankaru 1964, Conover 1964, Gaudy 1973, Ikeda 1974). This was also clear in this study. The low mesozooplankton biomass, dominated by female and young copepods, is typical of the area and season (McKellar & Hobro 1976, Forsskåhl et al. 1982, Kuparinen et al. 1984).

4.1 Abundance and biomass

The abundance and biomass values of ciliates in our study were lower than those reported from the coastal areas of Kiel, Askö, Riga Bay and Tvärminne (McKellar & Hobro 1976, Smetacek 1981, Stegmann & Peinert 1984, Boikova 1984, Kivi 1986). The non-loricated species predominated in our study. As the samples were preserved with Lugol's iodine solution, their abundance may be underestimated, especially that of the most fragile *Mesodinium rubrum* (Dale & Burkill 1982). Sorokin (1981) even argues that up to 95 % of the naked ciliates can be lost by fixation. Since the results of the above-mentioned works are also based on fixed material, it is most probable that the difference is caused by the open character of our study site.

4.2 Processes

Extrapolation of the results of laboratory experiments, as well as reports from other sea areas, to our field observations can be misleading. The basic assumption for all the calculations presented in this paper is that the process: biomass ratios are stable. Environmental factors and the physiological state, as well as the life cycle strategies of the organisms can, however, produce wide variation in these ratios (Ankaru 1964, Small & Hebard 1967, Winberg 1971, Gaudy 1973, Ikeda 1974, Tseytlin 1977, Corkett & McLaren 1978, Smith & Barber 1979, Heinle 1981, Nicholajsen et al. 1983, Valiela 1984, Turley et al. 1986).

4.2.1 Food intake

According to our estimates, the daily food intake of ciliates varied widely, but on average equalled the body weight. This is slightly lower than the previous findings: the feeding of non-loricate ciliates has been observed to range from 1-2 times the body weight (Beers & Steward 1971) to 5-6 times the body weight (Rassoulzadegan 1982). The calculated ingestion values most likely represent potential ingestion, since the selected size fraction of the POC is probably not totally suitable for the food items of ciliates. On the other hand, as pointed out by MacKinnon & Haves (1961), Smetacek (1981) and Rassoulzadegan (1982), placing restrictions on the size of the food (smaller than 43 % of the diameter of the oral opening of the animal, as was used in this study), does not necessarily apply to the non-loricate ciliates, which can adapt their shape to that of the ingested particles. Ciliates are often considered to be a link between bacteria and mesozooplankton (e.g. Smetacek 1981, Burkill 1982). According to Ferguson & Rublee (1976), bacteria are not important food items for ciliates in open marine areas. Fenchel (1980) even argues that bacterivorous ciliates do not occur in open water with a low bacterial abundance. He concluded that the minimum concentrations sustaining the growth of ciliates are $2x10^6$-$2.5x10^7$ cells cm^{-3}. During our study the bacterial abundance varied from 0.7 to $11x10^5$ cells cm^{-3} (Lahdes et al. 1988). The most probable food items of the ciliates were thus small flagellates, which accounted for 10-60 % of the total phytoplankton biomass in the surface layer (Leppänen & Kononen, 1988). There are, however, indications that small aloricate ciliates might be significant consumers of bacterioplankton at bacterial abundances of 10^6 cells cm^{-3} (Albright et al. 1987).

The feeding measurements performed during this study with an electronic particle counter indicate that mesozooplankton mainly ingested particles with a mean volume of 11,500 μm^3, corresponding to a sphere diameter of 28 µm (Bruun 1985). This value was used in our calculations. There are reports, however, that same mesozooplankton species can consume a wide spectrum of particles (Allan et al. 1977, Poulet 1977, Deason 1980, Peters & Downing 1984).

Despite the expressions "filter feeder" or "suspension feeder", zooplankters are not non-selective feeders, since the food items may be selected with the mouth parts and the taste may be one selection criteria (Paffenhöfer et al. 1982). Conover & Mayzaud (1984) argue that food which gives the highest net energy yield compared to the consumption energy, is preferred.

4.2.2 Production

The production of ciliates and rotifers was calculated using the equation of Galkowskaya (1965). However, this is valid for short time periods only, since biomass growth tends to be exponential during longer periods (Mann 1969). Doubling times from a few hours to some weeks have been presented (Gold 1971, Gold & Pollingher 1971, Heinbokel 1978, Capriulo 1982, Smetacek 1984). Laboratory experiments at optimal food concentrations indicate doubling times of 1-7 d over temperature ranges corresponding to the water temperature during this study (Capriulo 1982, Gold 1971). Ciliates are able to respond very rapidly to phytoplankton blooms, showing short generation times even at low temperatures. The doubling time of 1 d used in Fig. 3 is most probably applicable during short periods only, and cannot be used as an average value for longer periods.

4.2.3 Respiration

The respiration was calculated using the equations based on the relationship between the individual body weight and respiration with different modifications. All the equations, except the one of Laybourn & Finlay (1976), are primarily based on copepods and other larger animals. The equations of Ikeda (1970) and Vidal & Whitledge (1982) resulted in quite similar values (average difference ca. 10 %). The respiration values calculated with the equation of Dagg et al. (1982) were in general ca. 30 % higher than with the other equations. The equation of Laybourn & Finlay (1976) is intended for ciliates. It resulted in clearly lower respiration values for ciliates than the other equations. There is evidence, however, to show that the metabolism in benthic ciliates at least is in the same proportion to body weight as in larger animals (Vernberg & Coull 1974). The material collected by Fenchel (1980) indicates that the equation of Labourn & Finlay (1976) probably underestimates ciliate respiration by as much as one order of magnitude.

4.2.4 Energy allocation

Different species allocate their assimilated energy in widely different ways, but most consumers convert 40-80 % into respiration and 10-20 % into excretion, leaving 0-30 % for net production (Valiela 1984). When comparing the results of our calculations, the ratios between the processes varied temporally and also between the water layers. The growth efficiency values published for ciliates range from approximately 20 to 78 % (Heinbokel 1978, Smetacek 1981, Jansson 1986, Turley et al. 1986) and should, in general, be higher than those for metazoans (Fenchel 1974). The laboratory experiment of Heinbokel (1978) gives gross growth efficiencies of ca. 50 %. High growth efficiencies indicate efficient assimilation.

Reasonable conversion estimates for ciliates could be 50 % to respiration and 50 % to production. Smith & Barber (1979), however, report daily respiration values of up to 82 %, and Packard et al. (1978) 67 % of the photosynthesis for *Mesodinium rubrum*. Assuming that the respiration values for ciliates obtained with equations 1-4 are at the correct level, it would indicate an average doubling time of 4-6 d and 2-3 d for heterotrophic ciliates and *Mesodinium rubrum*, respectively. This is reasonable compared to the generation times presented by Larsson et al. (1986) for Askö during the spring. According to the above reasoning, the average assimilation efficiency for heterotrophic ciliates was 40 %. The high assimilation efficiencies obtained in the laboratory experiments are probably not possible in our case, since the food intake is calculated on the basis of POC values.

The average contribution of respiration to gross production and the assimilation efficiency of copepods and cladocerans were within the general ranges (e.g. Dagg et al. 1982, Falkowski et al. 1983, Kuparinen et al. 1984).

4.2.5 The role of zooplankton in the carbon cycle

During the whole study period the particulate primary production of phytoplankton was ca. 3.1 mol C m^{-2} (Leppänen & Kononen 1988). Despite the ability of *Mesodinium rubrum* for prominent vertical migration, it is most probable that the individuals below the halocline and even in the intermediate layer (30-80 m) cannot be included in the daily production figures, but only the individuals in the surface layer. Thus the autotrophic production of *Mesodinium rubrum* was ca. 0.4 mol C m^{-2} (average doubling time = 3 d), resulting in ca. 3.5 mol C m^{-2} for total particulate primary production. According to the reasoning concerning the zooplankton processes, ca. 40 % of the particulate primary production was cycled through the zooplankton.

During the actual vernal bloom period (April-May) a smaller portion of the primary production was cycled through zooplankton. Phytoplankton particulate production was then 2.8 mol C m^{-2}, and *Mesodinium* contributed almost 0.2 mol C m^{-2} of total primary production (average doubling time = 3 d). This gave a total of ca. 3 mol C m^{-2}. About one third was grazed by zooplankton, mostly by ciliates.

The consumption of primary production by ciliates, copepods and cladocerans is clearly dependent on the season and sea area (Tables 3 and 4). In this study only one third of the particulate primary production was grazed by zooplankton during the vernal phytoplankton bloom period, leaving ca. 2 mol C m^{-2} for potential sedimentation. This is very close to the values measured simultaneously by Leppänen (1988).

Since all the process estimates are based on equations developed in laboratory experiments or measurements from other sea areas, the quantification is rough. Nevertheless, this study clearly indicates that ciliates act as important primary producers and are the most important heterotrophic organisms during the vernal period in the open northern Baltic Proper. Furthermore, it demonstrates the importance of direct measurements of zooplankton processes in the decomposition of organic matter in the Baltic Sea food web.

Table 3. The consumption (%) of ciliates out of the primary production in different sea areas.

Sea area	% consumption	season	source
Long Island	43	whole year	Riley 1956
Long Island	27	whole year	Capriulo & Carpenter (1983)
California	7-52	April-Sept.	Beers & Steward (1971)
California	10	whole year	Heinbokel & Beers (1979)
Washington	17-52	October	Landry & Hasset (1982)
Narraganset Bay	11-18	whole year	Verity (1985)
Baltic Sea	28	spring bloom period	This study
Baltic Sea	30	whole study period	This study

Table 4. The consumption (%) of mesozooplankton out of the primary production in different sea areas

Sea area	% consumption	season	source
Bering Sea coastal	5-6	spring	Dagg et al. (1982)
mid shelf	15-87	spring	Dagg et al. (1982)
off shore	15-29	spring	Dagg et al. (1982)
Long Island	44	whole year	Capriulo & Carpenter -83
Nova Scotia Inlet	10-30	spring bloom	Conover & Mayzaud (1984)
Swedish W-coast			
(Kåsterfjorden)	3	spring bloom	Båmstedt (1981)
Öresund	1-2	spring bloom	Nicolajsen et al. (1983)
Gulf of Finland	1	spring	Kuparinen et al. (1984)
Gulf of Finland	67	whole year	Kuparinen et al. (1984)
Open Baltic Sea	7	spring bloom	This study
Open Baltic Sea	11	whole study period	This study

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CYCLING OF ORGANIC MATTER DURING THE VERNAL GROWTH PERIOD IN THE OPEN NORTHERN BALTIC PROPER. V. COMMUNITY RESPIRATION AND BACTERIAL ECOLOGY

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ABSTRACT

Development of bacterial numbers and production, as well as the decomposition rate of organic matter measured as total planktonic respiration, were followed during April-June in 1982 in the open northern Baltic Proper. Overall respiration was highest in the uppermost 10 meter layer and decreased abruptly below a depth of 30 meters. According to the respiration measurements about 45 % of the gross primary production was mineralized in the 0-30 meter layer during April 15 - June 17. Bacterial numbers remained relatively low ($0.1 - 1.1 \times 10^{12} m^{-3}$) throughout the whole observation period. Bacterial consumption in the 0-150 m water column was ca. 30 %, and production ca. 19 % of the net primary production. More than half of this activity took place during the vernal period. Almost 70 % of bacterial production and consumption took place in the 0-30 m water layer. The values agree reasonably well with the organic matter production and settling estimates obtained simultaneously during the comprehensive study.

Keywords: Baltic Sea, pelagial bacterial ecology, bacterial production, community respiration, oxygen consumption

1. INTRODUCTION

The biological processes taking place in the surface layer of the sea fundamentally determine the channelling of matter and energy in the food webs of the whole water column. The relationship between the rates of production and decomposition of the organic matter, in particular, has a decisive effect on the fate of the organic matter and oxygen consumption in the deeper water layers - a topic which is much discussed in connection with the Baltic Sea ecosystem.

The relative contribution of different organisms in heterotrophic decomposition varies. Bacteria are traditionally classified solely as decomposers although their actual role in these processes is still not yet clear. Recent findings emphasize the tight coupling in the microbial loop between bacteria, auto- and heterotrophic flagellates and microzooplankton (Azam et al. 1983, Linley et al. 1983, Goldman et al. 1985, Andersen & Sørensen 1986).

In this study the development of bacterial numbers and production was followed from April 15 to June 17. In addition, the decomposition rate of organic matter was estimated by measuring total planktonic respiration. The study is a part of a comprehensive ecosystem research project being carried out on the pelagial of the open northern Baltic Proper: hydrography, nutrient chemistry, biological production and the sinking of organic matter were followed during spring 1982 (cf. Lahdes & Leppänen 1988, Leppänen 1988, Leppänen & Alenius 1988, Leppänen & Bruun 1988, Leppänen & Kononen 1988).

2. MATERIALS AND METHODS

The samples were taken at a site located in the northern Baltic Proper (59°26.1'N; 21°31.4'E). A detailed hydrographic description of the area is presented by Leppänen & Alenius (1988).

Community respiration was measured as oxygen consumption after incubation of the water samples in the dark. The oxygen concentration was determined using the standard Winkler titration with some improvements. The samples were collected at depths of 0, 5, 10, 20, 30 and 50 meters. Water was taken from the same samples as for other biological and chemical analyses during the comprehensive study in question.

Four pairs of parallel samples were taken at each depth, every pair of blank and dark bottle being filled simultaneously through a distributor. The size of the glass stoppered bottles was ca. 125 ml. The blanks were treated with Winkler reagents immediately after filling, and the dark bottles were transferred to non-transparent plastic tubes and incubated either in the sea or deck incubator at *in situ* temperature for 21 to 95 hours.

The Winkler reagents were added at the end of the incubation period. All bottles were kept under water in the dark before being acidified with 85% orthophosphoric acid (H_3PO_4). The samples were titrated first with 0.015 M, and then for technical reasons with 0.030 M Na-thiosulphate solution using starch as the indicator. The coefficient of variation (CV) of the method was mostly between 0.1-0.4 %, being greater in only 14 % of cases. The detection limit of the method was reached with the incubation times used in the experiment.

Community respiration was determined as the difference between the oxygen concentration of the blank and that of the sample incubated in the dark. Oxygen consumption in the dark is considered to measure the amount of organic carbon mineralized during incubation, a respiratory quotient (RQ = CO_2 produced/O_2 consumed) being used to convert oxygen consumption to carbon. Extreme RQ values of 0.7 and 1.0 are obtained when fats or sugars, respectively, are catabolized. A value of 0.85 has been used in this study. This value has been proposed by Ogura (1972) for the easily degradable matter in surface water.

The bacterial samples were taken at depths of 0, 2, 5, 7, 10, 15, 20, 30, 40, 50, 60, 80, 100, 130 and 150 meters. Integrated samples presenting different water layers were prepared. The samples were preserved by adding formaldehyde to give a final concentration of 4 %. The bacterial numbers were determined by the acridine orange direct count technique (Zimmermann & Meyer-Reil 1974, Väätänen 1980b) in which at least 400 cells were counted with an epifluorescence (EF) microscope. The average cell volumes were determined separately for each sample with a scanning electron microscope (SEM) of the Department of Electron Microscopy, University of Helsinki, using ethanol and Kaltron 113 as dehydrating agents before air drying

(Zimmermann 1977, Krambeck 1978). A total of 200 cells were measured from the SEM-graphs, and the volumes calculated using formulae for a sphere and a cylinder. The conversion factor for converting volume to carbon was $3.5*10^{-13}$ gC μm^{-3} (Bjørnsen 1986).

In order to compare the volume determinations done with SEM and EF, EF measurements were made also using a Patterson-Cawood-grid (Patterson & Cawood 1936). The samples for this comparison were taken in 1983 at the entrance to the Gulf of Finland.

The bacterial growth rates and production were estimated using two methods in which it is assumed that 60% of the bacterial cells are active (van Es & Mayer-Reil 1982). The first method involved determining the frequency of dividing cells (FDC) as introduced by Hagström et al. (1979). At least 30 dividing cells were counted in each sample and the growth rate and production were calculated using the regression equations between FDC and growth rate given by Hagström et al. (1979) and Hagström & Larsson (1984). Production was also calculated using the growth rate obtained from the changes in bacterial biomass with the equation $P = \mu \times B$, where $\mu = (\ln B_2 - \ln B_1)/dt$, B_1 and B_2 are the biomasses on days t_1 and t_2, $dt = t_2 - t_1$ and B is the biomass of bacteria at a given instant (Stanier et al. 1981). The production values were converted to consumption and respiration values by assuming that carbon conversion efficiency is 60 %. These factors are based on the uptake of dissolved substrates (e.g. Azam et al. 1983, Newell & Linley 1984).

The data was divided, on the basis of the physical, chemical and biological features to correspond to the following three layers: 0-30 m, 30-80 m and 80-150 m (cf. Leppänen & Alenius 1988, Lahdes & Leppänen 1988). The time periods in the following calculations were selected on the basis of biological activity and succession, so that April - May was considered as the vernal period and the first half of June as early summer phase.

3. RESULTS AND DISCUSSION

3.1 Bacterial ecology

The bacterial population consisted predominantly of free living, small cocci, straight rods and vibrios (Fig. 1). The percentage of cocci varied between 33 % and 80 %, being highest in the uppermost layer in June and near the bottom in April (Table 1). The mean cell volume ranged from 0.033 - 0.125 µm^3, increasing towards the end of the study period.

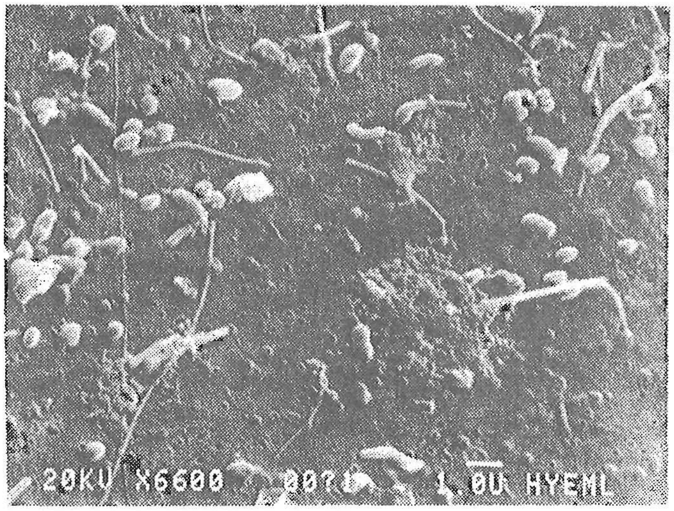

Fig. 1. Scanning electron micrograph of a bacterial sample taken on 17 June 1982 at a depth of 150 m. (SEM-graph taken by K. Kononen).

Bacterial number and biomass (Table 1, Fig. 2) increased in all water layers during the study period. In April and up until the middle of May the increase was fastest in the surface layer, and in June near the bottom. Bacterial numbers were of the same order of magnitude as those measured earlier at the entrance to the Gulf of Finland and in the northern Baltic Proper (Hagström et al. 1979, Väätänen 1980a, Virtanen 1981, 1985). The higher biomass values as compared to the results of Virtanen (1981, 1985) were due to the different carbon conversion factor.

The highest number of bacteria was found near the bottom in June. These bacteria were mostly free living. Rather little bacterial data have been published for the water below the permanent halocline in the Baltic Sea (Seppänen & Voipio 1971, Gocke 1977, Dawson & Gocke 1978, Gocke & Hoppe 1982). According to simultaneous sedimentation measurements made by Leppänen (1988), the organic matter that settled out from the euphotic layer was concentrated near the bottom. It is most probable that the increase in bacterial numbers is connected with the release of utilizable substrates from dead algal material.

Parallel bacterial volume and size distribution determinations (Fig. 3) with SEM and EF resulted in 37 % and 52 % smaller mean volumes with SEM. The differences were statistically significant ($p<0.001$).

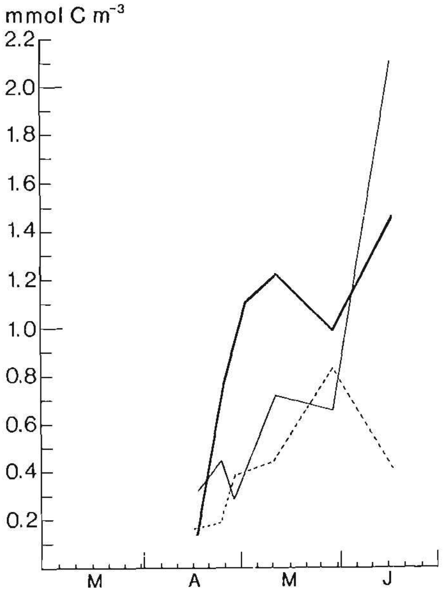

Fig. 2. Development of the bacterial biomass (mmol C m^{-3}) in the different water layers from 15 April to 17 June. The values for 27 May are not representative owing to missing data. (Thick line 0 - 30 m, dotted line 30 - 80 m, thin line 80 - 150 m).

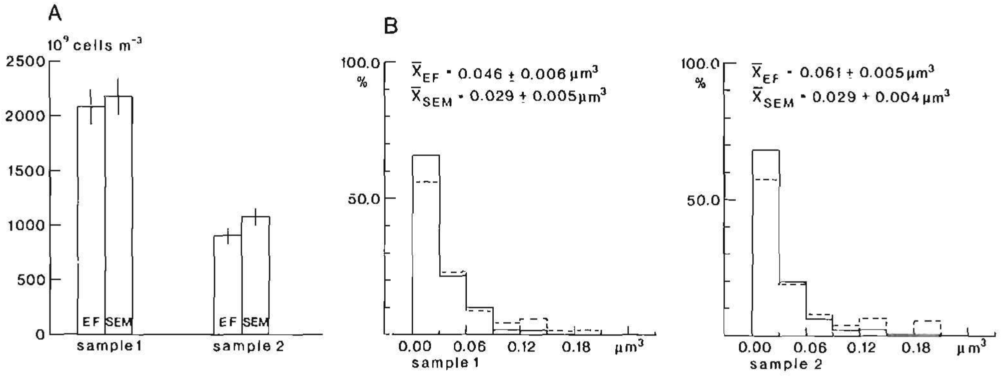

Fig. 3. Parallel bacterial number (A) and volume and size distribution (B) measured with scanning electron microscopy (SEM) and epifluorescence microscopy (EF) techniques, determined from two spring samples taken at the entrance to the Gulf of Finland (A. 4 May 1983 and B. 19 April 1983). For all parallel determinations n = 5.

The size distribution determinations showed that the frequency of small cells (< 0.03 µm^3) was 10 % higher when measured with SEM. In the larger size classes the situation was the reverse.

Table 1. Bacterial data collected during the observation period in the open northern Baltic Proper in 1982. The bacterial numbers are based on acridine orange direct counting.

Date	Depth (m)	Numbers x10^9 m^{-3}	FDC %	Average volumes µm^3 (SEM)	Cocci %	Biomass mmol C m^{-3}
April						
17	0-20	147	(5.1)	0.033	48	0.144
	30-50	65	7.4	0.050	65	0.101
	60-100	126 (SEM)	-	0.062	69	0.237
	130	173	1.9	-	57	0.323
24	0-20	404	2.4	0.073	55	0.890
	30-50	95	(1.4)	0.059	65	0.170
	60-100	265	2.3	0.035	68	0.283
	100-150	448	2.5	0.035	82	0.471
29	0-20	617	1.3	0.061	76	1.162
	30	297	3.4	0.094	64	0.843
	40-60	178	(2.5)	0.051	70	0.272
	80	336	3.3	0.058	62	0.587
	100-150	204	4.9	0.039	60	0.243
May						
12	0-20	518	3.8	0.092	59	1.439
	30-60	217	10.2	0.055	80	0.361
	80-100	295	2.8	0.085	71	0.757
	130-150	240	4.7	0.093	65	0.679
27	0-10	262	4.9	0.125	70	0.991
	80	370	4.9	0.074	52	0.824
	150	215	5.7	-	66	0.650
June						
17	0-15	568	(6.9)	0.093	72	1.595
	20-60	188	2.1	-	-	0.529
	70-80	178	4.8	0.098	52	0.529
	100	619	2.1	0.079	33	1.474
	50	1098	3.9	0.110	47	3.644

Shrinkage of cells in the SEM procedure has been observed by other authors, too (Fuhrman 1981, Krambeck et al. 1981). Montesinos et al. (1983) have shown that shrinkage varies in different bacterial groups. On the other hand, the low resolution of light microscopy compared to SEM means that small cells are less likely to be detected, thus resulting in an overestimation of the volume in EF results. These two effects partly compensate each other, and the biomass estimation is probably close to the real value.

Despite the increase in bacterial number and mean volume in all the water layers in April (Table 1, Fig. 3) the bacterial production was, however, still below the detection limit of the FDC method. Therefore the growth rates calculated from the change in biomass during April 17-24 were used for the 0-30 m, 30-80 m and 80-150 m water layers (0.245 d^{-1}, 0.070 d^{-1} and 0.044 d^{-1}, respectively) in the production calculations for the vernal period from April 15 to May 27. The FDC method already gave average growth rate values of 0.320 d^{-1}, 0.070 d^{-1} and 0.076 d^{-1} in the three water layers, respectively, for the two last samplings on May 27 and June 17. These values were used for the last period from May 27 to June 17. These growth rate values appear to be reasonable. Hagström & Larsson (1984) found that the growth rate *in situ* at 10°C is ca. 0.030 h^{-1}, and a transfer to 0°C would result in a growth rate of about 0.010 h^{-1}. This is near to the value which we obtained for the vernal period. Hanson et al. (1983) reported growth rates of 0.029-0.088 h^{-1} in cold waters of the Antarctic Ocean.

The bacterial production in the 0-30 m water layer for the whole observation period was 409 mmol C m^{-2}, which is ca. 13 % of the net primary production in the same water layer (primary production from Leppänen & Kononen 1988). Bacterial production in the whole 0-150 m water column was 600 mmol C m^{-2} i.e. 19 % of the net primary production. More than half of the bacterial production took place during the vernal period. As a whole, 20 % and 30 % of the net primary production was channeled through bacteria in the surface layer and the whole water column, respectively (Table 2).

Algal exudates (i.e. dissolved production) are an important carbon and energy source for bacteria but according to Jensen (1983) only about 60 % of the exudates are directly utilizable by bacteria. During this study the amount of dissolved production, calculated by Leppänen & Kononen (1988), was not sufficient for bacterial consumption, which should thus be based

Table 2. Bacterial production (P), respiration (R) and consumption (C) (mmol C m^{-2}d^{-}) in different water layers during the observation period in the open northern Baltic Proper in 1982.

Period	0-30 m			30-80 m			80-150 m		
	P	R	C	P	R	C	P	R	C
15 April -	$\mu = 0.245\ d^{-1}$			$\mu = 0.070\ d^{-1}$			$\mu = 0.044\ d^{-1}$		
12 May	104	69	173	17	11	28	21	14	35
12 May -	$\mu = 0.245\ d^{-1}$			$\mu = 0.070\ d^{-1}$			$\mu = 0.044\ d^{-1}$		
27 May	158	105	263	10	7	17	22	15	37
27 May -	$\mu = 0.320\ d^{-1}$			$\mu = 0.070\ d^{-1}$			$\mu = 0.076\ d^{-1}$		
17 June	147	98	245	29	19	48	92	61	153
TOTAL	409	272	681	56	37	93	135	90	225

on other sources of fresh dissolved organic matter originated e. g. from cell lysis of particulate matter. This substrate is important because algal exudates in general are poor in nitrogen (Lancelot & Billen 1985). The direct digestion of particulate matter by bacteria was considered negligible.

The estimation of bacterial carbon was based on a factor of $3.5*10^{-13}$ gC μm^{-3} for converting biovolume to carbon (Bjørnsen 1986). Factors ranging from $0.847x10^{-13}$ to $5.6x10^{-13}$ gC μm^{-3} have been published (Ferguson & Rublee 1976, Watson et al. 1977, Bratbak 1985, Heldal et al. 1985, Nagata 1986, Kuparinen 1988). The results obtained using the latest techniques by Nagata (1986) and Bjørnsen (1986), especially, suggest that the carbon content of bacterial cells is considerably higher than previously reported. It is assumed that this would considerably change the concept of the role of bacteria in carbon cycling but, at the moment, there is no general agreement about the preferable conversion factor.

3.2 Community respiration

The total plankton community respiration in the dark is the sum of the oxygen consumption of both autotrophic and heterotrophic organisms, and is considered to represent the amount of carbon mineralized by the community. The oxygen consumption was highest in the uppermost 10 meter layer, and decreased abruptly below 30 meters (Fig. 4). Some incubations from depths of 30 and 50 meters resulted in "negative respiration", i.e. a higher oxygen concentration in the incubated than in the blank bottles. Similar anomaly was observed by Tschumi et al. (1977), who proved that it is caused by the light shock on adding Winkler reagents to bottles incubated in the dark and the instability of the oxygen concentration in the water when the bottles are filled.

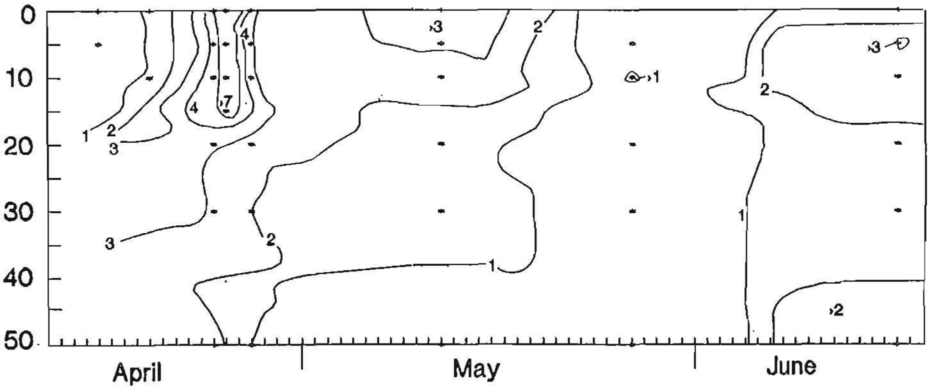

Fig. 4. Community respiration (mmol C m^{-3}d^{-1}) in the upper 50 meter layer from 15 April to 17 June.

The measured overall respiration values, as well as calculated values for different groups of plankton, are presented in Table 3 for the 0-30 meter water layer. Calculated respiration exceeded the measured value, especially during the phytoplankton bloom phase. Owing to technical problems (e.g. loss of incubation bottles in a storm, together with "negative respiration" values) at the beginning of the study period, the first two respiration activity results are approximations, and the measured values are most likely underestimations. Phytoplankton respiration was dominating during the whole observation period being about 85 % of the calculated total respiration. Both bacteria and ciliates were of more importance than mesozooplankton. The results of Väätänen (1979) and Kuparinen (1984) indicate the similar pattern.

There are several factors which affect the reliability of the results derived from both the respiration measurements and theoretical calculations. For instance the so-called "bottle effect" causes disturbances when measuring respiration directly while on the other hand the variation in cell metabolism and the physiological state of the organisms were not included in the equations (Christensen et al. 1980, Holligan et al. 1984, Kuparinen 1985). Therefore a certain range of unbalance is expected.

Table 3. Community respiration and the calculated respiration values for the different plankton groups (mmol m^{-2}) in the surface layer (0 - 30 m), in the open northern Baltic in 1982.

	15 April- 12 May	12 May- 27 May	27 May- 17 June	Total
Measured	1585	595	845	3025
Calculated:				
- phytoplankton 1)	2390	745	340	3475
- mesozoopl. 2)	5	20	45	70
- ciliates incl. Mesodinium 2)	130	115	125	370
- bacteria 3)	69	105	98	272
Calculated tot.	2594	985	608	4187
Primary gross production 1)	4080	1645	950	6675

1) Leppänen & Kononen (1988)
2) Leppänen & Bruun (1988)
3) See table 2

According to the measured overall respiration, 45 % of the phytoplankton gross primary production was mineralized in the surface layer during the period April 15 - June 17. The corresponding value for the vernal phase was 38 %. The measured respiration values fit reasonably well with the production estimates and the measured amount of matter which settled below the surface layer (Leppänen 1988, Leppänen & Kononen 1988).

When comparing the community respiration-primary production ratios to the results obtained in other studies, the physicochemical properties of the water layers and differences in biota should be taken into account. Kuparinen (1984) has found that the overall respiration accounted for only 12 % of the gross primary production in the 0-10 m water layer in the coastal waters of the Gulf Finland during the same spring as our study. Two years earlier the total respiration was found to have consumed 19 % of the gross primary production (Kuparinen et al. 1984) in the 0-10 m water layer in the same area. The corresponding value in our study was 38 % in the 0-30 m water layer as based on the measured respiration, and 63 % on the basis of the calculated total respiration. The difference in the results is self-evident considering the incompatibility of the water layers. Comparison to other sea areas is ambiguous and differing results have been obtained in studies dealing with the cycling of organic matter in spring. In Grand Banks (Newfoundland), for instance, community respiration consumed 33-100 % or even more of the gross primary production. Microheterotrophs dominated the respiration whereas the respiration of algae was negligible (Smith et al. 1986). Another extreme case occurred in the studies performed in the Belgian coastal water zone, where community respiration exceeded the primary production and phytoplankton respiration dominated on both a vernal and annual basis (Joiris et al. 1982, Joiris 1985).

4. CONCLUSIONS

Bacterial mean volumes varied between 0.033 - 0.125 μm^3, and numbers 65 - 1100 x 10^9 m^{-3}. This is about the same order of magnitude as measured earlier in the northern Baltic Proper and at the entrance to the Gulf of Finland. The volumes of bacteria generally increased toward the summer. Bacterial biomass had a maximum near the bottom in the middle of June, this most probably being connected to the decomposition of the organic matter which had settled in the bottom layer. Comparison between the epifluorescence and scanning electron microscope methods indicated that cells determined by the SEM method had shrunk. The SEM technique, on the other hand, better detected small bacterial cells.

Bacterial consumption of the net primary production in the whole water column was 30 % in April 15 - June 17. The corresponding value for vernal period was 20 %. 68 % of the bacterial consumption took place in the uppermost, 0-30 m water layer.

The community respiration measured as dark oxygen consumption consumed 45 % of the gross primary production. Respiration activity was maximal during the peak of the phytoplankton bloom. Phytoplanktonic respiration dominated throughout the whole observation period. Heterotrophic respiration was of some importance only after the end of May.

The methodology and amount of data used in this work suffice for only a roughly quantitative estimation of the decomposition of organic matter and the role of heterotrophic bacteria in the studied system. However, the measured values agree reasonably well with the production and settling estimates for organic matter made during the comprehensive study.

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CYCLING OF ORGANIC MATTER DURING THE VERNAL GROWTH PERIOD IN THE OPEN NORTHERN BALTIC PROPER. VI. SINKING OF PARTICULATE MATTER

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ABSTRACT

The deposition of particulate matter during the vernal growth period was studied using moored traps in the open northern Baltic Proper in 1982. The vernal diatom-dominated phytoplankton bloom settled rapidly from the euphotic layer after the bloom peak, and the sporulation of diatoms probably played an essential role in this process. Neither the weak thermocline nor the permanent halocline formed a barrier to the main flux of the particles. About 60 % of the particulate primary production of carbon settled out from the euphotic layer, while over 50 % of the nitrogen and phosphorus was recycled within this layer. The amount of phosphorus in the particulate matter increased in the layer below the halocline due to the adsorption of inorganic phosphorus onto the settling particles. During the vernal production stage, the settling matter was most probably decomposed near the sediment surface, after leaving the euphotic layer, rather than during sinking.

Key words: Baltic Sea, sedimentation, particulate carbon, particulate phosphorus, particulate nitrogen, particulate silicon.

1. INTRODUCTION

The sinking of organic matter is the most important link between the pelagic euphotic zone and the aphotic benthos in the sea. The biochemical, as well as the chemical and physical processes in the water column determine the quantity and quality of the organic matter that sinks to the bottom (cf. Lahdes & Leppänen 1988). The biochemical composition of the sinking matter determines, on the other hand, its nutritional value, energy content and decomposition rate in the sediment (e.g. Smetacek 1984, Wassmann 1984).

The areal and seasonal variation in the quantity and quality of the sinking matter is large (e.g. Steele & Baird 1972, Webster et al. 1975, Smetacek 1980, Bodungen et al. 1981, Fellows et al. 1981, Hargrave & Taguchi 1978, Billet at al. 1983, Wassmann 1983, 1985a, 1985b, Davis & Payne 1984). Most of the studies concerning the Baltic Sea have been carried out in the shallow coastal areas, where resuspended matter from the bottom plays a prominent role in the whole water column (Zeitzschel 1965, Niemistö 1971, Hendrikson 1976, Askö Laboratory 1977, 1978, 1979, Iturriaga 1979, Smetacek 1980, Forsskåhl et al. 1982, Kuparinen et al. 1984, Larsson et al. 1986). The aim of the present work is to measure the quality and quantity of particulate sinking matter in the open northern Baltic Proper during the vernal growth period. There are strong grounds to believe that this period is the most important for the annual material and energy input to the benthos (Jansson 1978, Laakkonen et al. 1981, Graf et al. 1984, Kuparinen et al. 1984). This paper is part of a comprehensive ecosystem research project being carried out at the Finnish Institute of Marine Research into the production, decomposition and sinking of organic matter in the pelagic food web of the northern Baltic Proper (Lahdes et al. 1988, Lahdes & Leppänen 1988, Leppänen & Alenius 1988, Leppänen & Bruun 1988, Leppänen & Kononen 1988).

2. STUDY AREA

The study area is situated in the open northern Baltic Proper (59° 26.1′ N; 21° 31.4′ E). The depth of the sampling site is 158 m, and is located in the node of two troughs (Leppänen & Alenius 1988). The sampling site is a sedimentary basin, where the annual sedimentation is high (ca. 2.2 mm a^{-1}, Niemistö & Voipio 1981). The bottom consists of soft, black, very fine-grained mud, with a high H_2S content. In addition to the autochtonous primary production, material is transported to the sampling site from surrounding non-deposition areas (Naik & Poutanen 1984). The water body was divided by a permanent halocline, which rose during the study period from a depth of ca. 90 m to a depth of ca. 65 m (Leppänen & Alenius 1988). For a more detailed description of the hydrography and currents, nutrient development, phytoplankton production and the role of zooplankton, as well as bacteria in the area, see Leppänen & Alenius (1988), Lahdes & Leppänen (1988), Leppänen & Kononen (1988), Leppänen & Bruun (1988) and Lahdes et al. (1988), respectively.

3. MATERIALS AND METHODS

The sinking material was collected with the buoy-supported, moored traps (Fig. 1). Two identical moorings were installed simultaneously in the area during the period 23 March - 17 June, 1982. Each trap consisted of three PVC cylinders. The height and diameter of each cylinder were 100 cm and 10 cm, respectively, resulting in an aspect ratio of 10. The traps were installed at depths of 30, 50, 80, 100 and 150 m.

The particulate matter deposited in the traps was usually collected every second week. Immediately after recovery of the traps, excess water was siphoned off and its particle content filtered on a Whatman GF/C filter for the determination of dry weight. The material which had settled on the bottom of the traps was deep-frozen on board the research vessel.

The surface of the bottom sediment was sampled with a gravity corer (Niemistö 1974). The slide of the uppermost 6 mm of sediment surface was subsampled as described by Niemistö (1974), and stored deep-frozen in petri-dishes onboard.

After lyophilization of the samples from the traps and sediment surface, the organic carbon content was analyzed using a high temperature combustion method (Salonen 1979). Nitrogen and phosphorus were determined by Kjeldahl digestion (Zink-Nielsen 1975).

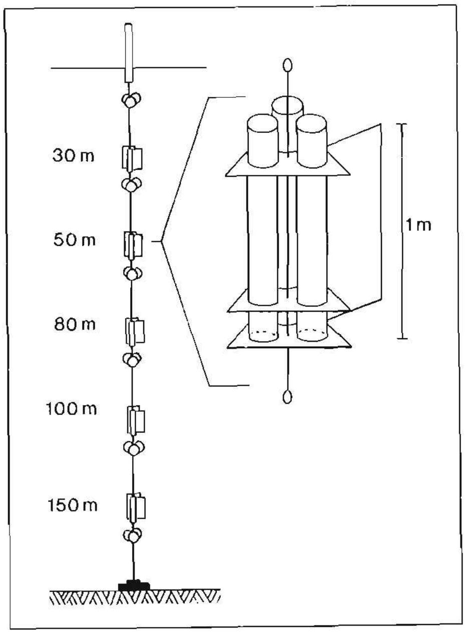

Fig. 1. The design and mooring of the sedimentation traps.

Chlorophyll *a* was extracted in 90 % acetone and determined fluorometrically (Edler 1979). Organic silicon was analyzed according to Paasche (1980).

The effect of remineralization of organic carbon in the traps was estimated by the following equations. Assuming that the remineralization of carbon follows first order kinetics, and the remineralization rate is constant during the exposure period, then the actual deposition rate of carbon (D) is:

$$C = Dk^{-1}(1-e^{-kt}) \quad (1)$$

$$D = Ck(1-e^{-kt})^{-1} \quad (2)$$

where C is the measured amount of deposited particulate carbon after the sampling, k is the decomposition rate and t is the sampling time (in days). The results from material collected with the traps in 1983 from the Tvärminne sea area (western Gulf of Finland) suggest that the average daily remineralization rate of carbon in the traps is 2 % during the vernal phytoplankton bloom period (unpubl. material of the Finnish Institute of Marine Research). This was used as the value for k, and is close to the values presented by Saunders (1972), Iturriaga (1979), Bloesch & Burns (1980), and Gardner et al. (1983).

3. RESULTS

The difference between the amount of sinking matter deposited in the two separate sets of traps was usually less than 10 %, and there was no systematic difference between them. The deposition rates were low in the whole water column up until the end of April, but then increased rapidly and remained high during May (Fig. 2).

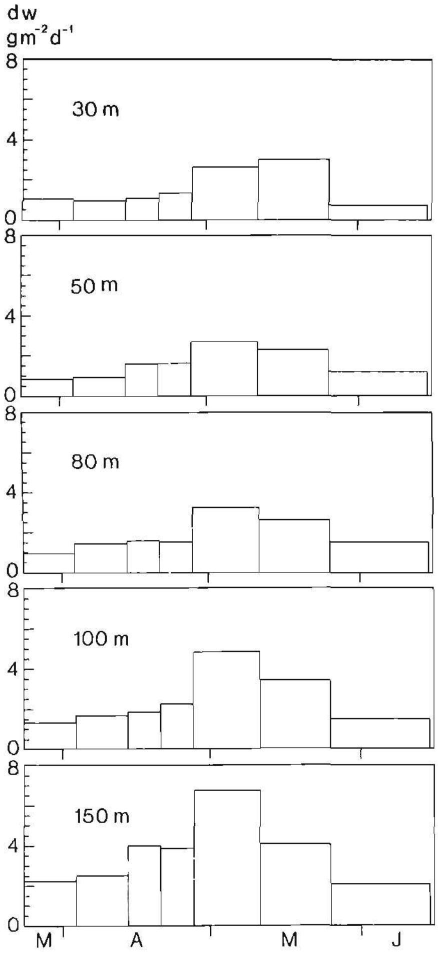

Fig. 2. Deposition rates of the particulate matter (dry weight) at different depths during the study period in 1982 in the open northern Baltic Proper.

The colour of the deposited matter was greenish at the depths of 30 and 50 m, but reddish dark brown in the deeper traps.

One general feature was the increase in the deposition rates toward the bottom (Fig. 3). The deposition rates of chlorophyll *a* followed the temporal pattern of the dry matter (Fig. 4). During the first exposure periods the deposition rates of chlorophyll generally decreased toward the bottom, but during the last two periods increased, especially during the last one.

The temporal pattern of the percentage contribution of carbon, nitrogen and silicon to the dry matter deposited in the traps was similar. The lowest values were recorded at the beginning of the study period (Fig. 5). The contents were

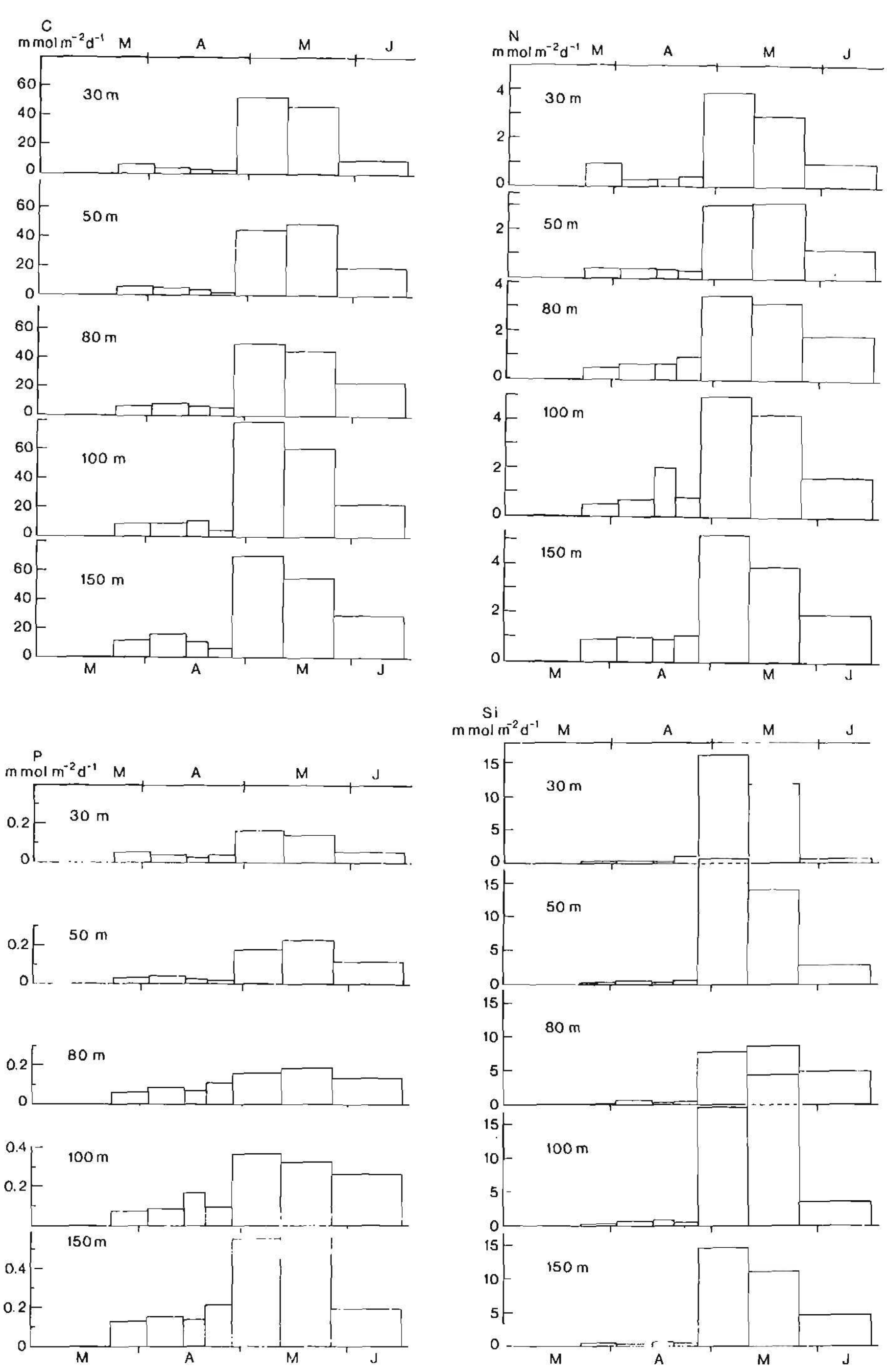

Fig. 3. Deposition rates of particulate carbon, nitrogen, phosphorus, and silicon at different depths during the study period in 1982 in the open northern Baltic Proper.

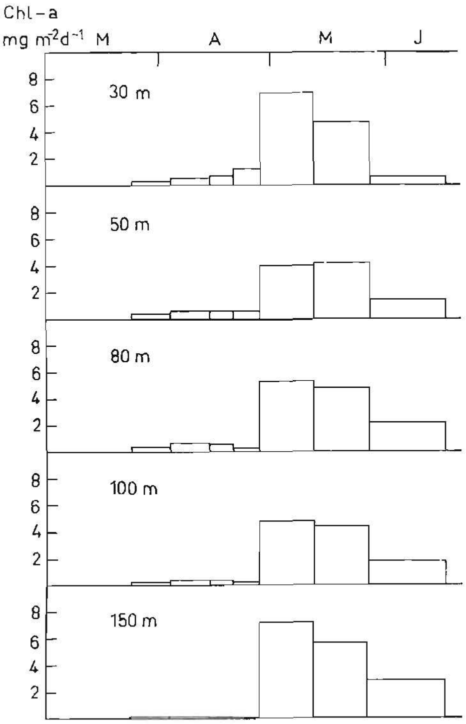

Fig. 4. Deposition rates of chlorophyll *a* at different depths during the study period in 1982 in the open northern Baltic Proper.

highest during the period of high deposition at the end of April and in May, and in general they decreased on moving toward the bottom. The phosphorus content was more constant, and the highest values often being measured in the deepest traps.

The molar C:N:Si:P ratios of the dry matter in the traps and the corresponding weight ratios of carbon to chlorophyll a are presented in Tables 1 and 2. The vertical variation in the C:N ratios, in particular, was smaller than that in the C:P ratios. The C:Si ratios were markedly low during the period of high deposition at all depths. The C: chlorophyll *a* ratios (Table 2) were lowest during the period of high deposition and in most cases showed a clear increase toward the bottom.

During the study period there was a 2 to 3-fold increase in the contribution of carbon, nitrogen, phosphorus, and silicon to the dry matter of the sediment surface (Table 3), the levels being highest at the end of the study period. The corresponding increase in the chlorophyll content was almost 9-fold (Table 3). The colour of the sediment surface was patchy, with gray-green-light brown areas always being different to the reddish dark brown matter deposited at the depth of 150 m.

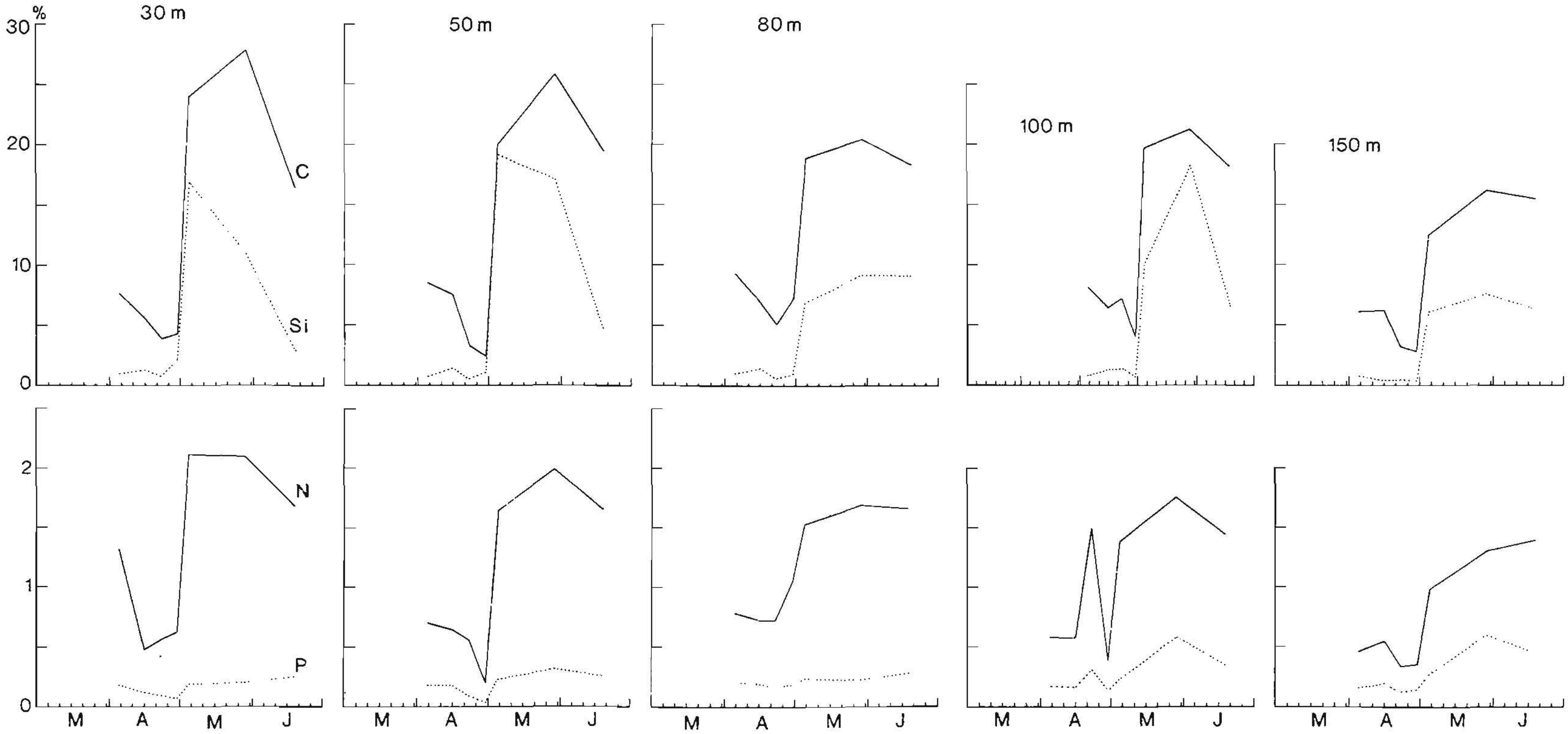

Fig. 5. Percentage contribution of carbon, nitrogen, phosphorus and silicon to the dry weight of the deposited matter at different depths during the study period in 1982 in the open northern Baltic Proper.

Table 1. The molar C:N:Si:P ratios of the deposited particulate matter at different depths during the exposure periods.

depth	23III-4IV	4-14 IV	14-21 IV	21-28 IV	28IV-12V	12-27 V	27V-17VI
m	C:N:Si:P	C:N:Si:P	C:N:Si:P	C:N:Si:P	C:N:Si:P	C:N:Si:P	C:N:Si:P
30	105:15:6:1	117:8:11:1	124:12:10:1	127:11:29:1	306:22:92:1	332:20:85:1	160:15:12:1
50	120: 8:4:1	109:7: 9:1	95: 8: 7:1	111: 9:23:1	241:16:99:1	203:12:58:1	160:10:23:1
80	115: 8:5:1	93:8: 8:1	92:10: 5:1	76: 8: 5:1	298:20: -:1	228:16: -:1	163:13: -:1
100	120: 7:5:1	98:7: 8:1	65:11: 5:1	75: 8: 5:1	210:13:47:1	89: 6: -:1	120: 8:20:1
150	90: 7:5:1	83:6: 2:1	73: 6: 4:1	40: 5: 2:1	112: 8:26:1	91: 6:19:1	152:10:24:1

Table 2. The ratios of carbon to chlorophyll *a* of the deposited particulate matter at different depths during the exposure periods.

depth	23 III-4 IV	4-14 IV	14-21 IV	21-28 IV	28 IV-12 V	12-27 V	27 V-1 7VI
30	215	118	58	44	91	118	214
50	198	109	93	65	130	142	157
80	245	136	143	376	112	113	125
100	390	295	313	308	198	165	144
150	750	860	880	755	116	116	126

Table 3. The percentage of carbon, nitrogen, silicon, phosphorus, and chlorophyll *a* out of the dry matter in the sediment surface (0-6 mm), as well as the elemental C:N:Si:P ratios during the study period.

date	C %	N %	P %	Si %	chl %	C:N:Si:P
23 III	3.1	0.44	0.10	1.5	1.0	81:10:16:1
3 IV	7.8	0.59	0.16	1.6	1.9	125: 8:11:1
14 IV	7.7					
21 IV	7.8					
24 IV	7.8	0.78	0.16		2.8	125:11: :1
29 IV	5.6	0.63	0.16	1.7	1.6	90: 9:12:1
27 V	10.0	0.86	0.16	1.5	3.3	160:12:10:1
16 VI	10.2	0.75	0.22	3.0	8.7	120: 8:15:1

4. DISCUSSION

The sampling efficiency of the traps and the decomposition of the deposited matter during the exposure periods are the most important factors that affect the reliability of the results. An additional problem in the material flux calculations is the estimation of the resuspension of "old" matter in relation to the primary sinking.

4.1 Sampling efficiency

The laboratory and field experiments performed by Gardner (1980a, 1980b), Bloesch & Burns (1980), and Blomqvist & Håkanson (1981) have proved that the simple cylinder is the most suitable form for a trap, when the diameter of the trap exceeds 4 cm and the aspect ratio (height:diameter) exceeds 5 in quiet water bodies and 10 in turbulent ones. However, according to Butman et al. (1986) and Butman (1986), biased particulate collection efficiencies are always possible in areas with complex flow and particle dynamics. The traps used in this study should gave a correct estimate of the sinking flux of the particulate matter under the low current velocities measured by Leppänen & Alenius (1988).

4.2 Resuspension and decomposition in the traps

The material deposited into the traps consists primarily of sinking and resuspended matter. There is no reliable method for quantitatively distinguishing between those components. The organic carbon content of dry matter, elemental ratios and carbon to chlorophyll ratios (Steele & Baird 1972, Webster et al. 1975, Smetacek 1980, Laakkonen et al. 1981, Wassmann 1983, 1984, 1985a, 1985b), microscopic analysis (Webster et al. 1975, Smetacek et al. 1978, Parmanter et al. 1983), as well as the proportions of the radionuclides of the natural decay series (Spencer et al. 1978, Tsunogai et al. 1980, Bacon 1984), have been used in determining the origin of the sinking material.

Resuspended "old" matter and the degradation of the primarily settling "fresh" particulate matter in both the water column while sinking and the traps during the exposure periods, introduce similar characteristics to the elemental ratios and contributions to the deposited matter. When algal material is degraded, labile low-molecular weight compounds are rapidly metabolized, while the degradation rate of the remaining more refractile fraction is low (Handa et al. 1972, Zsolnay 1973, Fukami et al. 1981, Matsunaga 1981, Ishikawa & Nishimura 1983, Poutanen & Morris 1983). The autolytic release of dissolved organic compounds is found to be important as the first stage in the degradation of algal matter (Garber 1984). During the degradation process the C:N and C:P rations increase, and the percentage contribution of the elements to the dry matter decreases. Below the halocline, especially, the adsorption of inorganic phosphorus onto particles increases their relative phosphorus content while sinking (Voipio 1969, Lahdes & Leppänen 1988) thus counteracting the effect of dissolution.

There was a considerable difference between the elemental ratios of the particulate matter in the traps and those in the water column at corresponding depths (cf. Lahdes & Leppänen 1988, Table 1). There is no reason *a priori* to suppose that the particles which settled in the traps should have the same elemental ratios as the average seston; the majority of the downward mass flux has been found to be associated with a few fast-sinking large particles with varying composition compared to the average seston where small particles are dominant (Honjo 1980, Fellows et al. 1981, Smetacek 1985). This might be the reason for the "fresher" appearance of the C:N:Si:P ratios in the deposited matter during the beginning of the study period. The low contributions of these elements to the dry matter indicate, however, that they are of resuspended origin. During the period of high deposition the difference in the C:N:P ratios in the trap material and seston was most probably caused by the decomposition of the trapped material. Neither fixation nor preservation were used in this study to prevent degradation of the material deposited in the traps. The accumulation of particles in high concentrations creates an environment favourable for decomposition. The biomass of heterotrophic ciliates and bacteria increased at this time in the water column (Leppänen & Bruun 1988, Lahdes et al. 1988). Sinking organic particles have been found to be rapidly colonized by bacteria and protozoa (Taylor et al. 1986).

The correction for carbon remineralization in the traps using equation (2) yields the deposition rates presented in Table 4. The corresponding loss of nitrogen and phosphorus during the last three exposure periods, when most of the sinking took place and the remineralization of these elements was most evident, can be corrected using the corrected deposition values of carbon (Table 4) and the C:N:P ratios of the seston during the same periods adopted from Lahdes & Leppänen (1988). The corrected total settling values for nitrogen and phosphorus are presented in Table 4. These corrections increase the deposition values of carbon by ca. 15 %, and roughly double the values for nitrogen and phosphorus. The increase in the deposition rates toward the bottom is evidence of resuspension. Thus the corrections for the traps below the halocline may be biased due to the increase in the contribution of resuspended material. The corrected settling values for phosphorus and nitrogen better corresponded to the net changes in the water than the measured ones.

Table 4. The measured and corrected amounts (mmol m^{-2}) of particulate carbon, nitrogen, silicon and phosphorus during the whole study period (23 March-17 June), and during the vernal phytoplankton bloom period (3 April-27 May) at different depths.

	Whole period							vernal bloom period (April-May)						
m	measured				corrected			measured				corrected		
	C	N	Si	P	C	N	P	C	N	Si	P	C	N	P
30	1811	136	433	7.3	2124	222	15.2	1543	106	414	5.4	1804	185	12.9
50	1948	127	542	10.4	2360	226	18.8	1490	97	483	7.3	1810	200	16.3
80	2131	161	362	11.2	2535	247	20.8	1580	118	258	7.6	1875	215	17.8
100	2784	201	671	22.8	3209	241	27.7	2243	162	597	18.3	3638	204	21.0
150	2791	205	483	25.0	3313	240	27.1	2080	154	383	19.8	2463	188	20.5

The relative amount of particulate silicon was high in the particulate matter deposited during the period of high deposition (Table 1). Lahdes & Leppänen (1988) observed that the decrease in dissolved inorganic silicon in the surface layer (0-30 m) was clearly higher than the corresponding increase in the particulate form. The measured downward flux of particulate silicon, however, corresponded well with the observed decrease in the initial reserve of dissolved inorganic silicon during the phytoplankton bloom period (cf. Lahdes & Leppänen 1988). The reason for this behaviour of silicon is probably the formation of resting spores of diatoms with a high silicon content. Spore-forming diatoms were the dominant group in the phytoplankton during the vernal peak (Leppänen & Kononen 1988). Since the spores are formed rapidly and sink fast (Smetacek 1985), their contribution in the seston remains low but they accumulate in the traps. A corresponding accumulation was, however, not observed at the sediment surface.

4.3 Sinking from the surface layer

Only a small proportion of the newly produced particulate carbon, nitrogen and phosphorus settled out from the surface layer (0-30 m) during the increasing phase of the bloom. The content of the elements at the sediment surface had, however, clearly increased already in the beginning of April. The diatom bloom collapsed after the depletion of dissolved inorganic nitrogen in the surface layer (Leppänen & Kononen 1988). This was followed by a period of high deposition when the daily flux of particulate carbon, nitrogen and phosphorus was ca. 5 % of the average reserve of the seston in the overlying water layer (Fig. 6). The daily flux of particulate organic silicon was as high as 20-54 %. Thus the total flux during that period exceeded the average total amount of particulate silicon in the 0-30 m water layer. Most of the vernal phytoplankton bloom sank from the euphotic layer during a period of about 1 month. The simultaneous increase in settling rates and the elemental ratios of the deposited matter at all depths indicate that neither the developing thermocline nor the halocline formed any barrier to the main particle flux during that period.

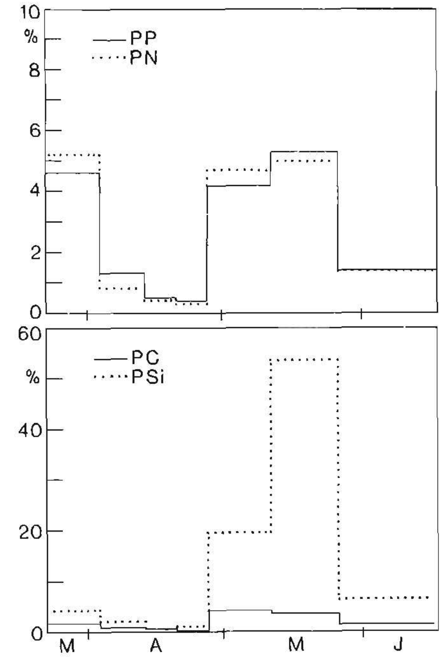

Fig. 6. Percentage daily flux of particulate phosphorus, nitrogen, carbon and silicon from the seston in the 0-30 m layer during the study period in 1982 in the open northern Baltic Proper. The concentration of elements in the seston are from Lahdes & Leppänen (1988).

It is most probable that deposition at a depth of 30 m was not markedly affected by the resuspended matter during the vernal bloom period (April-May). This thus represents the primary sinking of particulate matter from the euphotic layer. During the vernal bloom period ca. 60 % of the carbon assimilated in a particulate form by autotrophic organisms sank down from the surface layer, while the corresponding percentage for nitrogen and phosphorus was 38 % and 48 %, respectively (Table 5). The sinking flux of silicon exceeded the estimated autotrophic assimilation. The corresponding percentages for the elements were almost similar throughout the whole study period (Table 5).

Table 5. The amount of particulate primary production of carbon, nitrogen, silicon, and phosphorus in the surface layer (0-30 m) (adopted from Lahdes & Leppänen 1988 and Leppänen & Bruun 1988), the total deposition of the corresponding elements and chlorophyll *a* at the depths of 30 and 150 m during the whole study period (23 March-17 June) and during the vernal bloom period (April-May), as well as the measured accumulation in the sediment surface. All values are expressed as mmol m^{-2} $period^{-1}$ except for chlorophyll *a* which is in mg m^{-2} period $^{-1}$.

	Whole study period					Vernal bloom period				
	C	N	Si	P	Chla	C	N	Si	P	Chla
Primary production	3500	513	327	32		3000	481	280	27	
settling at 30 m	2120	220	430	15	203	1800	185	410	13	188
settling at 150 m	3310	240	480	27	248	2460	190	380	21	190
accumulation on the sediment surface (6 mm)	1920	70	170	13	250	590	60	0	0	46

4.4 Deposition on the bottom

Since the contribution of resuspension clearly increased on moving closer to the bottom, it is impossible to estimate the amount of primary sinking to the bottom. The topography of the basin causes a near bottom flow of particulate matter from the shallower non-deposition and erosion areas into the deep basin. This concentrated fresh matter into the deepest traps, as clearly shown, by the settling pattern for chlorophyll (Fig. 4 and Table 5).

The accumulation of carbon, nitrogen, silicon, phosphorus, and chlorophyll a in the 6 mm-thick layer of the sediment surface during the vernal bloom period (April-May) was small compared to deposition in the traps (Table 5). During the whole study period, only the accumulation of chlorophyll slightly exceeded the amount which settled out from the euphotic layer, while only ca. 90 %, 30 %, 40 %, and 87 % of the carbon, nitrogen, silicon, and phosphorus, respectively, were found in the sediment.

In theory, the amount of matter which accumulates in the sediment surface should be greater than the rate of direct deposition would permit. This was not, however, the case. The results indicate that the sinking matter probably first accumulates in the form of suspension layer above the actual sediment surface, and is not collected by the corer used in this study. This is supported by the fact that the colour of the sediment surface was always different than that of the matter deposited at a depth of 150 m.

The results of this study indicate that most of the vernal particulate production had already been decomposed in the euphotic layer and again in the layer near the sediment, rather than during the process of sinking.

4.5 Comparison with other sea areas

Due to the low heterotrophic activity during the vernal period, the growth of primary producers exceeds the carrying capacity of the system resulting in the extensive sinking of phytoplankton blooms. This is a well-known phenomenon in both coastal and open sea areas (Billet et al. 1983, Wassman 1983, 1985, Davies & Payne 1984, Smetacek et al. 1984). In the Baltic Sea 33-65 % and 20-38 % of the vernal particulate primary production of carbon and nitrogen, respectively, is lost through sinking from the euphotic layer (Table 6). The differences in the assimilation: sedimentation ratios do not necessarily reflect different recycling pattern. For instance methodological differences (trap design, preservation of trapped material etc.) and temporal and vertical limits for the calculations may produce values which vary by wide margins. The highest assimilation: sedimentation ratios are found in the Kiel Bight as well as in this study. In Kiel, chloroform was used in the traps to prevent the decomposition of material and in this study the effect of decomposition was corrected. The uncorrected values of this study are close to those measured in Askö and Tvärminne, where no preservation/correction was used.

Table 6. The ratios of carbon and nitrogen assimilation and sedimentation (%) during the vernal phytoplankton bloom period in different parts of the Baltic Sea. The values for Tvärminne area from Forsskåhl et al. (1982) and Kuparinen et al. (1984); C:N ratio of the sinking matter was 8:1 (Laakkonen et al. 1981). Values for Askö and Arkona Basin are from Wulff et al. (1986) and for Kiel Bight from Peinert at al.(1982) and Smetacek et al. (1984).

	Sedimentation/assimilation (%)	
	carbon	nitrogen
This study		
-measured	51	22
-corrected for decomposition in traps	60	38
Tvärminne	32-38	27-33
Askö	40	23
Arkona Sea	33	20
Kiel Bight	>50-65	

By removing a considerable portion of the initial reserves of nutrients bound in the euphotic layer, the sinking of particulate matter during the vernal growth period acts as an important link between the pelagial and the benthos, but can also counteract the eutrophication of the pelagial system. It is generally accepted (e.g. Melvasalo et al. 1981) that dissolved inorganic nitrogen (DIN) is the main factor limiting primary production during the vernal growth period and, if the observed increase in the initial amount of DIN (e.g. Nehring et al. 1984, Pitkänen et al. 1985) increases the peak of the bloom, due to the low heterotrophic activity, rather than its duration, then in this case sedimentation could remove most of this stored component from the euphotic layer. In areas which favor denitrification this process could then transform the nitrogen to N_2 and remove it from the system. As pointed out by Rönner (1985), for instance, when the organic content of the system reaches very high levels nitrogen may, in the long run, accumulate as ammonium rather than be lost through denitrification.

6. CONCLUSIONS

The vernal diatom dominated phytoplankton bloom rapidly settled down out of the euphotic layer after the bloom peak, and the sporulation of diatoms probably played a critical role in this process. Neither the weak thermocline nor the permanent halocline formed any barrier to the main flux of the particles. About 60 % of the particulate primary production of carbon settled out from the euphotic layer, while over 50 % of the nitrogen and phosphorus was recycled in this layer. The output of carbon and nutrients corresponded to the measured net changes in the water phase. The amount of phosphorus in the particulate matter increased in the water layer below the halocline due to the adsorption of inorganic phosphorus onto the settling particles. The contribution of resuspended matter to deposition in the deepest traps was evident during the whole study period, as well as in March and the beginning of April in the water layer above the halocline. Since the study basin is a deposition area where organic matter from the surrounding areas is also concentrated in the bottom sediment, estimating the contribution of primary settling to the observed accumulation of organic matter and elements in the sediment is difficult. It seems, however, that during the vernal production stage, after leaving the euphotic layer, most of decomposition of the settling matter most probably takes place near the sediment surface rather than during the sinking. The mass sedimentation of the particulate matter during the vernal phytoplankton bloom is an effective mechanism of removing nutrients from the euphotic layer, stored during the previous winter, and transporting them to the benthic system. Together with denitrification, this process may also counteract the eutrophication process.

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