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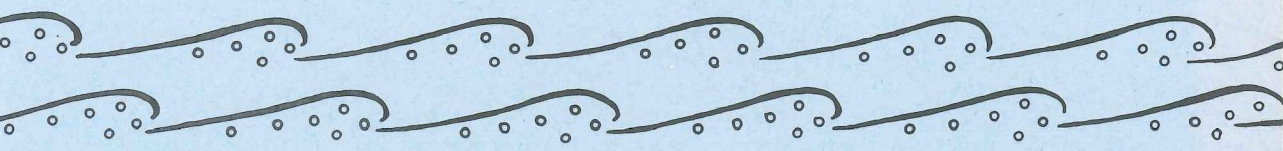
No 16

Carbon and nitrogen cycles during the
vernal growth period in the open northern
Baltic Proper

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The thesis consists of this summary and the following publications:

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Lahdes, E. & Leppänen, J.-M. 1988: Cycling of organic matter during the vernal growth period in the open northern Baltic Proper. II. Nutrient development and chemical composition of particulate matter. - Finnish Mar. Res. 255:19-35.

Leppänen, J.-M. & Kononen, K. 1988: 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. - Finnish Mar. Res. 255:37-54.

Leppänen, J.-M. & Bruun, J.-E. 1988: 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. - Finnish Mar. Res. 255:55-78.

Lahdes, E., Kononen, K., Karjala, L. & Leppänen, J.-M. 1988: Cycling of organic matter during the vernal growth period in the open northern Baltic Proper. V. Community respiration and bacterial ecology. - Finnish Mar. Res. 255:79-95.

Leppänen, J.-M. 1988: Cycling of organic matter during the vernal growth period in the open northern Baltic Proper. VI. Sinking of particulate matter. - Finnish Mar. Res. 255:97-118.

CARBON AND NITROGEN CYCLES DURING THE VERNAL GROWTH PERIOD IN
THE OPEN NORTHERN BALTIC PROPER

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ABSTRACT

The dynamics of hydrography, including currents, nutrients,
phytoplankton, zooplankton, bacterioplankton, primary production,
and the sinking of organic matter, were followed in the open
northern Baltic Proper during the vernal growth period in 1982.
Budgets for carbon and nitrogen cycles were constructed using
measured changes in the reserves, and by combining quantitative
plankton data with empirical equations from the literature in order
to estimate the major biological processes. The primary formation of
particulate matter was predominantly based on the initial reserves
of inorganic nutrients in the euphotic layer and in the intermediate
layer. Ciliates and bacteria were the most important heterotrophic
organisms. Most of the decomposition of organic matter took place in
the same water layer where it was produced and then again, after
leaving the euphotic layer, near the sediment surface rather than
during the sinking.

Key words: Nutrients, primary production, ciliates, mesozooplankton,
grazing, bacteria, sedimentation.

1. INTRODUCTION

In order to be able to evaluate the role of human impact on
changes in the environment, comprehensive knowledge is needed
about the ecological interactions and processes. One of the main
problems in the Baltic Sea has been to separate the effect of
natural long-term changes from anthropogenic ones on the develop-
ment of large anoxic areas in the bottom water. The complexity

of the problem has emphasized the need to develop models, deal-
ing with isolated processes or comprising the whole ecosystem.
The "model" can be a purely descriptive one including quantitat-
ive information about the reserves and cycling of matter (box-
models, flow diagrams) or a numerical one which attempts to
formulate aspects of the dynamic processes taking place in the
sea in mathematical terms. The models, the even simple ones,
have also been useful in forcing to multidisciplinary, comprehen-
sive ecosystem research, in evaluating the collected data and in
pointing out deficiencies in our knowledge. The predictive
models, needed for the planning of rational management of the
sea, especially require quantitative information about the main
pathways of organic matter circulation and the factors
controlling such pathways.

Ecological modelling of the Baltic Sea began at the end of
1960's, with material balances (oxygen and phosphorus, Fonselius
1969, Voipio 1969), and general ecosystem models (Aitsam 1972,
Jansson 1972). Today our ecological knowledge has reached a
stage where it has been possible to construct numerical models
to simulate the main nitrogen and oxygen dynamics of the Baltic
Proper (Stigebrandt & Wulff 1987). As the authors of this model
say, it is to be considered as the first step toward a detailed
ecological model, since a full account of the dynamics of the
Baltic systems goes way beyond the goals of the model.

In Finland the loan from the International Bank for
Reconstruction and Development (World Bank) initiated numerical
water-ecosystem modelling in the 1970's. One of the projects
concentrated on modelling the oxygen balance of the Bothnian Sea
(Mäkelä 1978). It become apparent during the work carried out at
the Finnish Institute of Marine Research that there is a signifi-
cant lack of knowledge about the exchange of gases between the
sea and the atmosphere, and about the decomposition and sedimen-
tation rates of organic matter.

The investigations on primary production and sinking of
organic matter in the Baltic have predominantly been carried out
in shallow coastal areas (e.g. Forsskåhl et al. 1982, Kuparinen
et al. 1984, Smetacek et al. 1984, Larsson et al. 1986). The
main purpose of the study in hand was to gather quantitative

data about the relationship between primary production, decomposition and sinking of organic matter in an open sea area where the permanent halocline divides the water, and where anoxia occurs near the bottom. The vernal growth period was chosen because there are strong grounds to believe that this period is the most important for the annual material and energy input, at least as far as the benthic system is concerned (Jansson 1978, Laakkonen et al. 1981, Graf et al. 1984, Kuparinen et al. 1984). The project was divided into sections covering the main physical features, nutrient chemistry, plankton dynamics, primary production, and the sinking of organic matter. The collected material provided an opportunity to combine the plankton data (abundances and biomass) with equations published in the literature, to calculate processes related to the cycling of organic matter in the food web, and to evaluate these calculated values in the light of measured ones.

This paper combines the results presented by Lahdes et al. (1988), Lahdes & Leppänen (1988), Leppänen (1988), Leppänen & Alenius (1988), Leppänen & Bruun (1988), and Leppänen & Kononen (1988) in a simple box-model together with the budgets for the carbon and nitrogen cycles. These elements were chosen on the basis of comparison with earlier studies, and because nitrogen is generally accepted as the main factor limiting primary production during the vernal growth period in the Baltic Proper (e.g. Niemi 1973, 1975). Some preliminary results concerning ciliates and the cycling of nitrogen have been published earlier (Leppänen & Bruun 1986, Leppänen et al. 1986).

This work has been carried out at the Finnish Institute of Marine Research. The Maj and Tor Nessling Foundation has supported the project financially. The ideas of prof. Aarno Voipio were the starting point for the whole project and he has provided advice during the planning stage the study and analysis of the results.

2. THE RESERVES AND REACTIONS OF CARBON AND NITROGEN IN SEA WATER

The main carbon and nitrogen reserves and the flows between them in a water ecosystem are schematically presented in Fig. 1. The
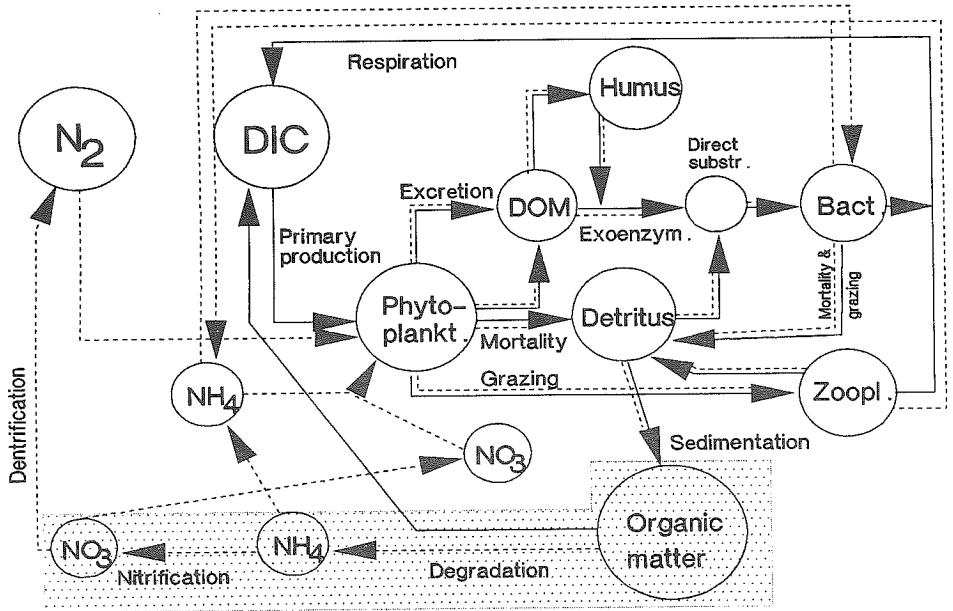

Fig. 1. Diagram of carbon and nitrogen cycling in a marine ecosystem. The solid arrows represent fluxes of carbon and the broken ones fluxes of nitrogen. The circles represent standing stocks. The shaded area is sediment. (Redrawn from Lancelot & Billen 1985).

total amount and distribution of the different carbon and nitrogen species in Baltic Sea water are dependent on the water depth and on the growth stage of the plankton. Most of the carbon and nitrogen is in the form of inorganic compounds (Fig. 2). Carbon is predominantly in the form of bicarbonate (ca. 80 %) while, in contrast to the other major elements, gaseous form is predominant in the nitrogen reserves (ca. 95 %). Dissolved organic compounds are dominating the rest of both carbon and nitrogen pools (Laakkonen & al. 1981, Lahdes & Leppänen 1988). The amount of dissolved organic matter is clearly higher in the Baltic Sea than in oceans, its composition is mostly unknown and its turnover time is long (Grasshoff & Voipio 1981).
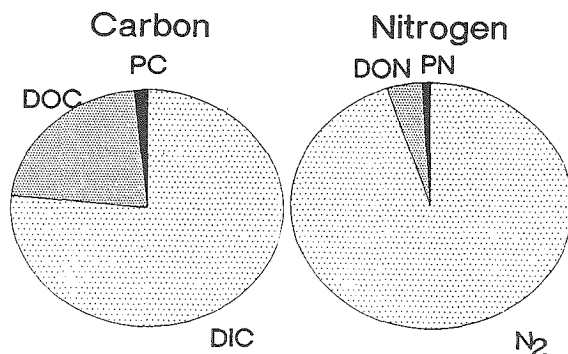
Carbon

Nitrogen

Fig. 2. Average distribution of carbon and nitrogen species in the Baltic Sea water (DOC = dissolved organic carbon, DIC = dissolved inorganic carbon, PC = particulate carbon, DON = dissolved organic nitrogen, PN = particulate nitrogen; compiled from Buch 1945, Laakkonen et al. 1981, Valiela 1984, Lahdes & Leppänen 1988).

During this study dissolved organic compounds were found to account for the major share of total nitrogen at all depths (ca. 70 %) when the gaseous form is excluded. In the euphotic layer the remaining fraction consisted mostly of dissolved inorganic compounds (DIN, i.e. NO_3-N, NO_2-N and NH_4-N) at the beginning of the study period, but became bound to particulate organic compounds (PN) during the phytoplankton spring bloom (Lahdes & Leppänen 1988). In the aphotic layer the contribution of DIN to total nitrogen was 10-30 % and showed a decreasing trend toward the end of the study period.

According to the results of Lahdes & Leppänen (1988) the particulate matter was predominantly autochtonous, originating from plankton organisms. The living part of the seston was concentrated in the surface layer (0-30 m), while detritus predominated below. Detrital interference in the surface layer was small for PN, but more distinct for particulate carbon (PC). The amount of dissolved organic carbon (DOC) was not measured. It seems that the contribution of allochtonous matter (e.g. humic terrigenous matter) to dissolved organic matter is probably higher than that to the particulate organic matter. Zsolnay (1975) reports that ca. 30 % of the total organic carbon in the euphotic zone of the Baltic Sea water is in the form of labile compounds and that their concentrations are correlated with phytoplankton biomass and productivity.

In the open Baltic Proper iorganic carbon is assimilated to form organic compounds in the euphotic layer by autotrophic organisms via photosynthesis. Dissolved organic carbon compounds (DOC) are produced by autotrophic organisms through exudation, released from dead particles through autolysis, from broken particles during zooplankton feeding, and by hydrolysis through the action of microbial extracellular enzymes. DOC is taken up by bacteria and transferred in the microbial loop. Organic car-bon is returned back to the inorganic pool through respiration by both autotrophic and heterotrophic organisms.

Nitrogen can occur in water in 8 oxidation states (Fig. 3). In organic matter nitrogen occurs predominantly in the reduced amino form (NH_4-N). Ammonium and nitrate are the most important forms of DIN in the biological nitrogen cycle.
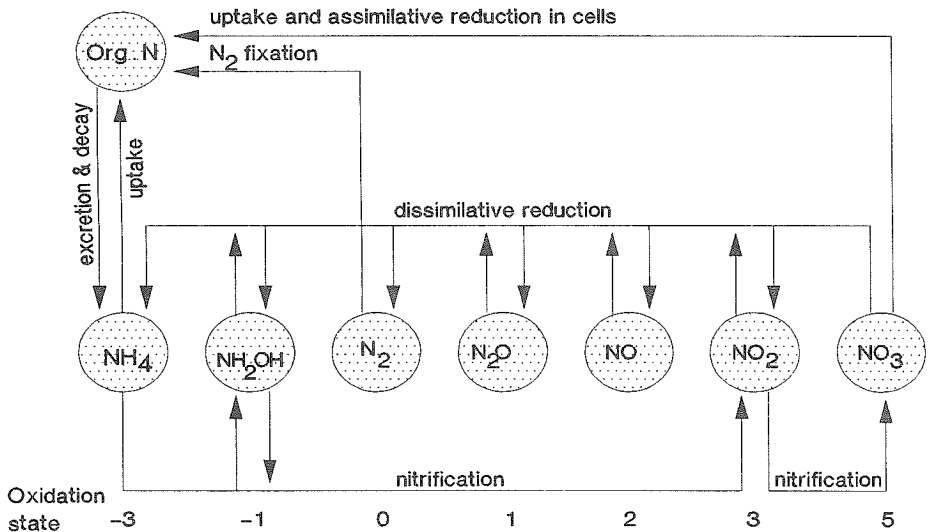

Fig. 3. Oxidation states of various nitrogen species in sea water. The arrows indicate the transformation processes (modified from Fenchel & Blackburn 1979).

DIN is assimilated primarily by phytoplankton in the euphotic zone but by bacteria in the layers below it. Ammonium uptake is preferred when it is available. Ammonium ions can be directly

incorporated into cellular material but in the assimilation of
nitrate it is first reduced in cells to the amino form prior to
its utilization in metabolic processes.

In dissimilatory nitrate reduction processes, nitrate is
transformed either to N_2 gas (denitrification) or ammonium
(dissimilatory ammonium production). The processes are carried
out by facultative anaerobic bacteria under anoxia or at low
oxygen concentrations either in the water column or in the sed-
iment. According to the measurements of Rönner (1983), nitrate
is not reduced dissimilatory to ammonium at significant rates in
the waters of the Baltic Proper.

Nitrogen fixation by cyanobacteria (blue-green algae) is a
process where gaseous N_2 is transformed to the amino form. This
process is restricted in the open Baltic Sea to late summer (e.
g. Leppänen et al. 1988 and the literature cited therein).

Dissolved organic nitrogenous compounds (DON) are formed
through the same processes as DOC. Phytoplankton exudates, how-
ever, contain only small amounts of nitrogen (Lancelot & Billen
1985 and literature cited therein). Consumers may excrete urea
and uric acid.

Organic nitrogenous compounds are decomposed to inorganic
forms through ammonification by heterotrophic organism. Ammonium
can be oxidized to nitrite and nitrate by obligatory aerobic
chemoautotrophic bacteria. Nitrifying bacteria should not be
able to compete with phytoplankton for ammonium in the euphotic
layer because both ammonium and nitrite oxidation are inhibited
by light (Enoksson 1980, Olson 1981). There is, however, evi-
dence that bacteria can assimilate DIN when growing in substrate
poor in nitrogen (Wheeler & Kirchman 1986).

3. DATA COLLECTION

The study area is located in the open northern Baltic Proper
(59° 26,1′ N; 21° 31,4′ E). The sampling site is a sedimentary
basin where the water depth is ca. 158 m.

The sampling for chemical and biological analyses was carried out between March 23 and June 17, 1982 at either one or two-week intervals, apart from the period April 14-29 when more frequent sampling was performed. The samples were taken between 8 and 11 am. The vertical temperature and conductivity profiles were measured with a CTD sonde. The sampling depths for chemical and most biological analyses were 0, 2, 5, 10, 15, 20, 30, 40, 50, 60, 80, 100, 130, 150 m, and occasionally 70 m. Mesozooplankton was sampled with a standard WP-2 net with a mesh size of 100 µm. The depth intervals for the vertical hauls were 0-30, 30-80 and 80-150 m. Currents and continuous temperature measurements were recorded between April 14 and June 17 using current meters placed at five depths: 30, 50, 80, 100 and 130 m (Leppänen & Alenius 1988). Solar radiation was recorded onboard R/V Aranda. Sedimentation of particulate matter was recorded with traps moored at the same depths as the current meters, and by taking samples from the sediment surface (Leppänen 1988).

Oxygen, pH, dissolved inorganic, particulate and total phosphorus and nitrogen, dissolved and particulate silicon, particulate carbon, adenosine triphosphate (ATP), chlorophyll a, primary production, community respiration, phytoplankton, ciliate and mesozooplankton species composition, abundance and biomass, as well as bacterial abundance and biomass were analyzed from the samples as described by Lahdes et al. 1988, Lahdes & Leppänen 1988, Leppänen & Alenius 1988, Leppänen & Bruun 1988, Leppänen & Kononen 1988.

No direct measurements of consumption, respiration and production of heterotrophic organisms were performed, but instead were calculated from the measured abundance or biomass values using the empirical equations obtained from the literature. For more details see Lahdes et al. (1988), Leppänen & Bruun (1988) and Leppänen & Kononen (1988).

In the nitrogen budget only the reserves and sedimentation were measured, all the other values being converted from carbon using the following assumptions:

- C:N ratio in phytoplankton and ciliates is 6.1 (Lahdes & Leppänen 1988),
- C:N ratio in zooplankton is 4.4 (Holligan et al. 1984)

- C:N ratio in seston is 8.2 (Lahdes & Leppänen 1988)
- C:N ratio in bacteria is 5 (Fenchel & Blackburn 1979).
- C:N ratio in feces is 8 (Turner & Ferrante 1979)
- C=P-E-F, where C is consumption, P is production, E is excretion, and F is feces.

Three successive stages could be distinguished on the basis of nutrient development and succession of the plankton community during the study period. The sampling done in March represented the winter stage, with a low plankton biomass and production and high concentrations of dissolved nutrients in the whole water body. The vernal phytoplankton production stage, i.e. the vernal growth period from its initiation to the sinking from the surface layer, took place in April-May. The last sampling in June represented the early summer phase. This paper concentrates on the vernal growth period.

4. GENERAL FEATURES

The hydrographic, chemical and biological features during the study period corresponded well with earlier observations made in the northern Baltic Proper and in the western Gulf of Finland (Simojoki 1946, Niemi 1973, 1975, Leppänen & Tamelander 1981, Alenius & Leppäranta 1982, Forsskåhl et al. 1982, Lassig et al. 1984, Kuparinen et al. 1984, Larsson et al. 1986). However, long-term monitoring of plankton communities in the Archipelago Sea (Vuorinen & Ranta 1987) and in the Gulf of Finland (Lassig et al. 1984, Kononen & Niemi 1984) have revealed the same general succession pattern, but also a large variation between years.

The water was divided by the permanent halocline. It rose from ca. 90 m by about 20 m during the study period. The developing thermocline divided the layer above the halocline into the mixing surface layer down to ca. 30 and the intermediate "winter water" layer. The surface layer was mostly somewhat deeper than the euphotic layer (Leppänen & Alenius 1988).

The currents were slow and the great variability in their direction and speed indicates small net water exchange in the

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area. On the other hand, this is contradictory to the rise of the halocline, especially since no clear correlation was found between the movements of the halocline and currents (Leppänen & Alenius 1988).
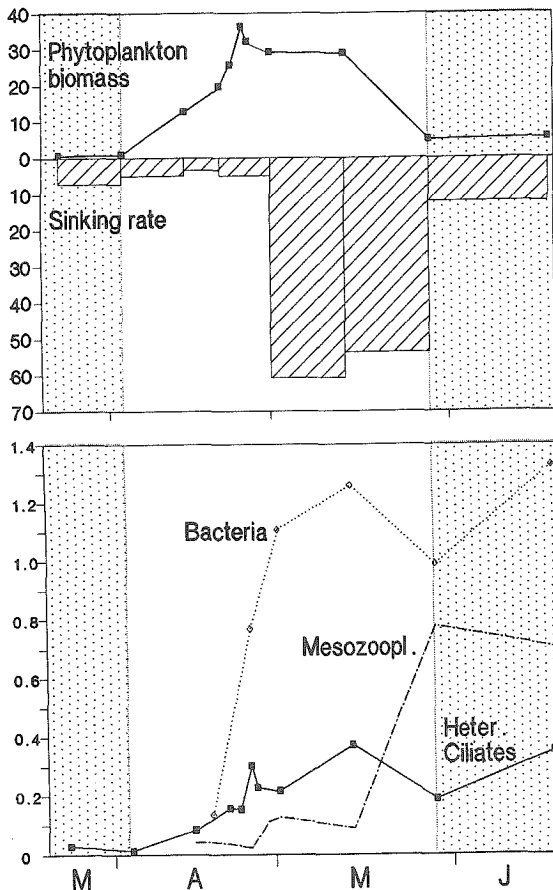
During the growth phase of the bloom, the sinking of phytoplankton was small and the biomass became concentrated in the surface layer (Fig. 4). The diatom bloom ended when dissolved inorganic nitrogen (DIN) was depleted in the euphotic layer (Lahdes & Leppänen 1988, Leppänen & Kononen 1988). The concentration of dissolved inorganic silicon was higher than the Michaelis constant reported by Paasche (1980) for silicon uptake by diatoms. The phytoplankton biomass settled rapidly down from the euphotic layer after the peak of the bloom (Leppänen 1988). The sporulation of diatoms seemed to play an important role in the sinking process of the bloom. Neither the

Fig. 4. The mean biomass of phytoplankton, heterotrophic ciliates, mesozooplankton and bacteria in the 0-30 m layer (mmolCm^{-3}) and the sedimentation rate of particulate matter at a depth of 30 m (mmolC m^{-2}d^{-1}), in the open nothern Baltic Proper during the whole study period 23 March-17 June 1982. The vernal period is indicated by a non-shaded area.

weak thermocline nor the permanent halocline formed any barrier to the main flux of the particles. The low zooplankton biomass was concentrated in the surface layer and was dominated by nonloricated ciliates and juvenile stages of copepods (Leppänen & Bruun 1988). Bacterial numbers remained relatively low throughout the vernal growth period (147-$617*10^9$ m^{-3} in the surface layer, Lahdes et al. 1988) but their biomass was highest among the heterotrophs (Fig. 4). For more details on hydrography, nutrient chemistry, phytoplankton, zooplankton, bacteria and sinking of particulate matter see Leppänen & Alenius (1988), Lahdes & Leppänen (1988), Leppänen & Kononen (1988), Leppänen & Bruun (1988), Lahdes et al. (1988), and Leppänen (1988), respectively.

Cluster analysis was carried out in order to detect natural grouping in the data (Fig. 5). This analysis must be considered more as an illustrative technique than as showing absolute linkages between the parameters. The close connection between phytoplankton parameters and the particulate nutrients and ATP shows the dominating role of phytoplankton in the development of particulate matter. The calculated processes for ciliates and mesozooplankton were closely connected to the biomass, which is the basic parameter in the calculations. Bacteria were not very closely connected to the phytoplankton parameters.
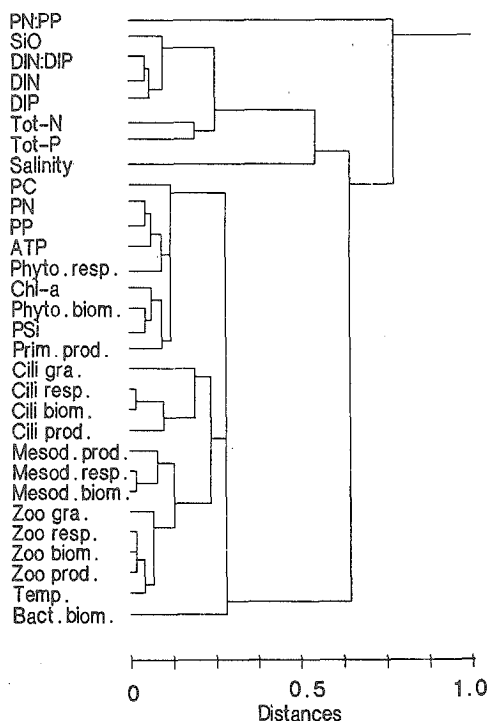

Fig. 5. Cluster analysis dendrogram of the variables (means of the 0-30 m surface layer) Cili. refers to heterotrophic ciliates, Mesod. to *Mesodinium rubrum* and Zoo to mesozooplankton.

5. RESULTS

The diagrammatic representation of the channeling of gross
primary production of carbon and nitrogen, assimilated by auto-
trophic organisms during the vernal growth stage (April-May) are
presented in Figs. 6 and 7, respectively. The system is assumed
to be a closed one. The small net exchange of water in the area
(Leppänen & Alenius 1988) provides grounds for this assumption.
According to the compilations of Elmgren (1984) and Poutanen
(1985), the input of allochtonous matter is of minor importance
(< 5 % of the total input). The system is simplified by dividing
it into two parts. The upper part represents the euphotic, mixed
surface layer and the intermediate layer above the halocline.
These two layers were combined because, as shown by Lahdes & Lep-
pänen (1988), the reserves of inorganic nutrients in the
intermediate layer were functionally connected to the uppermost
layer. The layer below the halocline represents an entirely
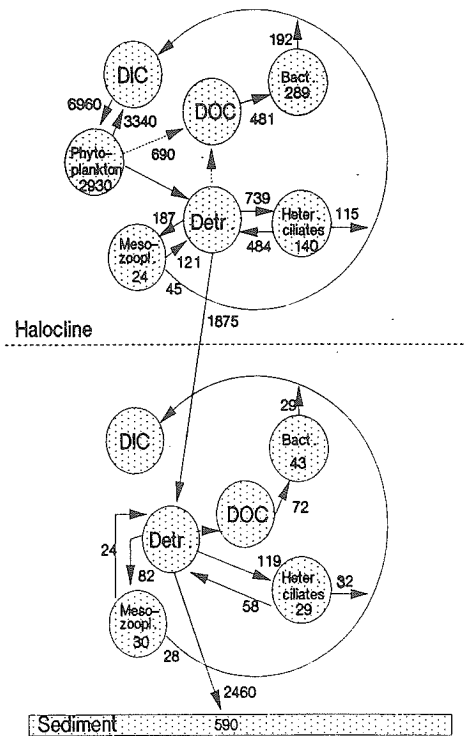aphotic system.

Fig. 6. The channeling of gross primary production of carbon in the open northern Baltic Proper during the vernal growth period (April-May) in 1982. The arrows represent the fluxes (mmolC m^{-2} period^{-1}), the dotted ones were not quantified, and the circles are standing stocks. The production figures (mmolC m^{-2} period^{-1}) are presented in the boxes.

5.1. Cycling of carbon

The gross production of carbon by phytoplankton and the auto-
trophic ciliate *Mesodinium rubrum* was almost 7 mol m^{-2}. The
respiration of autotrophic organisms returned almost half of the
gross primary production back to the inorganic pool (Fig. 6).
Thus ca. 0.1 % of the solar radiation (from Leppänen & Alenius
1988) was converted into primary production. 70 % of the exu-
dates was assimilated by bacteria in the water layer above the
halocline. 10 % of net primary production was respired through
heterotrophic organisms. About 30 % of the particulate primary
production was grazed by zooplankton, predominantly ciliates;
64 % was sedimented through the halocline.

   Below the halocline, ca. 15 % of the carbon sedimented from
the layer above was cycled through heterotrophic organisms and
5 % respired by them. The accumulation of carbon in the sediment
surface (uppermost 6 mm) was ca. 20 % of the particulate primary
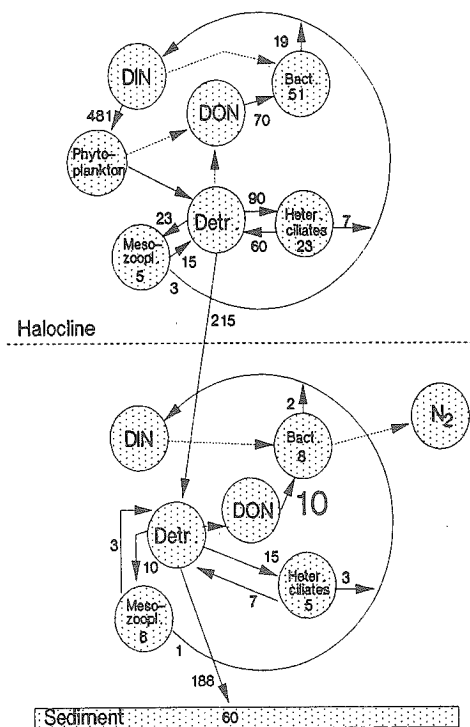production.

Fig. 7. The channeling of nitrogen assimilated by primary producers in the open northern Baltic Proper during the vernal growth period (April-May) in 1982. The arrows represent the fluxes (mmolN m^{-2}period^{-1}), the dotted ones were not quantified, and the circles are standing stocks. The production figures (mmolN m^{-2}period^{-1}) are presented in the circles.

5.2. Cycling of nitrogen

The channeling of nitrogen, assimilated by autotrophic organisms, is compiled in Fig. 7. Almost 40 % of this nitrogen was consumed by heterotrophs in the layer above the halocline, while 45 % was removed by sinking. Recycling through heterotrophic ammonification was small; most of the heterotrophic consumption was channeled to the detrital pool through defecation, or to production.

Only 13 % of the nitrogen assimilated by autotrophs was accumulated in the sediment surface.

6. DISCUSSION

The recycling of nutrients during the vernal growth period is small due to low heterotrophic activity and that the growth of primary producers exceeds the carrying capacity of the system. This results in extensive sinking of the phytoplankton bloom, which is a well-known phenomenon in both coastal and open temperate sea areas (Forsskåhl et al. 1982, Billet at al. 1983, Wassmann 1983, 1985, Bienfang & Harrison 1984, Davies & Payne 1984, Kuparinen et al. 1984, Smetacek et al. 1984, Larsson et al. 1986,). Assimilation by autotrophic organisms and the sinking of particulate matter were the predominating processes in the carbon and nitrogen cycles.

The calculated values for both carbon and nitrogen processes fitted very well with the measured values and the changes in the reserves in the water layer above the halocline. However, calculation of the metabolic structure of the plankton community on the basis of biomass values is a very subjective procedure which is largely dependent on the equation selected. The basic assumption for the calculations, the stable process:biomass ratio, does not apply to natural communities. Environmental factors (e. g. diel variation, depletion of nutrients or food), life cycle strategies of the organisms, and their physiological state can produce wide variation in the ratios. This approach is therefore more suited to explaining the observed changes in the carbon and

nitrogen pools, rather than to confirming the channeling of the elements in the food web.

Due to the lack of suitable equipment for distinguishing between auto- and heterotrophic flagellates at the time of the field study, the heterotrophic flagellates have been excluded. However, their role in the microbial loop can be important in that they feed on bacteria (e.g. Sieburth 1984). According to Niemi & Åström (1987), the contribution of heterotrophic flagellates to the biomass of "unidentified flagellates" can be high. Therefore the role of microheterotrophs is underestimated in this study.

6.1 Carbon cycle
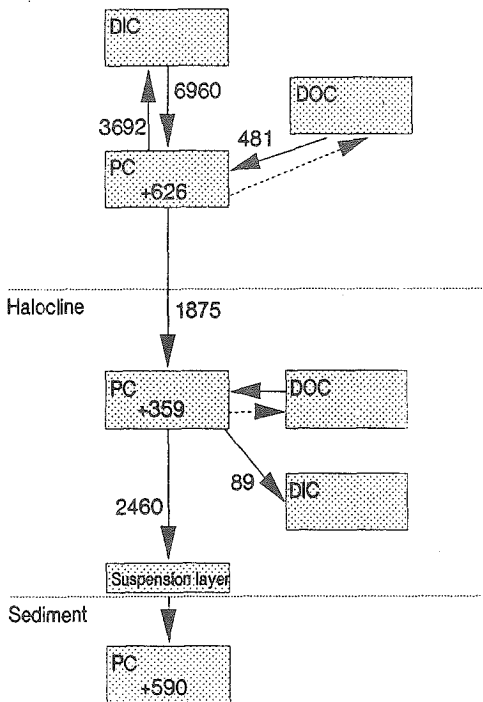
On the basis of the changes in the reserves and the measured and estimated processes a carbon budget for the vernal period is compiled in Fig. 8. In the layer above the halocline the reserves of PC increased by 626 mmol m^{-2}. In order to balance the budget almost the same amount of carbon, ca. 20 % of net primary production, should have been left in the dissolved organic pool. The amount of dissolved organic carbon was not, however, measured.

About 1/5 of the carbon sedimented through the halocline was accumulated in the water column, and ca. 1/3 in the sediment surface. The measured loss of

Fig. 8. Carbon budget for the vernal growth period in the open northern Baltic Proper. The arrows represent the flows and the figures inside the boxes net change in the reserves. All values are expressed as mmolC m^{-2} period^{-1}.

PC through heterotrophic respiration was small. The contribution of resuspension to the total deposition at a depth of 150 m was ca. 40 %. The excess is most probably not totally channeled into DOC pool, but rather accumulated in the form of a suspension layer above the sediment; this layer was not, however, sampled (Leppänen 1988).

[14]C incorporation, community respiration and the sinking of particulate matter were the only processes which were directly measured in this study. The ^{14}C incorporation rate during 2 h incubation, and the calculated daily production based on these rates, were assumed to estimate gross phytoplankton production (Leppänen & Kononen 1988). Bruun & Grönlund (1981) compared daily primary production rates obtained by a similar method to that used in this study with those measured *in situ* using 24 h incubation. The *in situ* measurements yielded on average 40 % lower values in the euphotic layer. If the 24 h *in situ* measurements are considered to estimate net production (e.g. Kuparinen 1985), then the difference should primarily be due to phytoplankton respiration. In this study phytoplankton respiration was calculated using the stable ratio between respiration and the maximum ^{14}C incorporation rate (Leppänen & Kononen 1988). According to these calculations, about half of the gross production was remineralized by phytoplankton respiration in the 0-30 m mixing surface layer. As the mixing layer was deeper than the euphotic layer (Leppänen & Alenius 1988), the proportion of algal respiration should be higher than that obtained in studies restricted to the euphotic layer only. This probably explains the smaller respiration estimates obtained by Bruun & Grönlund (1981) and Kuparinen et al. (1984) and Kuparinen (1984). The respiration of sedimenting algae below the halocline was assumed to be negligible, even though living cells were found to sink down at all depths (Leppänen & Kononen 1988).

The phytoplankton respiration estimate alone exceeded the measured total community respiration by 13-40 %, the difference being most pronounced during the peak of the phytoplankton bloom (Lahdes et al. 1988). One reason for this is the deviation from the stable respiration: Pmax ratio (e.g. Eppley & Sloan 1965). Although both processes increase along with the growth rate, the

increase in photosynthesis is relatively greater (Laws & Caperon 1976). On the other hand, the community respiration measurements are subjected to methodological errors. Long incubation times are needed to reach the sensitivity limit of oxygen determination in oligotrophic waters. Kuparinen (1985) found that oxygen consumption as a function of time is linear up to 128 hours when using incubation bottles of 300 cm^3. A deviation in linearity occurred when the respiration rates were high. The incubation times used in this study (21-95 h) were inside the above mentioned range, but the smaller size of the incubation bottles (125 cm^3) may have depressed the measured activity especially at times of intensive respiration. Holligan et al. (1984) observed that the respiration rate during the first 11 hours incubation was 1.5 times higher than that between 11 and 24 h. "Negative respiration values", i.e. a higher oxygen concentration in the incubated than in the blank bottles, occurred occasionally in this study and that decreased the integrated community respiration values (Lahdes et al. 1988). Tschumi et al. (1977) showed that the phenomenon is caused by the light shock on adding Winkler reagents to bottles previously incubated in the dark, and by the instability of the oxygen concentration in water when the bottles are filled.

Contributions of various plankton groups to overall community respiration have been analysed by size fractionating the samples by filtration (e.g. Williams 1981, Bell & Kuparinen 1984, Smith et al. 1986). It is claimed that this procedure disturbs the community metabolism (Salonen & Kononen 1984), and that filtration separates the organism only according to size and not according to their function in the food web. According to the calculated respiration rates of various plankton groups out of the total community respiration, phytoplankton was responsible for most of the respiration in the layer above the halocline, bacteria and ciliates being the most important heterotrophic groups. Kuparinen et al. (1984) and Kuparinen (1984) also report that phytoplankton respiration dominates the community respiration during the vernal growth period. Differing results have, however, been published for other sea areas during the spring. In Grand Banks (Newfoundland), microheterotrophs

dominated the respiration whereas the respiration of algae was negligible. The total community respiration consumed 33-100 % of the gross primary production (Smith et al. 1986). In Belgian coastal waters, Joiris et al. (1982) and Joiris (1985) reported that community respiration exceeded the primary production, and that phytoplankton respiration is predominant. In the open North Sea most of the gross primary production in spring was consumed by phytoplankton respiration (Weichart 1980). According to the compilation by Williams (1984 and literature cited therein), the contribution of phytoplankton respiration to total planktonic respiration ranges from 23 to 47 %, bacterial respiration from 29 to 68 %, mesozooplankton respiration from 8 to 32 %, and the respiration of protozoa from 0.1 to 11 %.

Low bacterial biomass and production during the vernal growth period is a commonly reported phenomenon in the area (e.g. Kuparinen et al. 1984, Kuparinen 1984). The bacterial abun-dances 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 1980, Virtanen 1981, 1985). The biomass values, on the other hand, are higher due to the higher coefficient used for converting bio-volume to carbon. There is no general agreement, at the moment, about the best coefficient, and the published coefficients range by a factor of about 5 (cf. Lahdes et al. 1988). The conversion factor used in this study is 2.56 times higher than that pre-viously used for this area (e.g. Kuparinen et al. 1984). However, the measurements of Kuparinen (1988) support this selection. The contribution of carbon in bacterial cell is then about three times higher than in other plankton groups, because the conversion factor of 0.11 is used for them, as recommended by the Baltic Marine Biologists (Edler 1979).

The temporal variation of bacteria and phytoplankton show tight coupling (Fig. 4), even though their coupling in the cluster dendrogram is loose (Fig. 5). Despite the fact that the amount of dissolved organic matter is considerably high after the winter (e.g. the amount of dissolved organic nitrogen during this study, Lahdes & Leppänen 1988), it is probably highly refractile and does not support bacterial growth. Bacterial

growth had therefore to be based on dissolved organic matter produced during the vernal period. Riemann & Søndergaard (1984) conclude that the total release of exudates represents a minor portion of the carbon fixed by the algae, exponentially growing algae release less exudates than stressed ones and the exudates are labile to heterotrophic assimilation. Jørgensen (1976) found that the production of dissolved organic matter by algae during optimum growth conditions (i.e. the increasing phase of the bloom) is small. The exudates of diatoms have shown to be less favourable for bacteria (Wolter 1982), and only about 60 % of the algal exudates are directly utilizable by bacteria (Jensen 1983). According to this reasoning, the amount of exudates was too small to support the estimated bacterial consumption. If direct digestion of particulate matter by bacteria is considered negligible (most of the bacteria were found to be free-living), a considerable part of bacterial consumption would have to be based on dissolved matter originating most probably from the lysis of dead algal cells. Release of dissolved organic matter by heterotrophic organisms is another possible source. According to the compilation of Peterson (1984), 14 % and 10 % of meso-zooplankton and microzooplankton carbon consumption, respectively, pass into the dissolved organic pool. In this study this would yield only ca. 15 mmol C m^{-2} in the whole 0-150 m water column.

The results of growth efficiencies (production/consumption = growth yield) published for bacteria vary over a wide range (e. g. Williams 1981, Newell et al. 1981, Linley et al. 1983). The value 0.6 used in this study may be reasonable when consumption is based on labile newly formed dissolved matter (Newell & Linley 1984 and literature cited therein).

Processes related to zooplankton were calculated using equations based on laboratory measurements and the results from areas other than the Baltic Sea. However, the temperature correction includes in most of the equations or they are derived under low temperatures. The close coupling between mesozooplankton and temperature in the cluster dendrogram (Fig. 5) reflects simultaneous development rather than the direct effect of temperature on the zooplankton processes.

The low assimilation efficiencies of both heterotrophic ciliates and mesozooplankton are somewhat contradictory with the values presented in the literature (Dagg et al. 1982, Falkowski et al. 1983 Heinbokel 1978, Jansson 1986, Smetacek 1984, Turley et al. 1986), especially during the studied growth period when fresh food was available. The calculated ingestion values most likely represent potential ingestion, since the selected size fraction of the particulate carbon is probably not totally suitable for the food items of zooplankton. On the other hand, the use of phytoplankton biomass as the amount of food items would have increased the grazing values. Ciliates are found to respond very rapidly to an increase in the food source and can form rapid blooms (e.g. Turley et al. 1986, Hagström & Larsson 1984). There is evidence that ciliates could potentially consume the whole daily primary production (Cosper & Stepien 1984) and, according to the compilation of Leppänen & Bruun (1988), the consumption of ciliates varies between 7 and 52 % of the primary production. The feeding of non-loricate ciliates has been observed to vary by 1-6 times their body weight (Beers & Steward 1970, Rassoulzadegan 1982), and they adapt their shape to that of the ingested particles (McKinnon & Haves 1961, Smetacek 1981, Rassoulzadegan 1982). Thus the restriction of the size of the food applied in this study (< 43 % of the diameter of the oral opening) may be too narrow. During the vernal growth period in the Baltic Sea large, chain-forming phytoplankton species predominate, decreasing the potential source of food for ciliates.

The Baltic Sea is characterized by a small over-wintering mesozooplankton population, and even though it starts to grow during the spring bloom, its development is too slow to utilize the vernal phytoplankton production peak (e.g. Hällfors et al. 1981). In oceanic areas the over-wintering mesozooplankton population can prevent, by grazing, the development of a distinct spring phytoplankton bloom (Dagg et al. 1982, Frost et al. 1983) or at least a large portion of the algal biomass is channeled to copepods (Conover & Mayzaud 1984, Peinert et al. 1987).

6.2 Nitrogen cycle

The reserves of total nitrogen decreased in all layers (Fig. 9). Sedimentation of particulate nitrogen through the halocline explained only 52 % of the decrease in the reserves of total nitrogen. The measured decrease in the reserves of DIN above the halocline supported ca. 80 % of the assimilation by the autotrophic organisms. The calculated remineralization of heterotrophic organisms was too small to support the rest of the autotrophic demand.
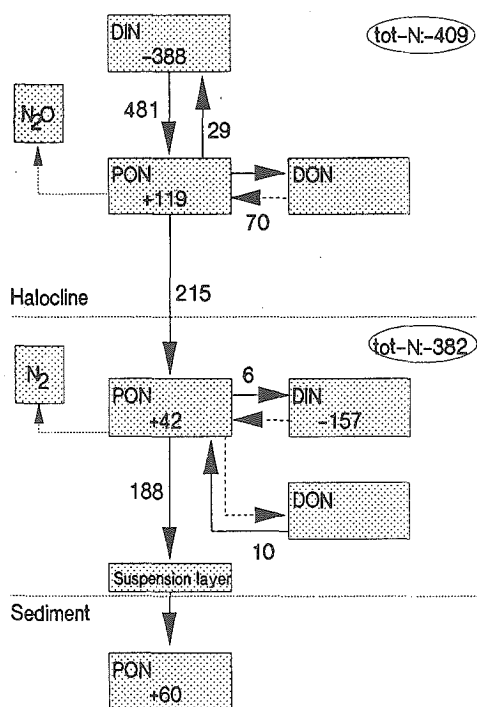
In the layer below the halocline, the measured and estimated processes could not explain the measured changes in the different nitrogen pools. Most of the measured decrease in the nitrogen reserves remained unexplained. Below the halocline resuspension balanced the potential loss of nitrogen from the sinking matter: deposition at a depth of 150 m was almost the same as at a depth of 80 m. The measured accumulation of nitrogen in the sediment surface was 32 % of the measured settling at a depth of 150 m.

Fig. 9. Nitrogen budget for the vernal growth period in the open northern Baltic Proper. The arrows represent the flows and the figures inside the boxes net change in the reserves. All values are expressed as mmolN m^{-2} period^{-1}.

The carbon and nitrogen cycles in the water ecosystem are closely coupled and mostly parallel as shown in Fig. 2. However, there are departures from the ideal Redfield C:N ratio (Lancelot

& Billen 1985) which affected the selection of the C:N ratios to convert the carbon flows to nitrogen in this study. The major causes of the nonparallelism in the carbon and nitrogen cycles according to Lancelot & Billen (1985) are the following:

- carbon uptake by phytoplankton is primarily controlled by light intensity,
- exudates have a different C:N ratio from phytoplankton,
- the C:N ratio of detritus changes during degradation, and nitrogen can be immobilized during the bacterial mineralization of organic matter,
- denitrification can result in a significant loss of nitrogen in anoxic or nearly anoxic conditions.

Owing to the nonparallelism, the use of stable stoichiometry may lead to misinterpretations. As the results of this study show, the use of stable C:N ratios can be useful, but it has to be kept in mind that it only gives a status of first approximation from which departures are important to take into account. This is probably one reason for the imbalance in the nitrogen budget.

In the nitrogen cycle, the primary formation of particulate matter was predominantly based on the initial storage of DIN in the mixed surface layer, and on its vertical transport from the intermediate layer. The contribution of recycled nitrogen through heterotrophic organisms was small, being typical for the vernal period of temperate sea areas (Båmstedt 1981, Joiris et al. 1982, Kuparinen et al 1984, Smetacek et al. 1984, Schulz et al. 1984).

In this study phytoplankton was assumed to be responsible for the DIN uptake, and bacteria were supposed to be utilizing only DON. Tempest et al. (1970), Brown et al. (1972) and Wheeler & Kirchman (1986) have shown that bacteria can be responsible for considerable DIN uptake and may compete with phytoplankton for nitrogen. According to Lancelot & Billen (1985) net uptake

instead of release of DIN occurs mostly when degradating organic matter with a C:N ratio higher than 10-17.

The calculated ammonification was small due to the low estimate for the assimilation efficiency of micro- and mesozooplankton, and the considerably high C:N ratio of the feces used (8:1). Therefore the role of these groups in nitrogen regeneration may be underestimated. The ratio of carbon and nitrogen assimilation by autotrophs to sedimentation of the respective elements indicates that nitrogen is recycled more effectively in the surface layer than carbon.

Sedimentation could explain only about half of the decrease in total nitrogen in the 0-80 m layer. The production of N_2O could be an additional reason for nitrogen loss in this layer. Using the emission rate given by Rönner (1983), this process could explain only < 1 % of the decrease in total-N. The water below a depth of 100 m was low in oxygen during most of the study period (Leppänen & Alenius 1988). This means that denitrification could take place in the 100-150 m layer at least. According to the measurements made by Rönner (1983), denitrification can transform NO_3-N to N_2 gas at a rate of 0.5-2.8 µg N l^{-1} d^{-1} when the O_2 concentration is < 0.2 ml l^{-1}. This would yield 90-500 mmol N m^{-2} during the study period, and could balance the nitrogen budget below the halocline. A decrease in NO_3-N, which would indicate denitrification taking place, was however not clearly evident until the end of May.

6.3 Sinking of particulate matter

The accumulation of particulate matter in the water column was small during the whole vernal period (April-May), and most of the phytoplankton bloom sedimented out from the layer above the halocline: 64 % and 45 % of the particulate primary production of carbon and nitrogen, respectively. Neither the weak thermocline nor the permanent halocline presented any barrier to the main particle flux. The effect of resuspended matter was small most probably above the halocline (Leppänen 1988). Near the bottom, at a depth of 150 m, resuspension contributed ca. 40 % and 10 % to the total deposition of carbon and nitrogen,

respectively. The low accumulation of carbon and nitrogen in the sediment surface indicates that the sinking matter first accumulates in the form of a suspension layer above the actual sediment surface. The suspension layer is an intermediate between bottom water and the sediment surface, a transition zone from water with a high content of particulate matter to an extremely soft sediment with a water content exceeding 90-95 % (Grasshoff & Voipio 1981). Its thickness is difficult to determine but may be characterized by the change in the sediment dry matter content (Fig. 10). The accumulation of a high amount of organic matter creates favourable conditions for degradation processes. Unfortunately this layer could not, for technical reasons, be sampled in the study.

When the assimilation and sedimentation of carbon and nitrogen during the vernal growth period are compared with some other localities in the Baltic Sea (Fig. 11), about 30-60 % and 20-40 % of the particulate primary production of carbon and nitrogen, respectively, are lost through sinking from the euphotic layer. The differences in the assimilation:sedimentation ratios do not necessarily reflect a different recycling pattern. For instance, methodological differences (sediment trap
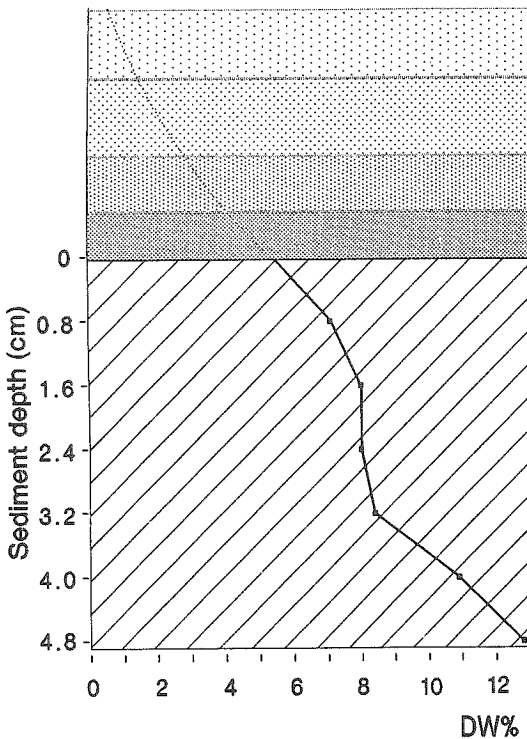
Fig. 10. Distribution of dry weight content (%) of a sediment core taken from the sampling site (Naik & Poutanen 1984). The suspension layer is hypothesized as lying above the actual sediment surface.

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 this study, in the Kiel Bight and in Tvärminne (in 1983). Preservation was used in the sedimentation traps in Kiel, and the effect of decomposition was corrected in this study as well in Tvärminne by an empirical equation (cf. Leppänen 1988). The uncorrected values of this study are close to those measured in Askö and Tvärminne, when no preservation/ correction was used.

It is possible to differentiate pelagic communities into "bloom" and "steady state" types according to the source of nutrient supply (Yentsch at al. 1977). In the bloom type primary production is based on "new" nutrients from outside the euphotic layer, while in the steady-state type nutrients are recycled through heterotrophs within the euphotic layer and production is based on regenerated nutrients. The concept of new and regenerated nutrients was presented by Dugdale & Goering (1967), and the two were differentiated in terms of nitrate
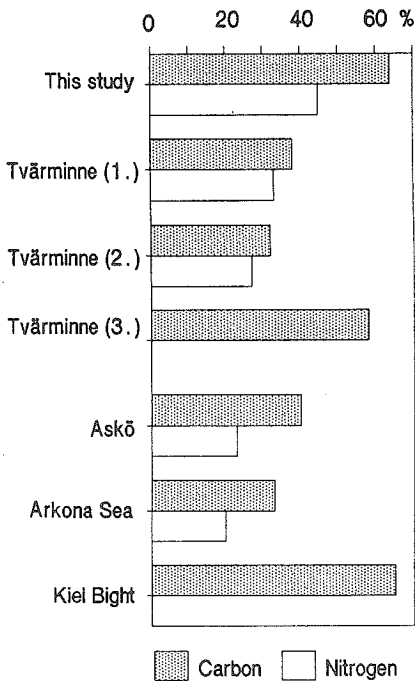
Fig. 11. The ratios of carbon and nitrogen assimilation and sedimentation (%) during the vernal growth period in different parts of the Baltic Sea. The values for the Tvärminne area are 1. from Forsskåhl et al. (1982), 2. from Kuparinen et al. (1984) where C:N ratios of the sinking matter was 8:1 (Laakkonen et al. 1981), and 3. from unpublished results of the Finnish Institute of Marine Research, measured in 1983. Values for Askö and Arkona Basin are from Wulff et al. (1986) and for Kiel Bight from Peinert et al. (1982) and Smetacek et al. (1984).

and ammonia, respectively. This does not strictly hold true in The Baltic Sea, where remineralized nitrogen can accumulate as ammonia below the halocline. The organic matter sedimenting out

from the euphotic layer is supposed to be equivalent to new production (Eppley & Peterson 1979). In the Baltic Proper the production during the vernal growth period is predominantly "new", based on the initial nutrient reserves that accumulated in the layer above the halocline during the previous winter. 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, rather than its duration, due to the low heterotrophic activity, then in this case sedimentation could remove most of this stored component from the euphotic layer. In areas which favour denitrification this process could then transform the nitrogen to N_2 and remove it from the system. This might explain why no clear signs of eutrophication have been observed in the open Baltic Sea (e.g. Wulff et al. 1986) 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. Changes in the duration of the bloom period and in the plankton community may, however, modify the cycling pattern of organic matmatin the food web. As already mentioned, ciliates are able to respond rapidly to the phytoplankton blooms, showing short generation times even at low temperatures. Therefore the increase in the duration of the vernal bloom or the decrease in the size of the phytoplankton species might increase the food intake of ciliates and enhance recycling of nutrients in the surface layer. This would result in a decrease in the sedimentation of particulate matter and, in this way, increase the pelagic production level after the vernal period as well.

7. CONCLUSIONS

Due to the scarcity of the measured processes the quantification of the different pathways of carbon and nitrogen cycle in this study is rough. Nevertheless, it clearly shows that, during the vernal growth period in the open Baltic Proper the primary formation of particulate matter is predominantly based on the

initial reserves of inorganic nutrients in the euphotic layer
and in the intermediate layer. Ciliates and bacteria are the
most important heterotrophic organisms. Most of the
decomposition of organic matter takes place in the same water
layer where it is produced and then again, after leaving the
euphotic layer, near the sediment surface rather than during the
sinking. This means that relatively almost the same amount of
sinking matter reach the bottom in deep areas as in shallow
areas. The sinking matter accumulates as a suspension layer
rather than as a deposit directly on the bottom sediment. The
mass sedimentation of the particulate matter is an effective
mechanism in removing nutrients from the euphotic layer, stored
during the previous winter, and transporting them to the benthic
system. The structure and function of the pelagic food web
determines how much nutrients from the initial reserves are
retained for later growth phases in the surface layer. The
vernal growth period holds a key position in following the
effect of the observed increase in the winter nutrient level on
the Baltic Sea ecosystem. To achieve reliable quantification of
the role of heterotrophic organisms, direct measurements of the
food intake of the most significant consumers, ciliates,
juvenile copepods and heterotrophic flagellates, as well as
bacterial production, should be performed during the vernal
growth period. Quantification of the sinking flux of particulate
matter offers a simple tool for monitoring the changes in the
pelagic system.

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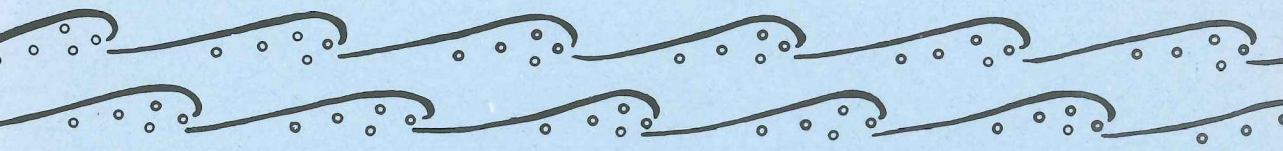   Prog. Ser. 33:265-277.

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