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Nitrogen dynamics of a cyanobacteria bloom in the Baltic Sea: new versus regenerated production

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ABSTRACT: A bloom of nitrogen-fixing filamentous cyanobacteria was studied at a drift station in the Baltic Sea in July–August 1982. Uptake of combined nitrogen nutrients (ammonium, nitrate and urea) was measured using ^{15}N labelled substrates, and was around 450 nmol l^{-1} d^{-1}. New production (based on uptake of nitrate and N_2) was only 27 % of total N uptake. The major nitrogen source was ammonium, which constituted about half of the total nitrogen uptake measured. The nitrogen fixers seemed to rely mainly on N_2 for their nitrogen demand, while the major part of nitrogen assimilation was carried out by smaller non-nitrogen-fixing phytoplankton, mainly utilizing regenerated nitrogen. The dissolved organic matter had a molar C/N ratio of over 20, and seemed mainly to be refractive. The particulate material had a C/N ratio of 8.5, and a N/P ratio of 19. From ATP measurements, the amount of 'living carbon' was estimated to be 23 % of the particulate carbon. Doubling time of the living fraction of the particulate nitrogen was approximately 1 d.

INTRODUCTION

The limiting nutrient for primary production in the pelagic marine environment is generally considered to be nitrogen. This seems to be true also for the brackish Baltic proper (Larsson 1984). This is indicated by e.g. the low molar ratio of inorganic nitrogen to phosphate (1.3 to 4) before the spring bloom (Fonselius 1978) and enrichment experiments with Baltic waters (Granéli & Granéli 1987). A substantial nitrogen input – 100000 to 130000 tons of N yr^{-1} (Lindahl et al. 1978, Rinne et al. 1978, Brattberg 1980), i.e. one-tenth of the total nitrogen input to the Baltic Sea (Larsson et al. 1985) – comes from blooms of filamentous cyanobacteria, of which *Nodularia spumigena* Mertens is often the most important nitrogen fixer. The blooms occur regularly in July and August every year, favoured by warm and calm weather after a turbulent period bringing phosphate to the surface water (Niemi 1979).

Most marine phytoplankton communities rely heavily on reduced-nitrogen sources such as ammonium and urea regenerated from organic compounds within the photic layer. The concept of 'new' and 'regenerated' production, based on the use of different nitrogen sources, was introduced by Dugdale & Goering (1967), and has been further discussed by Eppley & Peterson (1979). In the open sea, the amount of 'new' nitrogen uptake can give an estimate of the loss to deeper waters through sedimentation. In the present case, the nitrogen for 'new' production would be nitrate and dinitrogen gas (N_2), and the 'regenerated' forms would be ammonium and urea. The presence of a large population of nitrogen fixers might lead to the assumption that dinitrogen gas is the dominating nitrogen source. There are, however, several reasons why one should also consider the uptake of combined nitrogen sources. Firstly, organisms that fix nitrogen gas will use other nitrogen sources, especially reduced nitrogen like ammonium, if present. Secondly, in this area, there is usually a large population of primary producers present which is not capable of nitrogen fixation. These are mainly small flagellates, which have a high activity per biomass (Larsson & Hagström 1982).

In 1982 a heavy bloom, with *Nodularia spumigena* as the major nitrogen-fixing species, was followed in a drift study, during which the same water mass was sampled over a 1 wk period. This paper deals with the uptake of the most important combined nitrogenous nutrients, i.e. ammonium, nitrate and urea. In addition, concentrations of carbon and nitrogen in the particulate and dissolved matter are presented.

MATERIALS AND METHODS

The study was carried out between 26 July and 1 August 1982, as part of a joint Soviet-Swedish investigation concerning the physical and biological dynamics

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during a cyanobacteria bloom, on board the Soviet research vessel *Georgii Ushakov*. Stations were chosen by following a drogue at 15 m depth near the Landsort deep in the Baltic proper (starting at 58° 49.8' N, 19° 04.7' E and ending at 58° 35.3' N, 18° 40.5' E). Water was collected with a 30 l PVC Niskin-bottle at around 0800 h local time. Nutrients (ammonium, nitrate, urea, and phosphate) were analysed on board by the method of Grasshoff (1976). All filtration and separation into particulate and dissolved fractions was made through Whatman GF/F glass fibre filters, precombusted at 450 °C for 2 h to remove organic contamination. The filtrate was frozen for later analyses of dissolved organic carbon and nitrogen and the collected particulate material was dried in an evacuated desiccator with silica gel and stored dry until analysis. The analyses of dissolved and particulate matter were performed within 3 mo from sampling.

Analyses of particulate material. Total amounts of particulate carbon (PC) and nitrogen (PN) were determined with a Carlo Erba Model 1106 Elemental Analyzer. The phosphorus in the particulate matter (PP) was wet-oxidized to orthophosphate by autoclaving at 120 °C for 60 min, using persulfate as oxidant. This is essentially the method described by Valderrama (1981) for determinations of total phosphorus. ATP was extracted from the particulate material using boiling Tris-EDTA according to Lundin & Thore (1975) and analysed by the bioluminescence method, using Sigma FLE-50 enzyme extract and a Packard Picolite Model 6100 ATP-analyzer.

Analyses of dissolved organic matter. Total dissolved nitrogen was analysed as nitrate after wet oxidation in UV-radiation, using the method described by Enoksson & Samuelsson (1987). To obtain the concentration of dissolved organic nitrogen (DON), the amount of inorganic nitrogen was subtracted. Dissolved organic carbon (DOC) was analysed with an infrared carbon analyser (Beckman Total Organic Carbon Analyzer 915 B) by the Askö Laboratory, University of Stockholm.

Uptake rates of ammonium, nitrate and urea. These experiments started on July 27. Water samples from 0, 5, 10, and 15 m depth were enriched with 0.1 or 0.2 µmol N l^{-1} (95 atom % ^{15}N) of the ^{15}N labelled nitrogen compound of interest and incubated in 2.6 l polycarbonate bottles on deck. The samples were cooled with flowing surface water and the light conditions corresponding to the sampling depths were obtained with neutral density screens. Incubations were carried out around noon and lasted for 4 to 6 h. The particulate material was collected and converted to N_2 gas by Dumas oxidation in discharge tubes, according to Kristiansen & Paasche (1982). The $^{14}N/^{15}N$ isotope ratio in the N_2 was analysed by emission spectrometry (Statron NOI-5 ^{15}N Analyzer).

When *in situ* nutrient concentrations are low, the addition of a labelled nutrient might induce an increased uptake rate. The measured uptake values were corrected for this by using Monod kinetics. The K_s-values used, 0.22 and 0.02 µmol N l^{-1} respectively for ammonium and nitrate, were calculated from incubation series with different nutrient additions made during a later part of the cruise. For corrections of the urea uptake values a K_s-value of 0.27 µmol N l^{-1} was used. This figure is an average derived from summer studies in the North Sea (Kristiansen 1983). Daily nitrogen uptake was calculated by assuming a light dependency for the light period uptake (16 h), which means that the nitrogen uptake per unit of irradiance (Kipp & Zonen pyranometer) was constant over the day. To this was added a dark uptake estimated to 20 % of the average light period uptake. We consider the estimate of 20 % uptake in the dark to be a conservative estimate when comparing with other studies, e.g. during a similar cyanobacteria bloom in the nearby Askö area in 1984, the nitrogen uptake rate at midnight was 30 % of that at midday (K. Pettersson & F. Sörensson unpubl.).

RESULTS

Hydrography

The nutrient-depleted upper water mass had a temperature of 17 to 18 °C and was well separated from the deeper water by a sharp thermocline with a gradient of about 1 C° m^{-1}, located at 14 to 18 m. Salinity was around 7 ‰ down to the halocline at 70 m.

Nutrients

All nutrient concentrations above the thermocline were very low: 0.03 to 0.05 µmol l^{-1} of phosphate, 0.11 to 0.21 µmol l^{-1} of ammonium, and 0.17 to 0.30 µmol l^{-1} of urea-N. The nitrate concentration was always at or below the detection limit (0.10 µmol l^{-1}; Thorstensson 1987).

Particulate material

The average amounts of particulate carbon and nitrogen above the thermocline were respectively 22.6 µmol C l^{-1} (SD 1.2, n = 71) and 2.66 µmol N l^{-1} (SD 0.14, n = 71), with a PC/PN ratio of 8.5 (Table 1). Below the thermocline, the concentrations dropped to about one-fourth of the surface values. There was a slightly increased PC/PN ratio below 25 m, the average ratio being 9.9. This could be due to a faster mineralization of nitrogen than of carbon in sediment-

Table 1. Mean values of particulate C, N, and P, and dissolved organic C and N for depth interval 0 to 15 m or individual depths. All concentrations in μmol l^{-1}

Date (1982) and depth	Particulate material					Dissolved organics		
	C	N	P	C/N	N/P	C	N	C/N
26 Jul								
0–15 m	26.0	2.94	0.17	8.8	18	424	14.6	29
20 m	20.5	2.20	0.11	9.3	20	706	14.4	49
30 m	7.9	0.72	0.03	11.0	28	350	13.9	25
40 m	5.0	0.42	0.02	11.9	21	398	13.9	29
50 m	8.6	0.73	0.03	11.8	25	383	17.0	23
60 m	6.2	0.70	0.05	8.9	14	370	13.6	27
70 m	8.4	0.74	0.09	11.4	9	414	17.5	24
27 Jul								
0–15 m	20.8	2.48	0.16	8.4	15	452	15.9	28
20 m	17.1	1.77	0.12	9.7	14	447	15.7	28
30 m	6.2	0.69	0.04	9.0	20	342	20.4	17
40 m	6.6	0.54	0.01	12.2	49	304	16.5	18
50 m	4.5	0.49	0.04	9.1	14	290	15.9	18
60 m	4.4	0.49	0.02	9.0	31	343	15.0	23
70 m	5.7	0.55	0.02	10.4	26	462	–	
80 m	6.8	0.68	0.03	10.0	23	364	15.1	24
90 m	5.9	0.73	0.08	8.1	10	301	12.9	23
28 Jul								
0–15 m	24.3	2.88	0.13	8.4	22	410	15.7	26
20 m	23.6	2.78	0.18	8.5	16	355	13.6	26
29 Jul								
0–15 m	21.0	2.42	0.15	8.7	16	344	14.8	23
20 m	19.2	2.32	0.14	8.3	16	272	14.7	19
30 m	6.4	0.67	0.04	9.6	17	474	13.9	34
40 m	6.3	0.65	0.04	9.7	15	246	16.8	15
50 m	4.7	0.48	0.04	9.8	12	366	16.7	22
60 m	4.7	0.51	0.04	9.2	12	506	15.7	32
70 m	7.3	0.79	0.05	9.2	17	–	14.7	
80 m	6.7	0.66	0.04	10.2	17	–	14.0	
90 m	9.2	1.02	0.06	9.0	16	–	14.5	
30 Jul								
0–15 m	21.7	2.59	0.13	8.4	21	339	13.9	24
20 m	19.5	2.34	0.15	8.3	15	282	13.8	20
31 Jul								
0–15 m	21.8	2.65	0.12	8.2	23	369	13.4	28
20 m	12.7	1.35	0.11	9.4	12	324	13.3	24
25 m	9.7	1.11	0.06	8.7	20	359	14.5	25
1 Aug								
0–15 m	–	–	0.15			315	14.2	22
20 m	–	–	0.18			345	15.9	22
25 m	–	–	0.17			452	15.1	30

ing material. The average concentration of particulate phosphorus was 0.142 μmol l^{-1} (SD 0.011, n = 83) in the upper water mass, also showing a marked decrease below the thermocline. The PN/PP ratio was more variable than the PC/PN ratio and did not differ significantly above and below the thermocline. The PN:PP ratio was 19:1 in the upper water mass. The average ATP value above the thermocline was 190 ng l^{-1}. There was usually a small peak in concentration around the thermocline, at 15 and 20 m depth. Below 25 m the average ATP content was approximately half of the surface value.

Dissolved organic material (DOM)

Neither the dissolved organic carbon (DOC) nor nitrogen (DON) showed any significant concentration differences that could be correlated with density stratification. The concentrations of DOC were usually

between 300 and 500 µmol l^{-1}, with a slight decrease in the surface values with time (Table 1). Concentrations of DON were generally in the range of 13 to 18 µmol l^{-1} throughout the water column, showing a slight decrease with time. The C/N ratio of DOM was generally above 20.

Uptake of nutrients

The results indicated a 'steady state' situation for the uptake of nitrogenous nutrients throughout much of the 6 d drift study. The uncorrected results are shown in Table 2, and those corrected with Monod kinetics in Table 3. In the following text only the corrected rates will be used. Mean values (0 to 15 m depth) for the total uptake of combined nitrogen were 387 to 523 nmol l^{-1} d^{-1}, and showed no clear trends with time. Ammonium was the dominant nitrogen source, accounting for 37 to 67 % of the uptake of combined nitrogen, followed by urea-N, 24 to 44 %, and nitrate, 9 to 19 %.

Table 2. Drift study stations. Sum of uptake and percentages of the individual nitrogen sources of the sum. Means for depth interval 0 to 15 m

Date (1982)	Sum of uptake (nM h^{-1})	(nM d^{-1})	Percentage of uptake Ammonium	Nitrate	Urea-N
Jul 27	40	511	42	16	42
28	57	570	65	8	28
29	48	601	57	12	31
30	51	619	59	9	32
31	8	645	57	10	33
Aug 1	53	486	56	11	33
Mean	51	572	56	11	33
SD	6.6	62.5	8	3	5

DISCUSSION

The pronounced differences in amount of particulate matter showed that the water mass above the thermocline was very effectively isolated from the water below. Transport of nutrients into the upper water must therefore have been very small. This was also shown by Wilmot (1987) who, based on nutrient data and current measurements from the cruise, calculated that vertical transport was so slow that a period of 90 d was needed to double inorganic nutrients above the thermocline through entrainment. Production in the upper water mass had, except for input of N_2 to nitrogen-fixing organisms, to rely on regenerating processes.

Besides inorganic nutrients, another source for phytoplankton growth is dissolved organic matter, which dominated the organic nitrogen in the upper water mass to more than 80 %. At present, we lack appropriate methods for determining the amount of dissolved organic matter which is easily utilized by microorganisms, although the homogenous distribution of dissolved organic nitrogen and carbon throughout the water column indicates that the major part is degraded slowly and is not closely coupled to the biological processes in the photic zone. Ogura (1975) estimated the more stable, refractive part of the dissolved organic carbon to be 80 to 90 % in open sea water. It is probable that this part is even larger in the Baltic due to a discharge of refractive organic substances of terrestrial origin (Fonselius 1972). This is reflected in the high C/N ratio, generally above 20, of the dissolved organic matter (Table 1) which can be compared to for example the value of 8 given as a coastal average by Sharp et al. (1982). Gabrielson & Hamel (1985) showed that *Nodularia spumigena* cells, when decomposing, rapidly released both dissolved organic and inorganic nitrogen and phosphorus in forms available to other algae; thus decaying cells could constitute an important source for regeneration of nutrients. Some of the

Table 3. Same as Table 2, but corrected for enrichment effects. Calculated maximal uptake rate values (V_{max}) expressed as nmol l^{-1} h^{-1}, and individual nitrogen sources as percent of corrected total nitrogen uptake

Date	Sum of uptake (nM h^{-1})	(nM d^{-1})	Ammonium V_{max}	%	Nitrate V_{max}	%	Urea V_{max}	%
Jul 27	31	450	34	37	7	19	26	44
28	45	448	65	67	5	9	27	24
29	36	457	50	58	6	14	26	28
30	40	490	54	60	5	109	27	30
31	47	523	56	59	6	11	31	30
Aug 1	42	387	51	58	6	13	29	29
Mean	40	395	52	56	6	13	28	31
SD	5.9	52.7	10.1	10	0.9	4	2.2	7

regenerated nutrients might have been a suitable source for heterotrophic bacteria. Wheeler & Kirchman (1986) showed from ^{15}N uptake experiments off the coast of Georgia that about 80 % of the measured ammonium uptake could be due to bacterial assimilation. However, results from the present cruise (Hagström 1987) indicate that the bacteria played a minor role, having a low growth rate and a very low biomass.

The higher concentration of particulate matter above the thermocline indicated that the major part originated from biological activity in the photic zone. Although the total particulate carbon analysed comprised both living and dead fractions, ATP is only associated with the living, and may be used with some caution to partition between the 2 fractions. Applying the factor 250 for converting the ATP content to 'living carbon' (Holm-Hansen 1970) would give, as an average, 4 µmol C l^{-1} as living biomass in the water above the thermocline. This would constitute about 20 % of the total particulate carbon, which seems low when comparing with e.g. Gordon et al. (1979) who found 26 to 45 % when using the same conversion factor. Gabrielson & Hamel (1985) estimated the refractory part of *Nodularia spumigena* to be 34 % of the dry weight, and one source of the large proportion of dead particulate matter could be partly degraded cyanobacteria. The C/N ratio of 8.5 therefore seemed to largely reflect partly decomposed dead matter, and this ratio in the living organisms could well be lower. The PN : PP ratio of 19 : 1 indicated no pronounced imbalance of nitrogen to phosphorus, when compared to the ratio of 16 : 1 for phytoplankton composition (Redfield et al. 1963).

The average molar relation between measured uptake rates of carbon, measured by the ^{14}C-technique (Lindahl 1987), and nitrogen was 4.4 for combined nitrogen and 3.7 if the dinitrogen fixation (Lindahl 1987) was included. This is low when compared to the classical value of 6.6 for phytoplankton composition (Redfield et al. 1963), or to the mean C/N ratio of 8.5 in the particulate material. Lower uptake ratios than 6.6 were also observed by e.g. Eppley et al. (1973) in the Central Gyre of the North Pacific (3.0 to 7.7, integrated over the 150 m euphotic zone). The low assimilation ratio could indicate that the phytoplankton did not experience nitrogen limitation. It could, however, also indicate overestimation of the nitrogen uptake and/or underestimation of the carbon uptake.

One possible source of error for nitrogen uptake rate calculations found by e.g. Murphy (1980) could be that the biologically available *in situ* nutrient concentration was overestimated by the chemical analysis. This would lead to an overestimation of nitrogen uptake, especially at low additions of labelled substrate. This is probably the case for the nitrate uptake, where we used the detection limit (0.1 µmol l^{-1}) as the *in situ* ambient concentration, even if the concentration probably was lower. According to our kinetic studies during a later part of the cruise, the phytoplankton apparently had a low V_{max} for nitrate uptake, which indicated an adaptation to low concentrations. The addition (0.1 µmol l^{-1}) of nitrate to the water sample therefore only resulted in a small increase in uptake. The average nitrate uptake rate during our study was 59 nmol N l^{-1} d^{-1}. If the supply of nitrate through entrainment is negligible, the only other source available is nitrification. The highest nitrification rate obtained by Enoksson (1986) above 50 m was 9 nmol N l^{-1} d^{-1} in June (i.e. before the bloom period), in the same year and the same area as this study. Possible explanations for this apparent discrepancy between uptake and supply of nitrate could have been higher nitrification rates during our study period, or overestimate of the nitrate uptake rate.

Another feature that might be explained by overestimation of the biologically available *in situ* concentration was the results from the kinetic experiments on urea uptake performed during a later part of the cruise. The calculated rates decreased with increasing concentration, and no K_s or V_{max} could be determined. For this reason we used a K_s value from the literature. One approach, used by e.g. Murphy (1980), is to lower the value for *in situ* nutrient concentration used in the calculations of uptake until Monod kinetics is achieved. When lowering the value for ambient urea concentrations to 0.05 µmol N l^{-1} instead of the measured value of about 0.20 µmol N l^{-1}, the resulting kinetic constants gave an uptake of 30 % of the measured urea uptake rate. Applying this to the present data would give a corrected uptake rate of 57 nmol urea-N l^{-1} d^{-1}. Only 13 % of the total nitrogen taken up would then be urea, while nitrogen fixation would constitute 19 % of the total. Since an overestimation of the concentrations cannot be proven, we have used the uptake calculated from the measured urea concentrations throughout this paper.

On the other hand, the isotope dilution effect caused by regeneration of unlabelled nutrients during the incubation, probably most important for ammonium (Glibert et al. 1982, Harrison & Harris 1986), would lead to underestimation of the uptake rate. This error would, however, be expected to be more pronounced for long incubations (i.e. 24 h), while ours lasted 4 to 6 h. The effect of diluting the ^{15}N-labelled ammonium through regeneration would, if the regeneration rate equalled the uptake, underestimate our ammonium uptake values by at most 10 % under the prevailing conditions. We have not corrected our uptake data for this effect, but it would not have influenced the general conclusions. Nutrient concentrations and uptake rates showed little change over the 6 d drift study, and

therefore to maintain a steady state, regeneration would have had to be of the same size as uptake.

To use the concept of 'new' versus 'regenerated' production introduced by Dugdale & Goering (1967), one must be able to distinguish between the supply of the 2 classes of nitrogen nutrients. In waters where significant external sources of regenerated nutrients exist, the concept may be of no practical use. In the present case, all sampling was carried out far from the coast, and in stratified water masses with depths always exceeding 80 m. Any influence of ammonium or urea from land or sediments could have been of no practical consequence, and the use of uptake of these nutrients for estimating regenerated production is justified. The 'new' production, based on uptake of nitrate and N_2, constituted 27 % of the overall nitrogen uptake. The measured sedimentation rate, 85.7 nmol N l^{-1} d^{-1}, during the same study (Cederwall 1987) corresponded to 59 % of the new production. The difference could be due to degradation of organic material inside the sediment traps, to incomplete capture of sedimenting matter, to overestimation of nitrate uptake (see above), or to a temporary accumulation of nitrogen into different fractions in the upper water mass (e.g. floating patches of decaying cyanobacteria which were seen on the sea surface). The accumulation in the upper water mass would be equivalent to 0.3 µmol N l^{-1} during the investigated period, which is within analytical errors when analysing all nitrogen fractions.

The finding that ammonium was the preferred nutrient source, followed by urea, is in agreement with other studies from different parts of the world (e.g. McCarthy & Eppley 1972, Harvey & Caperon 1976). Even during this study, when there was a bloom of cyanobacteria, the nitrogen fixation rate, 86 nmol N l^{-1} d^{-1}, measured on parallel samples (Lindahl 1987), only reached 16 % of the total nitrogen (NH_4^+ + NO_3^- + urea-N + N_2) utilization, while the ammonium uptake constituted 47 %. The low contribution of nitrogen fixation to total nitrogen uptake might be explained by a rapid regeneration of reduced nitrogen, mainly utilized by the large number of small (less than 10 µm) phytoplankton (Wallström 1987). These were responsible for 80 % of the primary production, but no significant nitrogen fixation was shown in this fraction (Lindahl 1987).

The turnover time of particulate organic nitrogen was 3.8 d if nitrogen fixation is included. The living organisms were estimated to constitute 23 % of the total particulate organic nitrogen or 0.6 µmol l^{-1}, based on ATP measurements and assuming a ratio between C and N in phytoplankton of 6.6 : 1 (Redfield et al. 1963). The amount of nitrogen in the living phytoplankton has been calculated from microscopic wet weight estimates (Wallström 1987) assuming carbon content to be 11 % of wet weight (Edler 1979) and a Redfield C:N ratio. The phytoplankton biomass would then constitute on average 0.56 µmol N l^{-1}, i.e. 21 % of the total PN, giving a growth rate for the phytoplankton population of one doubling per day.

If we assume: (1) that total nitrogen uptake in the size fractions larger and smaller than 10 µm is proportional to primary production in these fractions, (2)

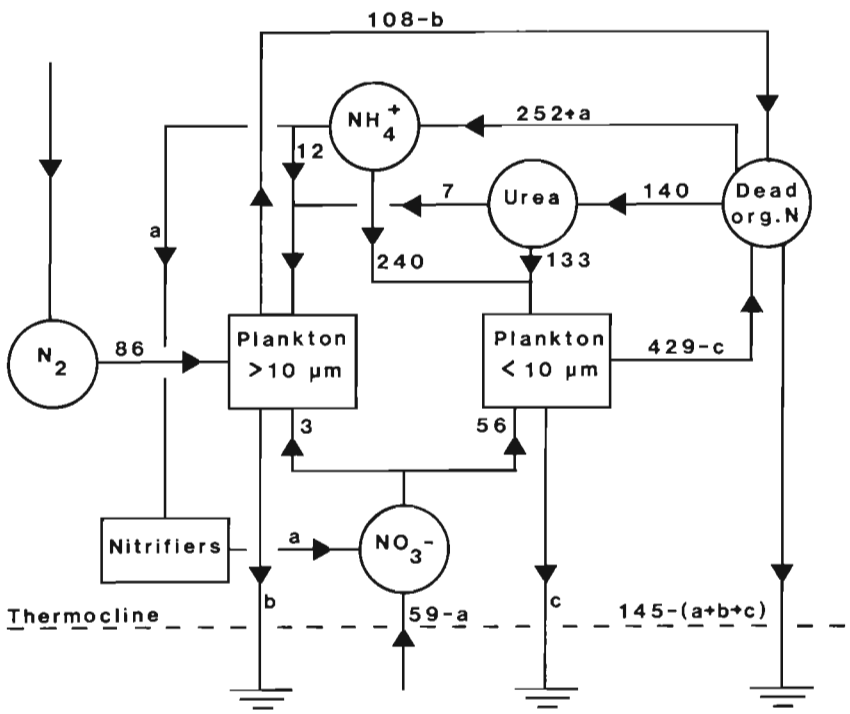

Fig. 1. Model of nitrogen transformations above the thermocline, assuming steady-state conditions and N-uptake in the 2 size fractions in the same proportions as C-uptake (Lindahl 1987). Only the fraction larger than 10 µm is assumed to fix N_2. Rates are given in nmol N l^{-1} d^{-1}. Rates a (nitrification), b and c (sedimentation of the 2 plankton compartments) are unknown

that the size fraction smaller than 10 µm does not fix N_2, and (3) that we have steady-state conditions, then a model of the nitrogen transformations above the thermocline can be constructed. This is shown in Fig. 1. According to this, small algal cells account for an N uptake of 429 nmol N l^{-1} d^{-1}, which means that they are responsible for 95 % of the total uptake of combined nitrogen. This is in good agreement with our measurements in the Askö area in the same season in 1984 and 1985, when more than 80 % of the uptake of combined nitrogen was associated with the fraction smaller than 10 µm (K. Pettersson, E. Sahlsten and F. Sörensson, unpubl.). For the fraction larger than 10 µm, nitrogen fixation would then account for 80 % of the nitrogen taken up. This could well be the case, since this fraction was dominated by filamentous cyanobacteria, capable of nitrogen fixation (Wallström 1987).

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