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Nitrogen cycling in the Barents Sea—Seasonal dynamics of new and regenerated production in the marginal ice zone

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Abstract

The uptake rates of nitrate, ammonium, and urea were measured with a ^{15}N technique during seven cruises in the marginal ice zone (MIZ) in the Barents Sea in 1984–1988. The results from all the cruises were pooled to obtain means for the prebloom, bloom, transition, and postbloom periods. New production—nitrate uptake as percent of total uptake—was high (92–96%) during the prebloom and bloom periods and decreased thereafter. Regenerated production—summed ammonium + urea uptake as percent of total uptake—increased through the bloom cycle and was at its maximum (75–93%) during the postbloom period. New production (as percent of the total) was higher in the ice-filled parts than in the ice-free parts, especially during the postbloom period. Nitrate uptake rates, however, were highest (9–25 nM h^{-1}) in open and ice-free parts during the bloom and transition period. Mean growth rate of phytoplankton-nitrogen was 0.5 doubling d^{-1} during the bloom and ranged from 0.3 to 0.4 doubling d^{-1} after the bloom. We hypothesize that primary production in the MIZ is not nutrient limited but is proportional to phytoplankton standing stocks.

Primary production in Arctic waters is characterized by a marked seasonality. Primary production increases during the spring as light availability increases and the water column stabilizes. Nutrient levels are maximal in the winter and decrease rapidly during the spring bloom. The concomitant depletion of surface nitrate and reduction of primary production has led to the hypothesis that primary production becomes nitrogen-limited during the Arctic summer (Harrison and Cota 1991). Zooplankton abundance also varies seasonally and follows the same pattern as primary production with a 2–3-week lag period (Skjoldal et al. 1987). Grazing by calanoid copepods consumes 5–20% of primary production in spring and 65–90% in summer (Eilertsen et al. 1989). In addition, grazing by microzooplankton becomes an important fate of phytoplankton production in summer (Vernet 1991).

Phytoplankton use both new (nitrate) and regenerated (ammonium and urea) nitrogen, and evaluation of nitrogen limitation should consider the availability of all nitrogenous nutrients. In temperate (Kokkinakis and Wheeler 1987) and Arctic waters (Harrison and Cota 1991), there is often a seasonal or upwelling-related shift from predominantly nitrate-supported production to predominantly ammonium- and urea-supported production. Regenerated nutrients are produced directly from grazing, and phytoplankton frequently use regenerated forms of nitrogen in preference to nitrate (Wheeler and Kokkinakis 1990). Thus, high new production during spring blooms and upwelling periods could result from a combination of high nitrate availability and low grazing pressure–low nitrogen regeneration. High regenerated production, on the other hand, could be due to either low nitrate availability or high grazing pressure and high ammonium regeneration.

Despite exhaustion of nitrate and reduction in phytoplankton productivity and biomass during summer in Arctic surface water, other physiological evidence indicates that phytoplankton may not be nitrogen limited. C:N assimilation ratios in the eastern Canadian

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Arctic are close to the Redfield ratio, suggesting little or no nutrient stress (Harrison et al. 1982). Kinetic studies and high growth rates of ice algae in Barrow Strait both indicate nutrient-sufficient conditions for primary production (Harrison et al. 1990). The absence of "surge" or enhanced uptake in the eastern Canadian Arctic (Harrison 1983) and in the open Barents Sea (Kristiansen and Lund 1989) also demonstrates nitrogen sufficiency for phytoplankton. In each of these environments, phytoplankton growth during much of the season is supported by ammonium and urea. Ammonium and urea are often present at low concentrations but are regenerated rapidly enough to maintain high phytoplankton growth rates. Thus, seasonal decreases in primary production could result from decreases in standing stock rather than changes in instantaneous growth rates of the phytoplankton.

In the present study, we examine the seasonal variation in nitrogen uptake in the marginal ice zone (MIZ) of the Barents Sea. An ice-edge phytoplankton bloom trails the receding ice edge during summer in the Barents Sea (Rey and Loeng 1985). Phytoplankton biomass and productivity are high during such blooms in the Arctic and Antarctic, and nitrate has been shown to be an important source of N for phytoplankton growth in the MIZ (Smith and Harrison 1991). Kristiansen and Lund (1989) found that nitrate was the most important source of N for phytoplankton growth in the outer part of the MIZ in the Barents Sea in May–June. Most of their samples were, however, collected south of the MIZ.

We examine nitrogen dynamics in this region to address three questions: Is there a change in the dominant nitrogen source used by phytoplankton over the seasonal cycle? Is there any physiological evidence for nitrogen limitation after the spring bloom? Is there any correlation between seasonal changes in nitrogen dynamics and food-web processes?

Methods

Sampling—Nitrogen uptake experiments were performed during seven cruises to the MIZ in the Barents Sea (Fig. 1). All samples were collected in the euphotic zone, usually in surface water (0.25–15 m) and occasionally at 20–50-m depths, with Niskin bottles fitted with silicon springs or by filling polyethylene carboys at 0.25-m depth by hand from the ice edge. Water from repeated casts at the same depth was mixed before subsampling and transferred to 1- or 2.4-liter polycarbonate incubation bottles within 2 h of collection.

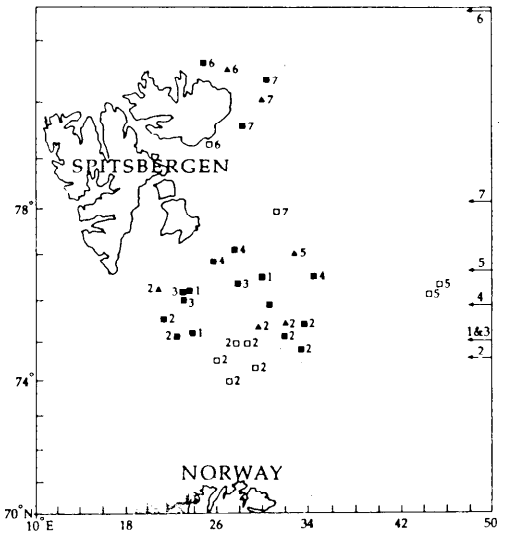

Fig. 1. Station locations in the close pack-ice (▲), open pack-ice (■), and ice-free zone (□) of the Barents Sea. Numbers refer to different cruises, and arrows denote the approximate southern limit of the ice edge during each cruise. 1—February–March 1987; 2—April 1986; 3—May–June 1988; 4—May–June 1986; 5—May–June 1984; 6—July 1984; 7—September 1988.

Analyses—Ammonium concentration was measured in triplicates within 2 h of collection according to Solórzano (1969). The samples with reagents added were heated to 50°C for 1 h before the extinction was read in 10-cm cells to ensure complete color development of the blue indophenol complex. The mean C.V. for 36 triplicates was 5.1%. Temperature, salinity, phytoplankton biomass as concentrations of chlorophyll *a* (Chl *a*), nitrate concentrations, and some particulate C and N (PC and PN) data were kindly supplied by scientists from the Institute of Marine Research in Bergen and from the University of Tromsø. The methods used are given by Kristiansen and Lund (1989) and Rey and Loeng (1985). For the September 1988 cruise, concentration of PN was measured by persulfate digestion (Grasshoff et al. 1983), and subsequent analysis of NO_3^- + NO_2^- was done on a Technicon autoanalyzer. Dilution cultures with five steps (diluted 10–

Table 1. Half-saturation constants (μM, means ± SE) used to calculate in situ rates for samples with high (≥1 μM) and low (<1 μM) ambient nitrate concentration. Number of experiments—*n*.

Ambient nitrate (μM)	Half-saturation constants			*n*
	Ammonium	Nitrate	Urea-N	
≥1	1.3±0.3	1.8±1.1*	0.2±0.1*	2–3
<1	0.1±0.0	0.2±0.1	0.1±0.0	4–7

* Mean of two values ± range.

10^5 times) and five replicates of each step were inoculated at selected stations for identification of phytoplankton species, especially the nonpreservable flagellates, according to Throndsen (1978).

Nitrogen uptake—Uptake rates of ammonium, nitrate, and urea at simulated in situ conditions were measured with ^{15}N isotopes (Kristiansen and Lund 1989). The uptake experiments were started within 2 h of collection. Additions of 4 μM ammonium (95 atom%), 4 μM urea-N (99 atom%), and 8 μM nitrate (96.8 atom%) were made to separate incubation bottles for all cruises except September 1988. In addition, kinetic experiments were conducted at three stations in nitrate-rich water (≥1 μM) and at four to seven stations in nitrate-poor water (<1 μM) with 0.05–8.0 μM additions of each of the three isotopes to separate bottles. A hyperbolic relationship was found between uptake rate and substrate concentration in all experiments. The saturation constant from each experiment was determined graphically (S/V plotted against S) according to Wright and Hobbie (1966). In September 1988, 0.5 μM additions were used for ammonium, nitrate, urea, and alanine.

The bottles were placed in incubators kept at in situ temperature and equipped with fluorescent light (Osram Daylight 5000 De Luxe) providing 290 μEinst m^{-2} s^{-1}, which is the typical irradiance in the surface layer (upper 10 m) during midsummer in the Barents Sea (Sakshaug and Slagstad 1991). The incubation bottles were covered with layers of neutral-density screening to adjust to in situ irradiance. Incubations were terminated after 6–12 h by filtering samples onto precombusted 25-mm Whatman GF/C glass-fiber filters (GF/F filters were used in September 1988). The filters were immediately frozen and later dried at 60°C. Filter samples were prepared for isotope analysis, and the atom% ^{15}N was determined by emission spectrometry with a Jasco model N-150 ^{15}N analyzer (Kristiansen and Paasche 1989). The uptake rates are given as nM h^{-1} and are, except for those from September 1988, calculated in situ rates assuming saturation kinetics (Paasche and Kristiansen 1982) and using the half-saturation constants given in Table 1.

The ammonium and urea-N concentrations were not measured at five of the 12 stations sampled in May–July. Concentrations for these stations were estimated as 0.2 μM based on mean values from measurements at the other seven stations. The ammonium and urea uptake rates estimated for these stations seem reasonable compared with rates from the other stations.

Ammonium regeneration was measured by isotopic dilution of 1 μM 95 atom% $^{15}NH_4^+$ on half of the stations sampled in April 1986. No significant dilution was found (data not shown). Except for the values from September 1988, the in situ rates presented here have therefore not been corrected for isotope dilution. The uptake rates from September 1988 have been corrected for isotope dilution (Wheeler et al. 1989). The ratio between ammonium uptake corrected and uncorrected for isotope dilution was 1.12±0.13 for ice-free zones and 1.18±0.11 for close and open pack-ice zones.

Dark incubations were run in parallel with some of the light incubations. The polycarbonate incubation bottles were wrapped in aluminum foil and black plastic. Isotopes were added 1 h later, and the bottles were incubated with the light bottles. Dark ammonium uptake was 28±4% (mean ± SE, $n = 4$), dark nitrate uptake was 4±1% (mean ± SE, $n = 17$), and dark urea uptake was 6% ($n = 1$) of light uptake of the respective nutrients. The daily uptake rates were calculated from the light and dark rates appropriate for the length of the light and dark periods for each cruise.

Phytoplankton growth rates—For all sampling periods, growth rates were estimated from the nitrogen uptake rates:

$$\mu = 3.32 \log_{10}[(P\text{-}PN_0 + P\text{-}PN)/P\text{-}PN_0].$$

μ is the growth rate in doublings d^{-1}, P-PN_0 is the initial phytoplankton PN concentration in μM PN and P-PN is the daily μM increase

in phytoplankton PN calculated from the in situ summed uptake rates.

Size-fractionation experiments—During September 1988, the role of picoplankton in nitrogen assimilation was determined by comparing uptake by unfractionated and <0.8-μm plankton. Uptake of ammonium, nitrate, urea, and alanine were measured as above but with 0.5 μM additions of ^{15}N-labeled nutrients. Plankton was size-fractionated after a 12–16-h incubation by gravity filtration through 142-mm 0.8-μm Nuclepore polycarbonate filters. The <0.8-μm fraction was then collected on 47-mm GF/F filters for isotopic analysis. This method of size fractionation has been used extensively in the subarctic Pacific (Kirchman et al. 1989), where <10% of the Chl *a* is in <0.8-μm particles.

Results

Grouping of the stations—The ice edge receded northward each seasonal cycle (Fig. 1). On the shorter time scales, however, the MIZ was also continuously moving as a result of winds and currents. During a 4-week cruise in April 1986, the "ice edge" drifted more than 1° southward in central parts of the investigated area. The stations have therefore been divided into three groups according to ice conditions: the close pack-ice zone, the open pack-ice zone, and the ice-free zone in the very outer part of MIZ. At some stations the water column was not yet vertically stratified, and these stations are referred to as prebloom stations.

Biomass and nutrients—Phytoplankton biomass as Chl *a* was very low at the prebloom stations (Fig. 2A). In April–June, the phytoplankton biomass was high but variable. The highest phytoplankton biomass concentrations were found at the stations in the open pack-ice zone. In September, the phytoplankton biomass tended to be higher in the close pack-ice zone than in the open pack-ice and ice-free zones. PN concentration (data not shown) followed the same general trend as Chl *a*, but the magnitude of the variation was less for PN (53-fold) than for Chl *a* (470-fold). The Chl : PN ratio showed a sharp peak at the beginning of the bloom, then decreased more rapidly than Chl *a* during the transition period (Fig. 2B).

Nitrate concentrations were high at the prebloom stations and at all stations in April (Fig. 2C). After April, the nitrate concentrations decreased rapidly, and by September nitrate was not detectable (<0.2 μM) in the ice-free zone. Concentrations of ammonium and urea were low but well above detection limits at most stations (Fig. 2D,E). High urea concentrations at some of the stations in May–June coincided with the observation of whales close to the ship during sampling.

Nitrogen uptake rates—During the prebloom, bloom, and transition periods with ≥1 μM nitrate, calculated in situ nitrate uptake rates averaged 77±3% of the measured "saturated" uptake rates (Table 2). Because nitrate uptake is close to saturation, the calculation of rates using the measured kinetic parameters provides a reliable estimate of in situ nitrate uptake rates. During the postbloom period, calculated in situ rates were only 41±6% of the measured saturated rates. The accuracy of the calculated nitrate uptake rates in this case is dependent on the accuracy and precision of the half-saturation constant, which has a 50% C.V. (Table 1). However, nitrate uptake is relatively low during the postbloom period, and a 50% error does not alter conclusions drawn below with respect to changes in the relative importance of nitrate-supported production during the season.

At the prebloom and bloom stations, the ammonium and urea uptake rates were very low. At low ambient nutrient concentrations, the kinetic approach yields an uncertainty of ~50% in the calculated in situ rate. However, because nitrate uptake is high during this period, the imprecision of the ammonium and urea uptake rates has little effect on the comparison of new and regenerated production presented below. The uptake rates of ammonium and urea increased dramatically after the bloom and account for most of the nitrogen used during the transition and postbloom periods. Calculated in situ ammonium uptake averaged 66±3% of the measured saturated rates (Table 2).

New production as a function of ice conditions—Total nitrogen production (summed nitrate + ammonium + urea uptake rate) can be divided into new production (nitrate uptake rate) and regenerated production (summed ammonium + urea uptake rate). Percent new production showed similar seasonal trends for all ice conditions (Table 3). New production

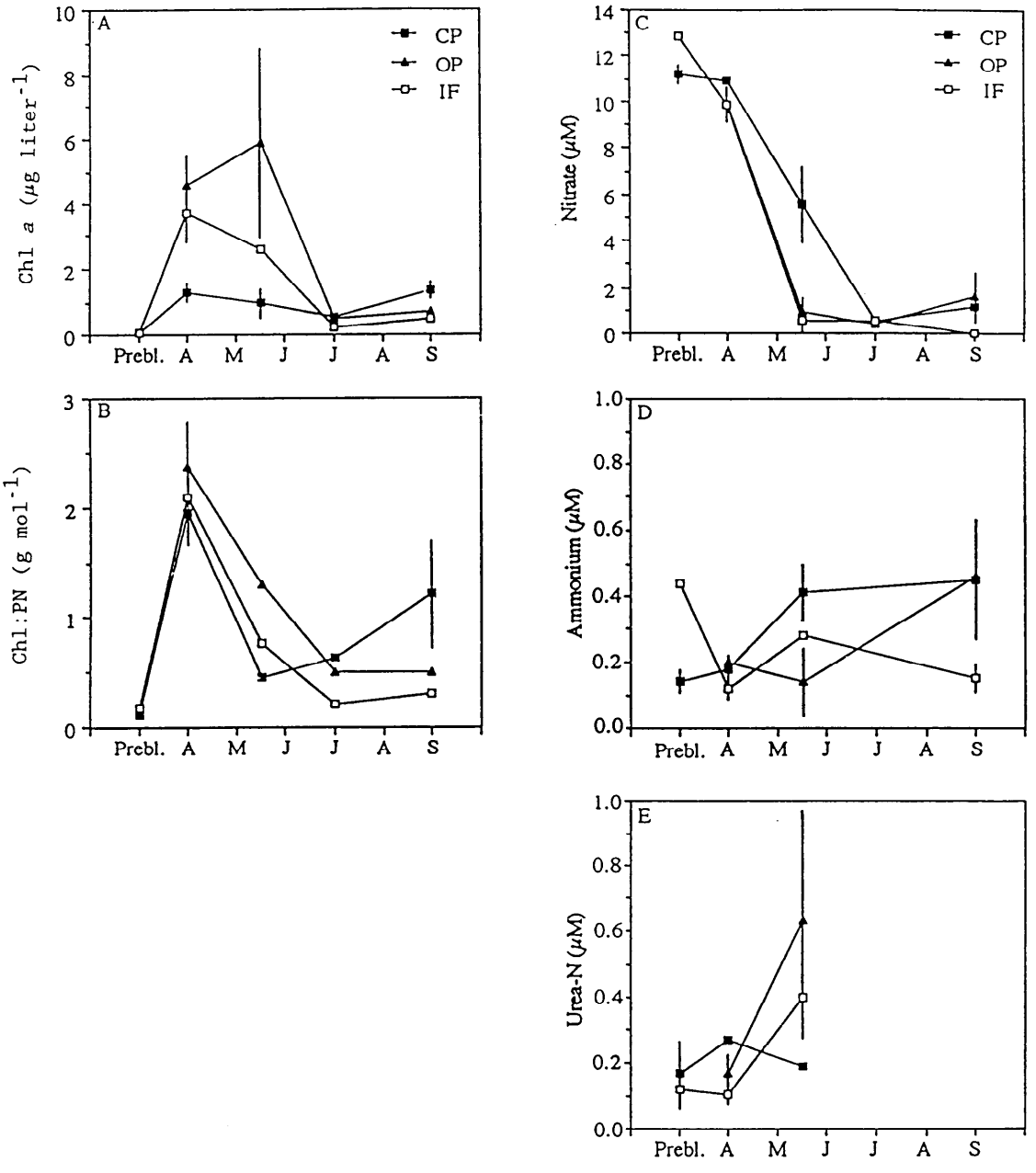

Fig. 2. A. Mean phytoplankton biomass as Chl *a*. B. Mean ratio of Chl *a* to PN concentrations. C, D, E. Mean concentrations of nitrate, ammonium, and urea. Vertical lines are ± SE. Close pack-ice—CP; open pack-ice—OP; ice-free—IF.

was uniformly high (>90%) during the prebloom and bloom periods, intermediate but variable (39–63%) in May–June, and consistently low (7–25%) during July and September. During the postbloom period, highest new production was in the ice-filled regions. Percent new production was hyperbolically related to nitrate concentration at low ammonium concentrations (Fig. 3). Overall means were close to 60% (Table 3), although these values are

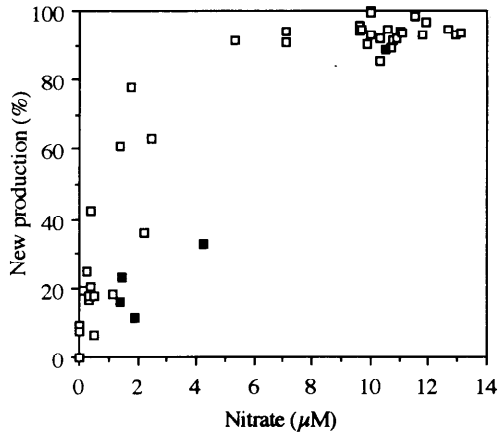

Fig. 3. New production vs. nitrate concentration. Ammonium concentrations: □— <0.5 μM; ■— ≥0.5 μM.

biased by the greater sampling frequency during the bloom compared to other times.

Absolute nitrate uptake rates (nM h^{-1}), however, were quite dependent on both time of sampling and ice conditions (Table 3). Uptake rates were lowest (0.2–4.2 nM h^{-1}) in the close pack-ice from April through June and afterwards were similar to rates in the open pack-ice and ice-free regions (0.2–2.1 nM h^{-1}). Very high rates (17–25 nM h^{-1}) were observed in the open pack-ice and ice-free parts during the April bloom as well as in the open pack-ice during the May–June period. Cumulative nitrate uptake was calculated using the average uptake rate for all the three regions in the MIZ for each period and assuming a 20-h day for April–July and a 15-h day for September. From April through September, 24.1 μM nitrate was taken up. This amount is twice the prebloom nitrate concentration and indicates that there is a significant additional input of nitrate into the euphotic zone by mixing and diffusion during the bloom cycle.

Nitrogen uptake and phytoplankton growth rates during an ice-edge bloom—During April 1986, phytoplankton in different stages of an ice-edge bloom were sampled intensively during a 2-week period. Ten stations sampled during this period are ranked in order of increasing levels of Chl *a* in Table 4. Salinity, temperature, and concentrations of nitrate and Chl *a* at stations before, early in, and toward the end of the bloom are given in Fig. 4. Examination of dilution cultures from stations 18 and 28

Table 2. Ambient nutrient concentration (μM), measured "saturated" uptake rates, and calculated in situ uptake rates. Means ± SE for all years grouped according to bloom condition. Measured rates are for 4 μM ammonium and urea and 8 μM nitrate. In situ rates are calculated for ambient nutrient concentrations.

Season	$[NO_3^-]$	NO_3^- uptake (nM h^{-1})		$[NH_4^+]$	NH_4^+ uptake (nM h^{-1})		[Urea]	Urea uptake (nM h^{-1})	
		Measured	In situ		Measured	In situ		Measured	In situ
Prebloom	11.5±0.4	0.7±0.5	0.6±0.4	0.20±0.07	0.2±0.1	<0.1	0.16±0.07	<0.1	<0.1
Bloom	10.2±0.4	16.5±3.4	13.7±2.8	0.17±0.02	3.8±0.7	0.5±0.1	0.19±0.04	0.7±0.1	0.3±0.1
Transition (≥1 μM NO_3^-)	4.5±1.3	20.9±15.6	11.3±7.8	0.34±0.08	15.6±11.5	2.8±1.9	0.28±0.06	3.8±3.0	2.2±1.7
Transition (<1 μM NO_3^-)	0.3±0.1	6.8±4.1	4.0±2.3	0.19±0.09	15.3±5.2	10.2±4.9	1.0	0.5	0.4
Postbloom (≥1 μM NO_3^-)	2.0±0.6	2.7±1.0	1.2±0.4	0.63±0.10	13.6±6.0	3.5±1.1			
Postbloom (<1 μM NO_3^-)	0.2±0.1	5.1±1.1	1.3±0.4	0.19±0.02	8.0±1.9	5.0±1.1			

Table 3. Seasonal new production and percent new production (nitrate uptake as percent of summed nitrate + ammonium + urea uptake rate) as a function of ice conditions. Means ± SE for $n \geq 3$, and mean ± range for $n = 2$. Number of samples given in parentheses.

Season	Close pack-ice	Open pack-ice	Ice-free
	% new production		
Prebloom	93±3(4)	–	93(1)
Apr	92±1(7)	94±1(6)	96±1(7)
May–Jun	63±15(3)	39±39(2)	52±9(2)
Jul	18(1)	21(1)	7(1)
Sep	17±2(6)	25±4(3)	8±0(3)
Mean *f*-ratio	0.63±0.08(21)	0.16±0.11(12)	0.65±0.11(14)
	New production (nM h^{-1})		
Prebloom	0.2±0.1(4)	–	2.2(1)
Apr	4.2±0.4(7)	17.1±4.9(6)	20.1±5.4(7)
May–Jun	3.8±2.9(4)	24.6±24.6(2)	8.7±2.7(3)
Jul	0.5(1)	0.6(1)	0.2(1)
Sep	1.2±0.3(6)	2.1±0.6(3)	0.7±0.1(3)

(both early bloom) and stations 31 and 52 (both late bloom) revealed that the dominating phytoplankton species during the bloom were diatoms (Throndsen pers. comm.). The dominating diatoms at stations 31 and 52 were *Bacterosira fragilis, Thalassiosira hyalina, Porosira glacialis, Nitzschia cylindrus,* and *Nitzschia grunowii* (Hasle 1990, pers. comm.). The bloom started in homogeneous nitrate-rich water containing <0.07 μg Chl *a* $liter^{-1}$. At the last stations, a strong pycnocline had developed near 50 m, the phytoplankton cells were blooming, and a substantial amount of the nitrate had been converted into particulate matter.

Table 4. Integrated nitrogen uptake in the euphotic zone (above the pycnocline) during a phytoplankton bloom at stations in the close pack-ice zone (CP), open pack-ice zone (OP), and ice-free zone (IF) in April 1986. Stations ranked by increasing Chl *a*.

Sta.	NO_3^- (mmol m^{-2})	Ice	Mixed layer (m)	N uptake (mmol m^{-2} h^{-1})	Chl *a* (mg m^{-2})	*P*-PN (% total)	Growth rate (dbl d^{-1})
15	641	IF	*	0.12	3	6	1.99
18	379	OP	30	0.11	14	23	0.70
39	265	CP	25	0.16	22	38	0.62
28	604	IF	*	0.19	23	24	0.71
43	721	CP	70	0.35	77	32	0.43
57	535	IF	50	0.84	124	62	0.60
24	511	OP	55	1.74	281	70	0.56
14	536	IF	60	2.08	346	76	0.55
31	304	OP	45	0.88	370	98	0.24
52	306	IF	55	1.91	451	62	0.41

* No pronounced temperature or salinity gradients at these stations. 50 m was used for depth of integration.

An estimate of phytoplankton-N (*P*-PN) is needed to calculate phytoplankton growth rates from the uptake rates. The Chl : PN ratio was linearly correlated with nitrate concentration for the stations in Table 4 (Chl : PN = 6.13–0.42[NO_3^-]; $F = 17.5$, $P = 0.0004$; Chl *a* as μg $liter^{-1}$, PN and NO_3^- as μM N). Consequently, subtraction of a fixed amount of non-phytoplankton PN to estimate *P*-PN was not appropriate. We therefore assumed that the maximum Chl : PN value (3.79 μg Chl μmol^{-1} PN) reflects seston which is dominated by phytoplankton, and we used this value to calculate *P*-PN from the Chl *a* concentration in Table 4. Phytoplankton nitrogen (as % total PN) was low at the first stations and higher at the last stations. On the assumption that all the nitrogen uptake was by phytoplankton, the mean phytoplankton growth rate was 0.53±0.05 doubling d^{-1} (means ± SE, $n = 9$). The low *P*-PN concentration at station 15 made the estimated phytoplankton growth rate at this station high and unreliable, and the value is not included in the mean phytoplankton growth rate. The Chl : *P*-PN ratio was assumed to be constant during the bloom because most of the algal biomass was diatoms (*see above*). The value of 3.79 μg Chl *a* (μmol *P*-PN)$^{-1}$ is in the upper range of available culture values, typical for diatom cultures growing at low irradiance (Sakshaug et al. 1991).

Regenerated production—Regenerated production increased through spring and summer, and except for two samples in May–June, high

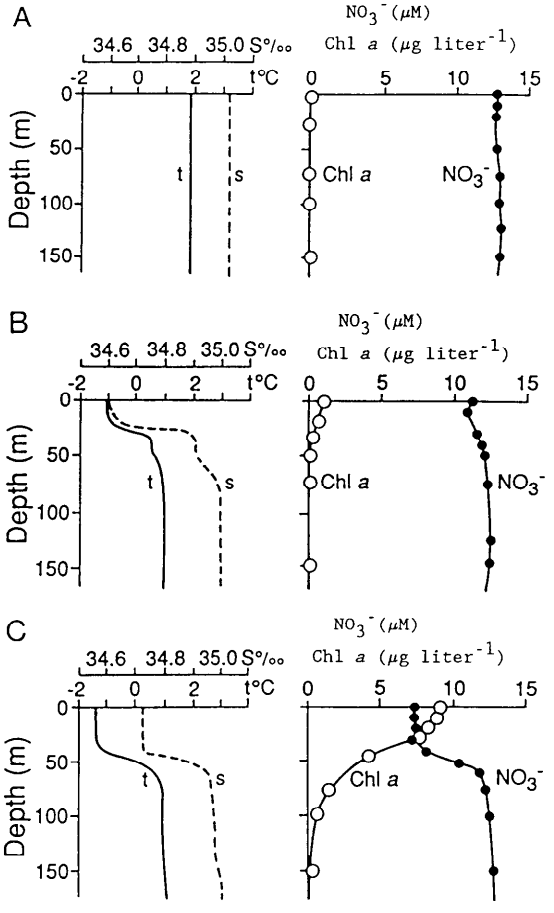

Fig. 4. Vertical profiles of salinity, temperature, nitrate concentration, and Chl *a*. A. Prebloom, Sta. 15. B. Early bloom, Sta. 39. C. Late bloom, Sta. 31.

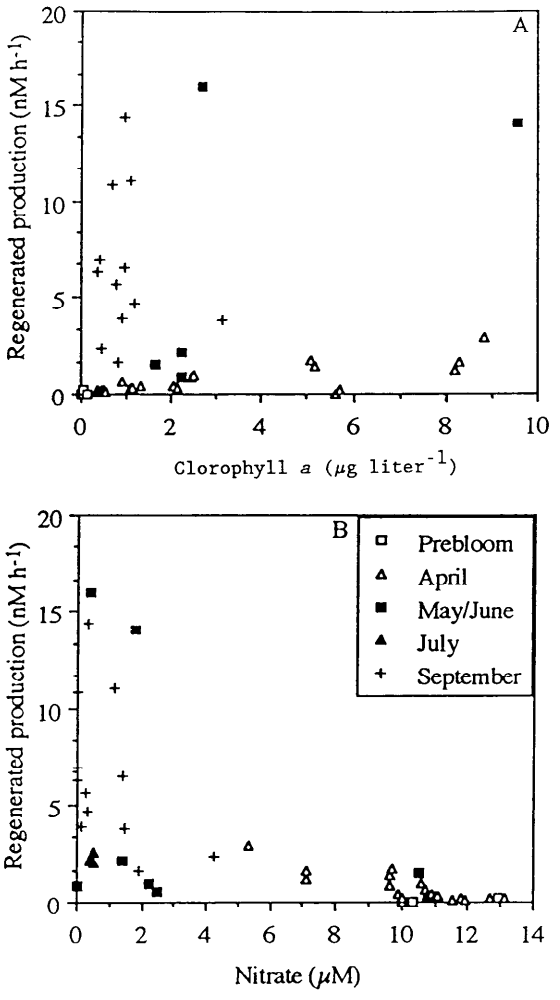

Fig. 5. A. Regenerated production vs. Chl *a*. B. Regenerated production vs. nitrate concentration.

regenerated production was found in water with low concentrations of both nitrate and Chl *a* (Fig. 5). For the two exceptions, nitrate concentrations were <2 μM, and Chl *a* was 2–9 μg liter^{-1}, but the phytoplankton was clearly sinking out of the surface layer. Total nitrogen uptake was similar during the bloom and transition periods (14.4 and 16.4 nM h^{-1}), despite a decrease in mean percent new production from 94 to 53% (Table 3). Maximum mean regenerated production occurred during the transition period (5.9 nM h^{-1}) but was significantly lower than the maximum mean new production (13.7 nM h^{-1}) during the bloom period.

Nitrogen-specific and Chl-specific uptake rates—Nitrogen-specific uptake rates showed a 5-fold range, with low but variable rates during the prebloom period, maximum rates (0.20 d^{-1}) during the bloom period, and intermediate rates during the transition and postbloom periods (Table 5). Nitrogen-specific rates underestimate phytoplankton-specific activity due to the presence of detrital nitrogen and PN from heterotrophic protozoans and microzooplankton. To obtain a better estimate of phytoplankton-specific activity, we compare uptake rates normalized to Chl *a* in Table 5. The mean Chl-specific uptake rate was high but extremely variable during the prebloom period and is not discussed further. Chl-specific uptake increased 2-fold [from 0.11 to 0.19 μmol

Table 5. Seasonal percent new production (nitrate uptake as percent of summed nitrate + ammonium + urea uptake rate), N-specific uptake rate (d^{-1}), Chl-specific uptake [μmol (μg Chl)$^{-1}$ d^{-1}], and estimated phytoplankton growth rates (dbl d^{-1}). Means ± SE; *n*—number of samples.

Season	New production	N-specific uptake	Chl-specific uptake	Growth rate	*n*
Prebloom	93±2	0.04±0.03	0.22±0.19	0.24±0.19	5
Bloom	94±1	0.20±0.02	0.11±0.01	0.49±0.04	20
Transition	53±11	0.08±0.03	0.14±0.04	0.32±0.10	5–7
Postbloom	17±2	0.09±0.01	0.19±0.03	0.44±0.06*	12–15

* Calculated assuming a doubling of Chl: *P*-PN for September as the expected response for a 50% reduction in light intensity (Sakshaug et al. 1991).

(μg Chl)$^{-1}$ d^{-1}] between the bloom and postbloom periods. During the same period, N-specific uptake decreased by a factor of two (Table 5). This diametrical change in Chl-specific and N-specific uptake rates probably reflects a change in phytoplankton species (*see below*) as well as an increase in abundance of heterotrophic and detrital particles after the spring bloom.

Phytoplankton growth rates were estimated from the Chl-specific N uptake rates and the expected Chl: *P*-PN ratio for the phytoplankton community during each period. We assumed that the prebloom period was dominated by flagellates, which usually have a Chl: *P*-PN of 1.00 (McCarthy and Nevins 1986). The bloom phytoplankton community was dominated by diatoms, which have a Chl: *P*-PN of 3.79 (*see above*). We used a Chl: *P*-PN ratio of 1.89 (Kokkinakis and Wheeler 1987) to characterize the mixed diatom and flagellate phytoplankton community during the transition period. The postbloom community was dominated by flagellates, and we included an estimated 2-fold increase in Chl: *P*-PN as an adaptation to reduced light levels during that period (Chl: *P*-PN = 2.00). The resulting growth rates ranged from 0.32 to 0.49 d^{-1} (Table 5), showed little seasonal variation, and indicated the presence of active phytoplankton communities throughout the transition and postbloom periods. Thus, although the N-specific uptake rates suggest a seasonal decrease in rates, Chl-specific uptake suggests little seasonal change.

Table 6. Uptake of nitrogenous nutrients by <0.8-μm plankton during September 1988. Rates were determined for three depths in the euphotic zone and are reported as means ± SD for five stations.

Nitrogen source	Uptake (nM h^{-1})		<0.8-μm uptake (% of total)
	Total	Corrected*	
Ammonium	3.81±1.37	5.43±1.72	53±26
Nitrate	1.11±0.69	1.67±0.98	48±17
Urea	2.17±0.94	2.18±1.04	24±13
Alanine	0.82±0.38	1.54±0.60	70±22

* Total uptake plus estimated uptake by bacteria passing through GF/F filters.

Uptake by picoplankton—A significant fraction of total nitrogen uptake can be attributed to picoplankton (organisms <0.8 μm). During September 1988, picoplankton accounted for 53, 48, 24, and 70% of ammonium, nitrate, urea, and alanine uptake, respectively (Table 6). About 50% of heterotrophic bacteria from subarctic waters will pass through GF/F filters (Kirchman et al. 1989). If the retention efficiency for picoplankton in the Barents Sea is similar, the measured uptake rates for the <0.8-μm fraction should be increased by a factor of 2 for a better estimate of picoplankton uptake rates. Similarly, total uptake may also be underestimated by inefficient retention of picoplankton on glass-fiber filters. Ammonium and nitrate uptake rates adjusted for the likely inefficient retention of picoplankton indicate that traditional measurements with glass-fiber filters may underestimate postbloom uptake rates by ~30% (Table 6).

Discussion

The kinetic approach for determination of uptake rates—Large additions of ^{15}N isotopes were used to obtain measurable uptake for the low biomass and cold temperatures found in the Barents Sea (Kristiansen and Lund 1989). The rates reported here were adjusted to ambient concentrations by assuming saturation kinetics and using experimentally derived half-saturation constants. Half-saturation constants are known to be higher in eutrophic waters than in oligotrophic waters (Goldman and Glibert 1983); thus we used one set of con-

stants for nitrate-rich samples (≥ 1 μM) and another for nitrate-poor samples (< 1 μM). The half-saturation constants for urea uptake were not significantly different, but this may result from the low urea uptake at the nutrient-rich stations.

The dominating phytoplankton species during the spring bloom in the Barents Sea are usually diatoms and occasionally the colony-forming flagellate, *Phaeocystis pouchetii,* while flagellate species usually dominate in the nutrient-poor surface layer (Rey and Loeng 1985). Taxonomic studies (including dilution-culture experiments) for a limited number of cruises and stations confirm this shift from diatom-dominated to flagellate-dominated systems (Syvertsen and Throndsen pers. comm.; Throndsen and Kristiansen 1991). The difference in ammonium and nitrate half-saturation constants for high (≥ 1 μM) and low (< 1 μM) nitrate waters may be attributed to this shift in species composition.

Although the kinetic approach introduces some uncertainty into estimated in situ uptake rates, the errors are largest when ambient nutrient concentrations are low or close to the half-saturation constants. The seasonal shifts in nitrate and ammonium availability during this study resulted in uptake rates that were close to saturation for nitrate early in the season and for ammonium later in the season. As a consequence, the measured uptake rates in conjunction with a correction to adjust to ambient nutrient concentrations provided reasonable estimates of in situ uptake rates.

Nitrate uptake during the spring bloom—The phytoplankton standing stock (Chl *a*) and timing of the ice-edge bloom were typical for the Barents Sea (Rey and Loeng 1985). The highest Chl *a* concentrations were 8–10 μg liter^{-1} in April–May. Some nitrate (2–7 μM) was still left in the water at these biomass-rich stations, however, and the phytoplankton standing stock probably increased even more the next few days. The sequence of stations in Table 4 was representative of most of the ice-edge bloom from its initiation until a few days before the peak.

Nitrate was the dominating nitrogen source for phytoplankton growth during the April 1986 bloom, and the mean N-specific uptake rate was 0.011 ± 0.001 h^{-1} (or 0.32 doubling d^{-1}). The estimated phytoplankton growth rate (corrected for nonphytoplankton-PN) in the MIZ was 0.53 d^{-1}, which is 77% of Eppley's maximum phytoplankton growth rate at the in situ temperatures (Eppley 1972) during our study. Similar growth rates have been found in natural phytoplankton assemblages in polar regions and in culture experiments with diatoms isolated from the Barents Sea (Gilstad and Sakshaug 1990).

New vs. regenerated production—Overall means of percent of new production in the close pack-ice, the open pack-ice, and the ice-free zones were 61–65% and were not significantly different. There was, however, a pronounced seasonal trend and a pronounced geographical trend (from close pack-ice to ice-free zones) in new and regenerated production. Absolute and relative new production was highest during the bloom period and part of the transition period, while absolute and relative regenerated production was highest during the postbloom period. During the postbloom period, percent new production decreased from the close and open pack-ice zones to the ice-free zones and into the oligotrophic surface layer south of the MIZ. Indications of such a geographical trend appeared during the transition period.

With the exception of the *f*-ratios from the EPOS cruise to the Weddell Sea during early spring (Kristiansen et al. 1992), the mean *f*-ratios of all available studies in the MIZ in polar regions are ≤ 0.74 (urea uptake not included, Table 7). Corrected for urea (using 50% of the ammonium uptake rate as an estimate of urea uptake), the published mean *f*-ratios decrease to ≤ 0.61. Our values of percent new production are very high during winter and spring. Similar *f*-ratios have been determined during early spring in the Antarctic and occasionally in other studies in polar regions (Table 7). No pronounced seasonal or geographical trends in new and regenerated production were found in the studies in Table 7. The hint of a seasonal trend, however, was found during the EPOS cruise to the Weddell Sea (Goeyens et al. 1991; Kristiansen et al. 1992). We speculate that the very high initial values of percent new production in the Barents Sea may be typical of polar regions, but are often missed as a result of inadequate sampling.

Correlations between changes in nutrients, biomass, and nitrogen uptake—The phyto-

Table 7. Mean and range of *f*-ratios from the marginal ice zone in the Arctic and Antarctic derived from the literature.

Region	Season	Mean *f*-ratio	Range	Reference
Antarctic				
Scotia Sea	Early spring	0.48	0.37–0.70	Olson 1980
Weddell Sea	Early spring	0.99*	0.97–1.00	Kristiansen et al. 1992
Weddell Sea	Spring	0.85*	0.85	Kristiansen et al. 1992
Weddell Sea	Spring	0.52	0.35–0.70	Smith and Nelson 1990
Weddell Sea	Early summer	0.57	0.30–0.83	Goeyens et al. 1991
Ross Sea	Summer	0.65	0.35–0.93	Nelson and Smith 1986
Scotia Sea	Summer	0.48	0.24–0.79	Glibert et al. 1982
Weddell Sea	Autumn	0.72	0.60–0.84	Smith and Nelson 1990
Arctic				
Bering Sea	Spring	0.74	0.68–0.76	Müller-Karger and Alexander 1987
Fram Strait	Summer	0.62	0.28–0.86	Smith and Kattner 1989
Barents Sea	Winter (prebloom)	0.93*	0.87–1.00	This study
Barents Sea	Sprilg (Apr)	0.94*	0.89–1.00	This study
Barents Sea	Summer (May–Jul)	0.42*	0.00–0.89	This study
Barents Sea	Autumn (Sep)	0.17*	0.08–0.33	This study

* Urea was included in these studies.

plankton biomass increased during the bloom when new production was high and regenerated production was low. During the transition period, the phytoplankton biomass decreased slightly, and regenerated production increased from 6 to 47%. Total production was, however, similar during the bloom and transition periods. During the postbloom period, the percent regenerated production was at its maximum. The indicated 4-fold decrease in the Chl *a* : PN ratio during the bloom cycle suggests a shift from a system dominated by autotrophic organisms during the bloom to a system dominated by heterotrophic organisms and detritus during the transitional and postbloom periods (Fig. 2).

Phytoplankton standing stock (Chl *a*) during the postbloom period was reduced to 28% of the mean value found during the bloom period. This reduction in phytoplankton standing stock was accompanied by a reduction in total nitrogen uptake. Although the N-specific uptake rates decreased after the bloom, the Chl-specific rates remained relatively constant. The decrease in N-specific uptake rates and the switch from primarily new to regenerated production are expected consequences of increased grazing after the spring bloom. The high phytoplankton growth rates as well as the high and nearly constant Chl-specific nitrogen uptake rates argue against any severe nitrogen limitation of the phytoplankton. Thus, although nitrate concentrations decrease, the supply rates of nitrate and ammonium are sufficient to support a healthy phytoplankton population. The low standing stocks of phytoplankton are most likely due to grazing by copepods (Eilertsen et al. 1989) and microzooplankton (Vernet 1991) rather than by limitation of growth rates per se.

Nitrogen uptake by picoplankton—Picoplankton (operationally defined here as particles <0.8 μm) contain both small phytoplankton and heterotrophic bacteria. Procaryotic photosynthetic picoplankton are not abundant in the Barents Sea (Throndsen and Kristiansen 1991), and the most abundant phytopicoplankton range in size from 1 to 3 μm. Thus, our <0.8-μm fraction is likely to be dominated by heterotrophic bacteria. Bacteria use both inorganic and organic forms of nitrogen (Kirchman et al. 1989) and may play a significant role in nitrogen assimilation in the euphotic zone. Bacterial production (and nitrogen assimilation) appears to increase relative to phytoplankton production during the decline of seasonal blooms (Ducklow et al. 1993). We have insufficient data to describe a seasonal cycle in bacterial nitrogen use in the MIZ of the Barents Sea. Nonetheless, our September size-fractionation results do indicate that during the postbloom period, most alanine uptake and little urea uptake is by heterotrophic bacteria. A significant portion of both nitrate

and ammonium uptake appeared in the bacterial size fraction. However, the proportions are similar and do not affect our conclusions with respect to new and regenerated production by phytoplankton.

Seasonal variations in new and regenerated production—Our results on the seasonal dynamics of nitrogen utilization in the Barents Sea MIZ argue against the simple notion of a spring phytoplankton bloom followed by a period of decreased production caused by nitrogen limitation. Nitrate concentrations do reach low levels early in the season, but in the open and close pack-ice, significant influx of nitrate into the euphotic zone supports moderately high nitrate assimilation after the bloom. In addition, regenerated production increases after the bloom. Grazing of the phytoplankton community by copepods and microzooplankton and degradation of organic material by bacteria are processes contributing to the production of ammonium. Grazing (Eilertsen et al. 1989) and bacterial activity (Thingstad and Martinussen 1991) increase after the spring bloom, providing an additional source of N for phytoplankton. The high Chl-specific uptake rates and high growth rates observed in this study indicate that the phytoplankton community is nitrogen-sufficient throughout the season. The observed decreases in primary production can be attributed to the maintenance of a low standing stock of phytoplankton by copepod and microzooplankton grazing rather than nitrogen limitation of phytoplankton growth.

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