

New production in the Northeast Water Polynya: 1993

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Abstract

The Northeast Water Polynya has been suggested as acting as a sink for carbon, especially during the spring and summer when phytoplankton growth is active. During 1993 the polynya was sampled for the entire growing period (late May through mid-August) in order to more accurately assess the magnitude, controls and patterns of new and total (ammonium, nitrate and urea) nitrogen production. This represents the first assessment of new production throughout an entire season in the Arctic. We found that, in 1993, new production, based on ¹⁵N-tracer techniques and integrated over the euphotic zone, was 0.141 mmol N m⁻² h⁻¹ (0.361 g C m⁻² d⁻¹ when converted using observed C/N ratios). Measured *f* ratios averaged 0.65 and demonstrate that the system, to a great extent, was using nitrate as a nitrogen source. In general *f* ratios were greatest early in the season and minimal in mid-summer. Urea uptake was highly variable and contributed slightly less than ammonium to phytoplankton nitrogen demand. Nitrate uptake at stations with low (< 0.5 μM) nitrate concentrations was significantly reduced, implying that nitrate concentrations limited phytoplankton growth late in the growing season. Long-term new production rates calculated from nutrient depletion patterns from the polynya as a whole as well as a time-series constructed from a single location were ca. 0.144–0.281 g C m⁻² d⁻¹. The relationship between new production as measured by incubations and nutrient depletion budgets suggests that phytoplankton growth is the dominant factor influencing the nitrogen budget of the polynya. The amount of material available for removal from the euphotic zone is limited and constrains the degree to which the polynya can act as a regional carbon sink.

Keywords: Arctic; polynya; production; nitrogen

1. Introduction

Polynyas (areas of substantially reduced ice cover surrounded by high concentrations of ice) are known to be the sites of large accumulations of biomass of

higher trophic levels relative to the ice-covered waters in the same region (Stirling and Cleator, 1981; Massom, 1988), but the reasons for the enhanced higher trophic level abundances are unclear. For example, bird numbers might be greater, due to increased sites for nesting, whereas some marine mammals may select polynyas as regions in which to feed. Some polynyas do appear to be the site of

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increased productivity (Arrigo and McLain, 1994), and others have been suggested to act in a manner similar to laboratory chemostats, where nutrients flow into the region from under the ice and are converted into biogenic matter in the stratified, high irradiance environment of the polynya (Arctic Ocean Sciences Board, 1991). Therefore, the increased productivity of polynyas might be transferred to higher trophic levels and result in a higher biomass, but accumulations independent of productivity are also possible. Similarly, it has been suggested that production within a polynya is efficiently transferred to the benthos (Ambrose and Renaud, 1995), and that a coastal polynya can act as a small net sink of carbon on an annual basis (Yager et al., 1995). However, the extent to which polynyas act as a source of production is far from clear, as is their roles as sites of new production.

The Northeast Water polynya has been studied intensively in the past few years. Hirche et al. (1991) compared a single station occupied in the polynya to those in the Fram Strait and found that it had higher phytoplankton and zooplankton biomass than those elsewhere in the Greenland Sea, but the temporal and spatial influences on these data are unclear. Lara et al. (1994) analyzed the hydrographic and biological conditions during one week (June 9–16, 1991) from the region and concluded that phytoplankton standing stocks would be limited by nitrogen without additional input of nutrients via physical processes. Smith et al. (1995) and Smith (1995) occupied 81 stations in July–August, 1992 and measured biomass, productivity and new production in the polynya. They found a complex pattern of phytoplankton biomass and growth which could not be attributed solely to irradiance, ice distribution, grazing or nutrient concentrations. Nitrate concentrations were found to be low, so they also concluded that ultimate control of phytoplankton standing stocks would be via nutrients. Despite the reduced nitrate levels, productivity was largely nitrate-based. Little evidence for upwelling or lateral advective inputs was found during this period. However, no studies to date have sampled the entire period of phytoplankton growth (i.e., late May through mid-August when the polynya's concentrations of open water are maximal).

In 1993 an international, multidisciplinary study was conducted in the Northeast Water polynya. The

goal of the project was to characterize the region's biological and physical processes throughout the entire period in which phytoplankton might be reasonably expected to grow (i.e., late May through mid-August). Two ships (RV *Polarstern* and USCGC *Polar Sea*) sampled the region continuously during this period, assessing phytoplankton biomass, nutrients, hydrography, primary productivity, and new production (as well as other variables). This paper describes the rates of new production as calculated by two independent procedures and the potential control of new production by nitrogen availability.

2. Materials and methods

Observations were conducted in the Northeast Water Polynya from May 25 to July 29, 1993 from the RV *Polarstern* (PSt) and from July 18–August 14, 1993 from the USCGC *Polar Sea* (PS). A total of 30 stations in which new production was measured were conducted on the *Polarstern* (Fig. 1a) and 38 on the *Polar Sea* (Fig. 1b). A time series was constructed using stations occupied within a small (25 × 25 km) area (PSt stations 21, 26, 27, 28, 29, 30, 31, 57, 58, 59, 60, 138, 159, 161, 165, 167, 168, 169, and 217; PS stations 2, 7, 8, 9, 10, 11, 16, 17, 37, 84 and 86). Using a rosette sampler equipped with a CTD, a LI-COR 185B underwater PAR sensor and Niskin bottles fitted with Teflon-coated closure springs, we recorded temperature, salinity and downwelling irradiance profiles and collected water samples at seven photic depths (100, 50, 30, 15, 5, 1 and 0.1% of surface irradiance).

Nitrate, ammonium, and nitrite in seawater were quantified using a Technicon Autoanalyzer-II system prior to the production measurements by standard automated techniques. Urea concentrations and standards were quantified on frozen samples at Laval University after the cruise using an Alpkem Autoanalyzer, with the procedure being based on the urea-diacetyl monoxime method (Koroleff, 1983). Chlorophyll and phaeopigment concentrations were determined using a Turner Model 112 or a Turner Designs Model 10 fluorometer (Holm-Hansen et al., 1965) on samples filtered through Whatman GF/F glass-fiber filters. All samples were extracted in 10 ml acetone at 4°C in the dark, and the fluorometers

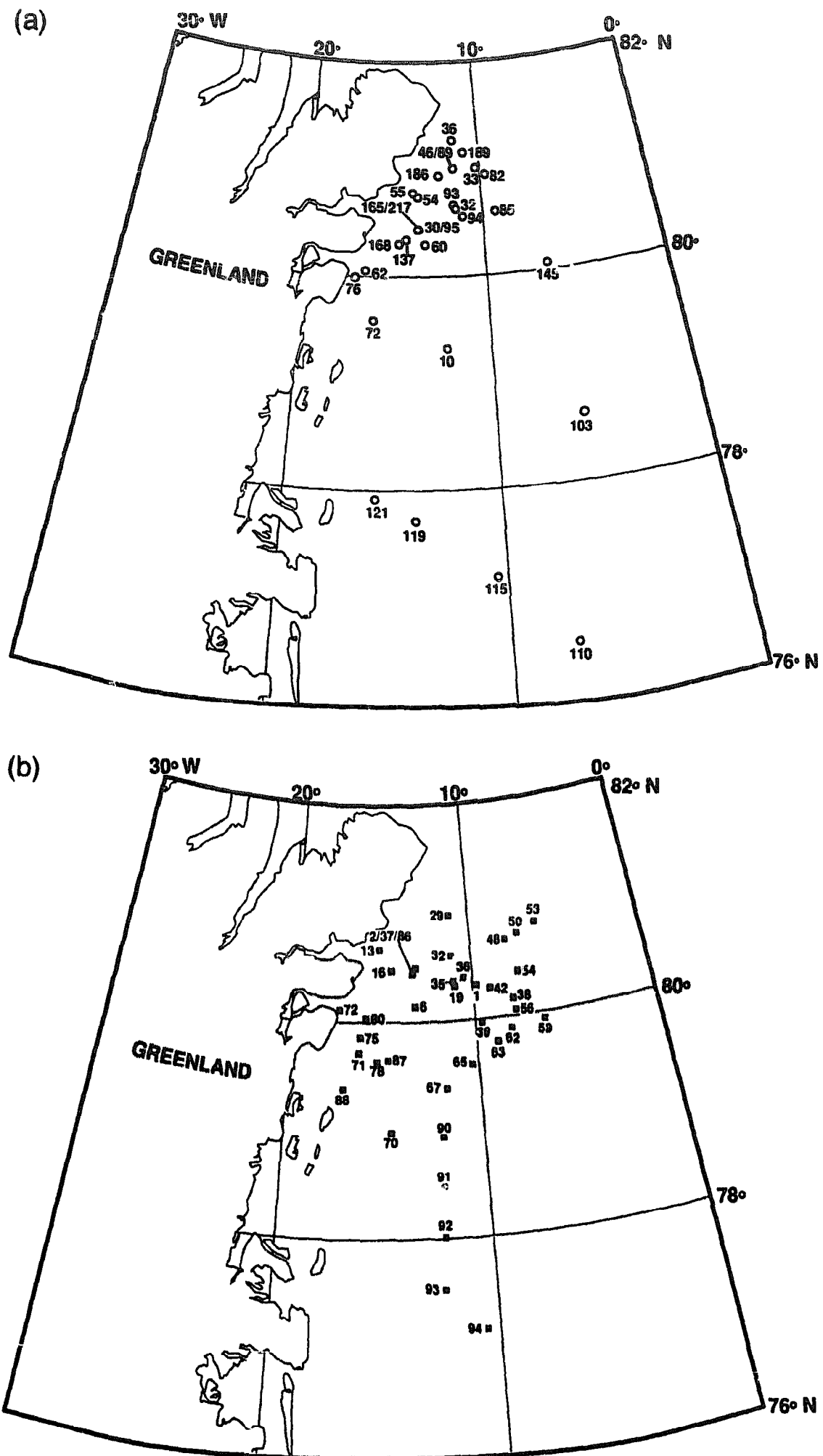


Fig. 1. Map showing the location of the stations where ^{15}N -nitrogen uptake was measured during (a) *Polarstern* cruises ARK IX/2 and 3, and (b) *Polar Sea* Cruise NEWP-93.

were calibrated using commercially prepared standards (Smith et al., 1995).

Rates of nitrate, ammonium and urea uptake were quantified using stable-isotope tracer techniques and simulated in situ incubations. Stock solutions of ^{15}N -labelled nitrate, ammonium and urea (95–99% carrier free) were prepared from crystalline salts and stored in Teflon bottles. For the *Polarstern* cruise, isotopic additions were such to create final concentrations of $0.1\ \mu\text{M}$ of labelled ammonium or nitrate or $0.05\ \mu\text{M}$ of labelled urea. For the *Polar Sea* cruise, an amount equal to 10% of the ambient nitrate or ammonium concentration was added to each sample (urea uptake was not assessed during the *Polar Sea* cruise). If nutrient concentrations were less than $0.5\ \mu\text{M}$, $0.05\ \mu\text{mol l}^{-1}$ were added to insure analytical sensitivity. All incubations were conducted in 500 ml screw-capped polycarbonate bottles. The simulated in situ incubators were positioned on deck in unshaded locations, and running seawater flowed through them to maintain surface temperatures. Each incubator was equipped with troughs, each of which was wrapped with appropriate quantities of neutral density screen (Cinemills, Inc.) to reduce the irradiance to the amounts from which the samples were collected. To account for spectral quality changes with depth, one layer of screen used was a blue filter, which was applied to the troughs simulating 30% or less of surface irradiance.

After 24 h incubation, the samples were filtered through precombusted (450°C for 2 h) Whatman GF/F filters and rinsed with cold, filtered seawater. All filters were placed in precombusted glass vials, capped with combusted aluminum foil, dried at 60°C and stored for return to the laboratory for analysis. The samples from the *Polarstern* were analyzed using a mass spectrometer (Europa Scientific), and the samples from the *Polar Sea* were analyzed on a Jasco emission spectrometer after microDumas combustion. All particulate nitrogen concentrations were determined on either a Europa mass spectrometer or a Carlo-Erba Model EA-1108 elemental analyzer. PN samples for the *Polarstern* were collected after incubation, but for the *Polar Sea* cruise they were collected before incubation. Given the standing stocks of particulate nitrogen and the rates of inorganic nitrogen uptake, the difference between pre- and

post-incubation PN concentrations was, on average, less than 4%. Rates of nitrogen uptake were calculated using equation 3 of Dugdale and Wilkerson (1986), and uptake was expressed as hourly rates by dividing by the total incubation period. No corrections for isotope dilution were made because corrections as calculated by the method of Kanda et al. (1987) were small. Furthermore, potential isotope dilution effects calculated from assumed regeneration rates (based on microplankton abundance and literature remineralization rates) and our uptake data also suggested that isotope dilution was in most cases small. Calculated f ratios (the ratio between nitrate uptake and total (i.e., nitrate plus ammonium plus urea, when available) uptake) included no corrections for uptake of dissolved organic nitrogen forms other than urea.

3. Results

The local hydrographic conditions in the polynya in 1993 in general resulted in increasing amounts of stratification through time, and by mid-summer the waters were highly stratified, as had been found previously. The stratification was by no means uniform or of equal strength, but did appear to increase through time as local melting of ice and thermal heating of the surface layer continued. Nutrient concentrations at a location which was repeatedly occupied (ca. $80^\circ 25' \text{N}$, $13^\circ 40' \text{W}$) were initially high but decreased through time (Fig. 2); conversely, the stratification at those stations became stronger with time (Fig. 2). Initial nitrate concentrations (i.e., those not influenced by biological uptake) in the surface layer at most stations were ca. $4\ \mu\text{M}$, which is typical for the local East Greenland Shelf Water.

Phytoplankton biomass was initially low, and did not exceed $1\ \mu\text{g chl } a\ \text{l}^{-1}$ until June 6 at PSt Station 53. The maximum chlorophyll a concentrations observed by the *Polarstern* and *Polar Sea* were 9.9 (PSt 223) and $7.4\ \mu\text{g l}^{-1}$ (PS 57), respectively, although the maximum within most stations was less than $2\ \mu\text{g l}^{-1}$ (Legendre et al., 1994a; Wallace et al., 1995a). Integrated chlorophyll a levels increased through time and were maximal in mid-July (Fig. 3). Maximum surface productivity during the *Polarstern* survey was $7.08\ \text{mg C m}^{-3}\ \text{h}^{-1}$ (Legendre et al.,

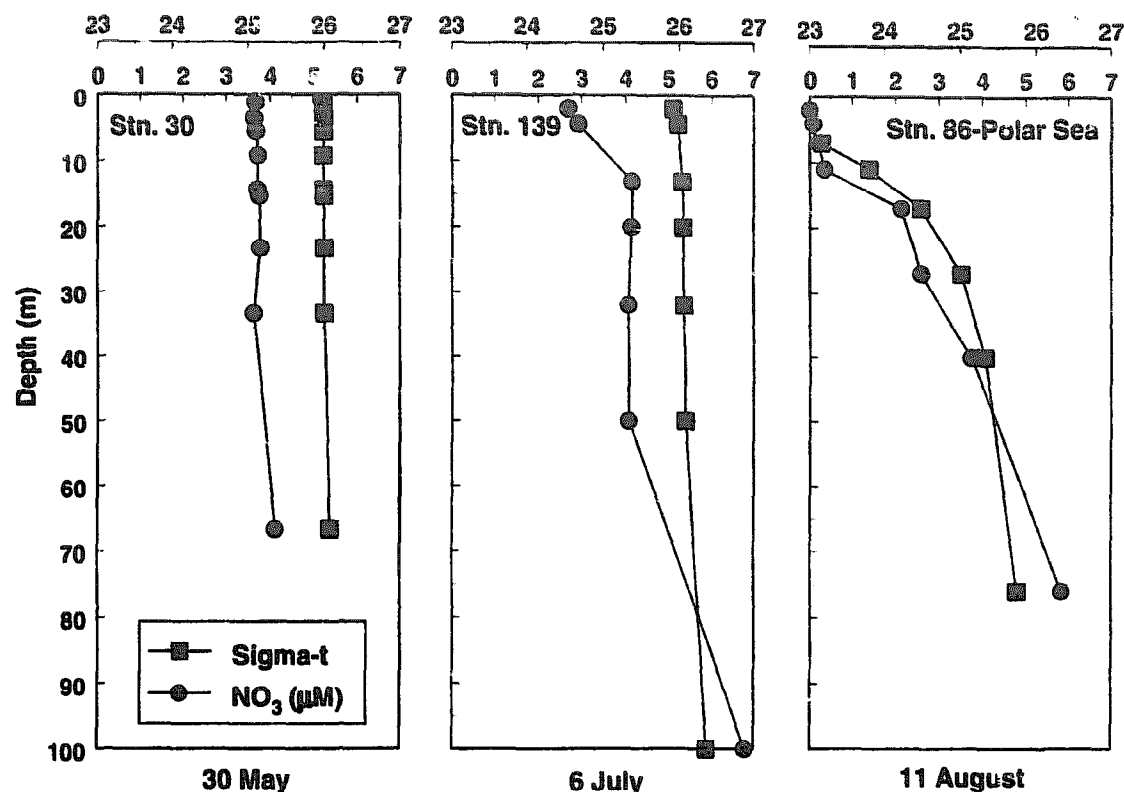


Fig. 2. The vertical distribution of σ_t (a measure of density) and nitrate at selected stations. (left) PST 30 ($80^{\circ}44'N$, $13^{\circ}20'W$). (middle) PST 139 ($80^{\circ}27'N$, $10^{\circ}56'W$). (right) PS 86 ($80^{\circ}23'N$, $13^{\circ}26'W$). The data were collected from stations occupied at intervals of approximately 5 weeks.

1994b), whereas during the *Polar Sea* cruise it was $6.92 \text{ mg C m}^{-3} \text{ h}^{-1}$ (Smith, unpublished; data available from the NSIDC, Boulder, CO). Although the spatial distribution of phytoplankton biomass and productivity was very uneven, autotrophic growth was proceeding throughout the region, and biogenic material was accumulating in the surface layer (Fig. 3).

Nitrogen uptake and rates of new production varied substantially through time, as determined by ^{15}N uptake measurements, and also varied spatially within the polynya. Mean rates of integrated, euphotic-zone nitrate, ammonium and urea uptake during the *Polarstern* cruise were 0.097 , 0.044 and $0.075 \text{ mmol m}^{-2} \text{ h}^{-1}$, respectively, whereas during the *Polar Sea* cruise average rates of nitrate and ammonium uptake were 0.167 and $0.075 \text{ mmol m}^{-2} \text{ h}^{-1}$ (Table 1). For the entire region the mean rate of nitrate uptake increased throughout the summer, except during the last 2 week period when it declined slightly (Fig. 3). Ammonium uptake was low initially, but increased markedly during the middle of the summer (Fig. 3). F ratios from both cruises averaged 0.65 , which suggests a strong dependence of growth on nitrate. For the first 11 stations of *Polarstern* cruise (through Station 100, June 20), f ratios averaged

$0.81 (\pm 0.24; n = 11)$, whereas those collected from June 21–July 19 from the same cruise averaged $0.49 (\pm 0.22; n = 11)$, indicating a significant ($p < 0.01$) decrease through time in the dependence on nitrate. Rates of nitrogen uptake were analyzed relative to ice concentration present at the time of sampling, but no statistical relationship was observed (Table 2). However, the average integrated water column ni-

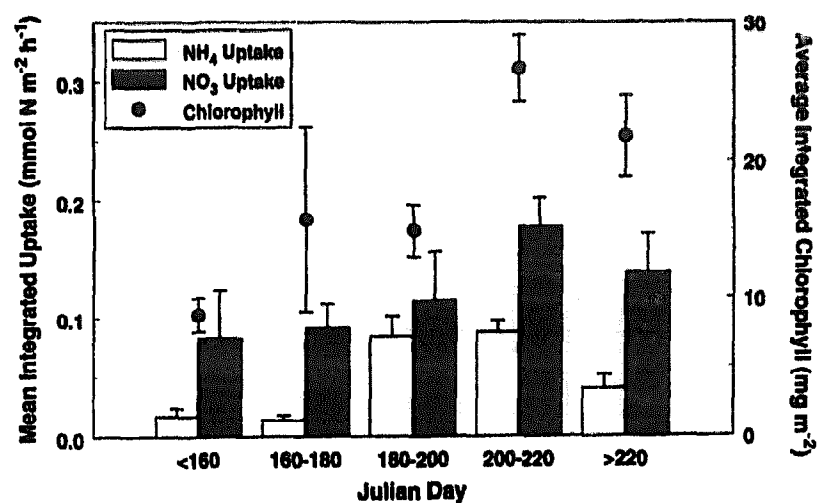


Fig. 3. Average nitrate and ammonium uptake rates during five, 20 day periods during the study. Also included are integrated euphotic zone concentrations of chlorophyll for the same stations and periods. The bars represent the standard error for each interval. Mean f ratios for the five periods were: 0.82 , 0.87 , 0.58 , 0.57 and 0.77 .

Table 1

Mean, standard deviation, minimum and maximum values of integrated nitrate, ammonium and urea uptake rates in the Northeast Water Polynya region in 1993

| Cruise | Statistic | Nitrate uptake (mmol m ⁻² h ⁻¹) | Ammonium uptake (mmol m ⁻² h ⁻¹) | Urea uptake (mmol m ⁻² h ⁻¹) |
|-------------------|-----------|---|--|--|
| <i>Polarstern</i> | Mean | 0.097 | 0.044 | 0.038 |
| <i>Polarstern</i> | σ | 0.108 | 0.090 | 0.055 |
| <i>Polarstern</i> | Maximum | 0.439 | 0.181 | 0.178 |
| <i>Polarstern</i> | Minimum | 0.006 | 0.0013 | 0.0007 |
| <i>Polarstern</i> | n | 22 | 23 | 22 |
| <i>Polar Sea</i> | Mean | 0.167 | 0.075 | ND |
| <i>Polar Sea</i> | σ | 0.125 | 0.054 | ND |
| <i>Polar Sea</i> | Maximum | 0.622 | 0.269 | ND |
| <i>Polar Sea</i> | Minimum | 0.0049 | 0.0045 | ND |
| <i>Polar Sea</i> | n | 38 | 38 | ND |

n = number of samples, σ = standard deviation, ND = no data. All integrations are from the surface to the 0.1% isolume.

trate uptake was greatest at locations with the lowest ice concentrations. Urea uptake was highly variable (Table 1), and in general was nearly equal to that of ammonium uptake. The maximum rate of urea removal (0.023 $\mu\text{mol l}^{-1} \text{h}^{-1}$ at 10 m; PSt 145) reduced the *f* ratio from 0.39 to 0.073. Urea uptake appeared to increase in mid-summer, but lack of data during the *Polar Sea* cruise precludes a quantitative assessment for the entire period of growth.

During middle and late summer, nitrate concentrations in the surface layer were reduced to less than 0.5 μM at many locations. The mean uptake rate of nitrate-depleted stations was compared to that for samples with nitrate concentrations greater than 0.5 μM to test if the low nitrate concentrations reduced

measured uptake rates (Table 3). At the low nitrate stations, both specific and absolute nitrate uptake rates were significantly ($p < 0.001$) reduced, and specific and absolute uptake at the low nitrate stations were 23% and 29% of those of the nitrate replete stations. Furthermore, *f* ratios were also significantly reduced (Table 3), with the average *f* ratio being lowered from 0.71 to 0.39.

Rates of nutrient removal were also estimated from the changes in nutrient concentrations through time (Sambrotto et al., 1993; Smith, 1993). Given the complex flow patterns and the magnitude of exchanges within the region (Budéus and Schneider, 1995; Johnson and Niebauer, 1995; Schneider and Budéus, 1995), it is difficult (if not impossible) to

Table 2

Surface and integrated water column nitrogen uptake rates (means and standard deviations) as a function of ice concentration

| Variable | Ice concentration | | |
|--|--------------------------|--------------------------|--------------------------|
| | 0–2/10 | 3–6/10 | 7–10/10 |
| Surface ammonium uptake ($\mu\text{mol l}^{-1} \text{h}^{-1}$) | 0.0024 \pm 0.0029 (87) | 0.0027 \pm 0.0024 (22) | 0.0018 \pm 0.0021 (30) |
| Integrated ammonium uptake (mmol m ⁻² h ⁻¹) | 0.063 \pm 0.049 (40) | 0.073 \pm 0.070 (11) | 0.053 \pm 0.49 (11) |
| Surface nitrate uptake ($\mu\text{mol l}^{-1} \text{h}^{-1}$) | 0.0056 \pm 0.012 (84) | 0.0026 \pm 0.0025 (20) | 0.0045 \pm 0.0053 (30) |
| Integrated nitrate uptake (mmol m ⁻² h ⁻¹) | 0.162 \pm 0.138 (40) | 0.131 \pm 0.070 (10) | 0.072 \pm 0.057 (11) |
| Surface urea uptake ($\mu\text{mol l}^{-1} \text{h}^{-1}$) | 0.0021 \pm 0.0039 (35) | 0.0008 \pm 0.0006 (4) | 0.0007 \pm 0.0021 (19) |
| Integrated urea uptake (mmol m ⁻² h ⁻¹) | 0.037 \pm 0.058 (15) | 0.091 \pm 0.062 (2) | 0.019 \pm 0.022 (6) |
| Surface <i>f</i> ratio | 0.59 \pm 0.30 (84) | 0.46 \pm 0.29 (20) | 0.67 \pm 0.30 (29) |
| Integrated <i>f</i> ratio | 0.67 \pm 0.22 (40) | 0.63 \pm 0.13 (10) | 0.79 \pm 0.56 (11) |

Surface values represent the pooled values from the 100% and 50% isolumes. *f* ratios are the ratios of nitrate uptake to the sum of nitrate and ammonium uptake and do not include the effects of urea uptake. Numbers in parentheses indicate the number of samples for each variable. All integrations are from the surface to the 0.1% isolume.

Table 3

Rates of nitrate uptake as a function of nitrate availability in surface waters of the Northeast Water Polynya

| Parameter | [NO ₃] < 0.5 μM | [NO ₃] > 0.5 μM |
|--|-----------------------------|-----------------------------|
| Mean specific rate of nitrate uptake (h ⁻¹) | 0.0018 ^a | 0.0078 |
| Standard deviation | 0.0019 | 0.0098 |
| Number of observations | 34 | 33 |
| Mean absolute rate of nitrate uptake (μmol l ⁻¹ h ⁻¹) | 0.0019 ^a | 0.0063 |
| Standard deviation | 0.0016 | 0.0066 |
| Number of observations | 34 | 33 |
| Mean <i>f</i> ratio | 0.39 ^a | 0.71 |
| Standard deviation | 0.24 | 0.25 |
| Number of observations | 34 | 33 |

Surface uptake values were split into two groups, the first which had less than 0.5 μM nitrate at the start of incubations and the second with more than 0.5 μM nitrate. Low concentrations of nitrate resulted in reduced rates of nitrate uptake, suggesting nitrate limitation in the summer.

^a $p < 0.001$.

isolate only those waters that reflect in situ removal of nutrients. Despite this complication, two independent analyses of nutrient removal were conducted. The first simply pooled all nitrate data from all stations where nitrogen uptake experiments were conducted and which were dominated by East Greenland Shelf Water, and the nitrate concentration was regressed against time (Fig. 4). The resultant regression [NO₃ = -0.0463DAT + 10.47 where DAT is the Julian date; $n = 140$, $r^2 = 0.58$] gave a net nitrate uptake at the surface (using a Model II regression) of 0.061 μmol l⁻¹ d⁻¹ (Fig. 4), which can be

compared to the average surface (100% and 50% isolumes) ¹⁵N-nitrate uptake rate for all stations ($n = 134$) of 0.0049 μmol l⁻¹ h⁻¹ (0.12 μmol l⁻¹ d⁻¹). Using the same data, the nitrate uptake rate was computed by approximating the nitrate uptake at the beginning of the study from a nitrate concentration for Polar Water which had not been influenced by biological uptake (ca. 4 μM; PSt St. 17, 80°00'N, 17°16'W), selecting the date of the earliest observed zero-nitrate value (Julian date 188), and computing the slope from a line connecting those two points. The initial nitrate value of 4 μM was chosen to

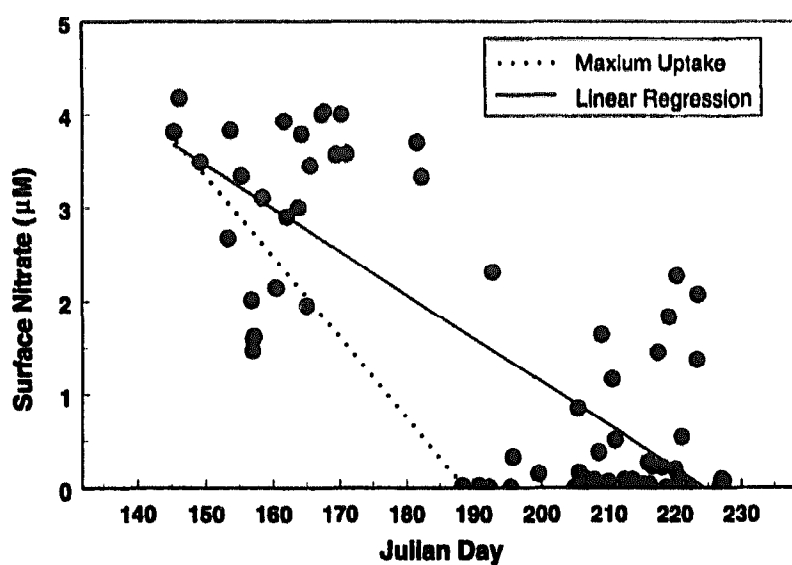


Fig. 4. A time series of surface nitrate concentrations from all stations where ¹⁵N uptake experiments were conducted. The solid line represents the linear regression (Model II; Laws and Archie, 1981) for these data, and the dotted line represents the maximum possible uptake rate as determined from the nitrate concentration prior to biological removal and the first observation of zero nitrate water (see text for details).

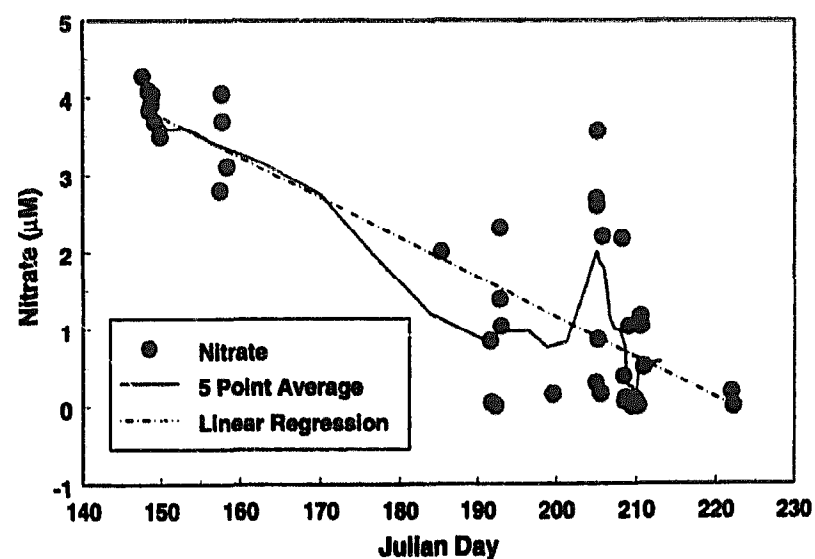


Fig. 5. A time series of surface nitrate concentrations near 80° 25'N, 13° 40'W. Only those stations which showed the upper 40 m being dominated by East Greenland Shelf Water were included in the analysis. The dashed line represents the linear regression (Model II; Laws and Archie, 1981) of unfiltered data, and the solid line connects five-point running means.

correspond with the maximal euphotic zone value observed in the cruise. This procedure resulted in a net nitrate uptake rate of $0.091 \mu\text{mol l}^{-1} \text{d}^{-1}$ (Fig. 4).

The second method used to assess net nutrient removal was to analyze surface nitrate concentrations at one location occupied repeatedly during the study. Using this approach, the temporal pattern of nitrate removal at stations in which the upper 40 m were dominated by East Greenland Shelf Water (salinities less than 32.4 p.s.u.) at one location ($80^{\circ} 25' \text{N}$, $13^{\circ} 40' \text{W}$) was assessed (Fig. 5). The nutrient removal rate for the restricted data set from this location was determined by linear regression (Fig. 5), as was done previously for the entire cruise data set (Fig. 4). Simple regression [$\text{NO}_3 = -0.0520\text{DAT} + 11.56$; $n = 42$; $r^2 = 0.69$] gave (using a Model II regression; Laws and Archie, 1981) a surface nitrate uptake of $0.063 \mu\text{mol l}^{-1} \text{d}^{-1}$. A five-point running average also demonstrated the same trend. The data tend to be variable because the location was near the boundary of the nutrient-rich flow which emerged from the Norske Øer ice barrier. Because the spatial extent of this water mass varied in time, its influence on the surface nutrient concentrations also varied temporally.

4. Discussion

Based on extensive summer observations in 1992, the Northeast Water Polynya had been characterized as a moderately productive region (Smith, 1995). However, the sampling period at that time did not include the period during which nutrient concentrations are elevated and algal biomass is low (i.e., early in the growing season). That earlier study also did not consider interannual variability, since no other data were available for comparison. The results of this study demonstrate that the nitrate uptake rates in July–August, 1993, were similar to those measured using the same techniques in July–August, 1992. The 1993 seasonal data clearly demonstrate the degree of spatial and temporal variability that is encountered in the polynya. The data were collected from an incredibly complex physical region, with extremely wide ranges of ice concentrations, ambient nutrients, irradiance levels, and vertical stratification.

This natural variability would reduce the strength of any statistical analysis of the trends we observed. Furthermore, the biotic assemblages (both autotrophic and heterotrophic components) were also markedly different in time and space (Smith et al., 1995; Booth and Smith, 1997-this volume), and thus this amount of variability in the rate process data was not unexpected.

The mean integrated nitrate and ammonium uptake rates in 1992 were 0.210 and $0.052 \text{mmol m}^{-2} \text{h}^{-1}$, respectively, similar to those measured in 1993 from the *Polar Sea* during the same months (0.167 and $0.075 \text{mmol m}^{-2} \text{h}^{-1}$; Table 1). Integrated f ratios found in 1993 were very similar to those found in 1992 (0.66 vs. 0.69). The overall mean nitrate uptake rate for the seasonal study ($0.141 \text{mmol m}^{-2} \text{h}^{-1}$) was not greatly different from that observed in July–August, 1992, although the seasonal trend of increasing new and regenerated production was apparent (Fig. 3). Urea uptake has never been measured in the polynya before, but the rates we observed are similar to those found by Harrison et al. (1985) in Baffin Bay. The contribution of urea was approximately equal to that of ammonium (Table 1).

If the mean integrated ^{15}N -nitrate uptake rate for the entire sampling period ($0.141 \text{mmol m}^{-2} \text{h}^{-1}$) is converted into daily carbon production using the average C/N atomic ratio observed in 1993 (8.9 ; Daly, 1995), new production rates equal $0.361 \text{g C m}^{-2} \text{d}^{-1}$. The measured C/N ratio was greater than that of the Redfield ratio (6.6), and other extreme variations have been observed in field studies (e.g., Sambrotto et al., 1993). Clearly the use of one ratio introduces uncertainty into the quantitative assessment of new production, but we use the observed ratio in all further estimates. During the summer of 1992, the average new production (based on changes in nitrate concentrations and an assumed onset of productivity of May 1) was $0.245 \text{g C m}^{-2} \text{d}^{-1}$ (Smith, 1995); hence, the mean new production rates were not markedly different, despite the differences in dates and positions of sampling and methods of calculation. One possible cause of this similarity is that, on average, the polynya's phytoplankton assemblage was growing at close to its temperature-mediated maximal growth rate (Eppley, 1972) and, because nutrient levels were the same at the onset of the growing season, the average rate of new produc-

tion would also be similar. If this were so, then the new production should be quantitatively similar each year, but the timing of the production might vary as a function of ice cover. Other physical factors might stimulate new production rates by providing inputs of nitrate to surface waters (vertical mixing over sills and topographic features, upwelling, etc.). Lara et al. (1994) suggested that upwelling or emergence of nutrient-rich waters along the Norske Øer ice barrier might be common enough to increase rates of new production appreciably.

The maximum rate of integrated new production as measured by ^{15}N -tracer techniques was $0.622 \text{ mmol m}^{-2} \text{ h}^{-1}$ (Table 1), which is equal to $1.59 \text{ g C m}^{-2} \text{ d}^{-1}$ and was over twice that of the average ($0.361 \text{ g C m}^{-2} \text{ d}^{-1}$). Similarly, the maximum rate of uptake as determined from the disappearance of nitrate in the surface layer was $0.091 \mu\text{mol l}^{-1} \text{ d}^{-1}$ (Fig. 4). If the same ratio that was found between the surface ^{15}N -uptake rate and the integrated ^{15}N -based new production is assumed for nitrate removal (28.82), then productivity would equal to $0.281 \text{ g C m}^{-2} \text{ d}^{-1}$. Using the same relationship, the linear regression-derived uptake rate using all the nitrate data ($0.061 \mu\text{mol l}^{-1} \text{ h}^{-1}$) would suggest a long-term (i.e., over weeks to months) new production of $0.144 \text{ g C m}^{-2} \text{ d}^{-1}$. New production estimates from the time-series station gave a similar result ($0.161 \text{ g C m}^{-2} \text{ d}^{-1}$). Wallace et al. (1995b) estimated new production in 1992 based on nutrient changes at selected stations along the axis of a trough in the region. The production they estimated from their regression ($41.4 \text{ mmol C m}^{-2} \text{ d}^{-1}$, or $497 \text{ mg C m}^{-2} \text{ d}^{-1}$) had a standard deviation of $16.1 \text{ mmol C m}^{-2} \text{ d}^{-1}$, which implies a 'range' of $304\text{--}694 \text{ mg C m}^{-2} \text{ d}^{-1}$. Although our estimates converge on the lower end of the Wallace et al. estimate, they are not grossly different, given the different data used in each analysis as well as the different techniques.

All nutrient depletion calculations depend on the value used for the initial nitrate concentration. In most areas of the ocean, this value can be easily measured or predicted, but in the Northeast Water Polynya no samples have been collected in winter. Furthermore, mixing throughout the entire water column is likely in certain locations (Wallace et al., 1995a), and hence surface nitrate concentrations might be expected to be similar to those of North

Atlantic Intermediate Water (nitrate concentrations from 5 to $7 \mu\text{M}$; Wallace et al., 1995b). Our earliest occupation of the polynya (early June) showed euphotic zone concentrations of ca. $4 \mu\text{M}$, indicating that their origin was from Polar Water. We used $4 \mu\text{M}$ as the initial value, but recognize that new production calculations would be increased by 50% if winter nitrate concentrations were indeed derived from mixing with NAIW.

These values are also only slightly less than those determined by direct ^{15}N incubations; in fact, it is surprising that the rates of new production derived from nitrate disappearance (which result from processes over the time scale of months) are so close to those measured by tracer incubations (seasonal mean of $0.141 \text{ mmol m}^{-2} \text{ h}^{-1}$ or $0.361 \text{ g C m}^{-2} \text{ d}^{-1}$). This was unexpected because the nitrate concentrations of the surface layer can be influenced by physical processes which introduce nitrate from below into the surface layer, thereby reducing the calculated new production. Furthermore, they can also be augmented by in situ nitrification (not measured during our study). Nutrient dilution via ice and terrestrial glacial meltwater addition might reduce surface concentrations, thereby creating overestimates of calculated production rates (salinity corrections were not included in our analysis). Isotopically derived rates, however, can be overestimates, because of grazer exclusion and placement in an optimal irradiance environment in the deck incubators. It is also possible that the low ambient concentrations of nitrate observed (nitrate was below $0.5 \mu\text{M}$ at 34 of the 71 stations) caused a significant drop in the rates within the 24 h incubations and resulted in lowered ^{15}N -uptake rates. However, ^{15}N -nitrate uptake time courses at low nitrate stations did not substantiate this hypothesis (Smith, unpubl. data). The most important result is that *all* estimates suggest that new production is not large, at least relative to other regions. For example, new production during blooms in the Greenland, Bering and Barents seas has been measured to be 3.3 , 2.4 and $2.8 \text{ g C m}^{-2} \text{ d}^{-1}$, respectively (Sambrotto et al., 1986; Smith, 1993; Kristiansen et al., 1994), which can be compared to our maximum new production of $1.6 \text{ g C m}^{-2} \text{ d}^{-1}$. It also emphasizes that the environmental mosaic present in the polynya over long time periods produces a 'mean' environment, which results in a

much more uniform new production rate than might be inferred from short-term sampling.

Previous investigations have suggested that phytoplankton growth in the polynya is limited by nitrogen concentrations (e.g., Lara et al., 1994; Smith, 1995). Our results found that the mean summer production was greater than that in the spring (but not significantly, given the variability encountered), and that only a small decrease in the average occurred in the late summer (Fig. 2). However, if the mean uptake rate for those samples with nitrate concentrations less than $0.5 \mu\text{M}$ is compared to that for samples with nitrate concentrations greater than $0.5 \mu\text{M}$, the uptake rate at nitrate-depleted stations is only one-third that of non-limiting nitrate levels and is significantly different (Table 3). This strongly suggests that nitrate does indeed limit productivity at selected locations within the polynya, and that the coarse seasonal (and spatial) description we have provided does not adequately resolve this limitation. Furthermore, the diffusive input of nitrate was calculated using the equations of King and Devol (1979) for selected stations in the polynya. In general, early in the summer when stratification was weakest, nitrate diffusive flux at times equalled uptake but, as stratification strengthened, the diffusive flux decreased to a small percentage of uptake. For example, at PSt Station 33 in mid-June the diffusive supply of nitrate through 25 m was greater than 50% of uptake, whereas at PS Station 86 the flux had decreased to less than 10% of uptake (assuming large diffusive coefficients to estimate maximum diffusive inputs). Hence, the role of nitrogen in limiting phytoplankton growth and yield was greater late in the summer when thermal stratification was strongest.

Yager et al. (1995) have suggested that the polynya might act as a regional carbon sink, by virtue of phytoplankton growth reducing the inorganic carbon levels and creating a flux of carbon into the water column from the atmosphere, and then the exchange with the atmosphere in winter being minimized as a result of the ice cover. The magnitude of any flux in summer would be dependent on the new production of the region. We have shown that the rates of new production in the Northeast Water Polynya are ca. $0.25\text{--}0.36 \text{ g C m}^{-2} \text{ d}^{-1}$ (depending on the method of calculation), and that reduced

surface layer concentrations of nitrate in the late summer result in decreased new production rates and nitrate limitation in this highly stratified environment. Use of these data (and other, such as ^{14}C uptake) in the context of system-wide carbon flux estimates may further refine our knowledge of the temporal and spatial variability within the polynya. The patterns and magnitude of new production may prove to be useful as a model for assessing the structure and function of other continental shelf systems of the high Arctic.

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