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increased productivity (Arrigo and McLain, 1994).

[redacted]

environment of the polynya (Arctic Ocean Sciences

[redacted]

of polynyas might be transferred to higher trophic

[redacted]

tions independent of productivity are also possible.

[redacted]

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

[redacted]

production.

The Northeast Water polynya has been studied intensively in the past few years. Hirche et al. (1991)

[redacted]

phytoplankton and zooplankton biomass than those

[redacted]

additional input of nutrients via physical processes. Smith et al. (1995) and Smith (1995) occupied 81

[redacted]

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

[redacted]

via nutrients. Despite the reduced nitrate levels, productivity was largely nitrate-based. Little evidence

[redacted]

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

[redacted]

Polar Sea) sampled the region continuously during

[redacted]

ents, hydrography, primary productivity, and new

[redacted]

describes the rates of new production as calculated

[redacted]

control of new production by nitrogen availability.

2. Materials and methods

[redacted]

Water Polynya from May 25 to July 29, 1993 from

[redacted]

14, 1993 from the USCGC *Polar Sea* (PS). A total

[redacted]

and 38 on the *Polar Sea* (Fig. 1b). A time series was

[redacted]

sor and Niskin bottles fitted with Teflon-coated closure springs, we recorded temperature, salinity and

[redacted]

and 0.1% of surface irradiance).

[redacted]

quantified using a Technicon Autoanalyzer-II system prior to the production measurements by standard automated techniques. Urea concentrations and stan-

[redacted]

University after the cruise using an Alpkem Autoanalyzer, with the procedure being based on the urea–

[redacted]

mined 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

[redacted]

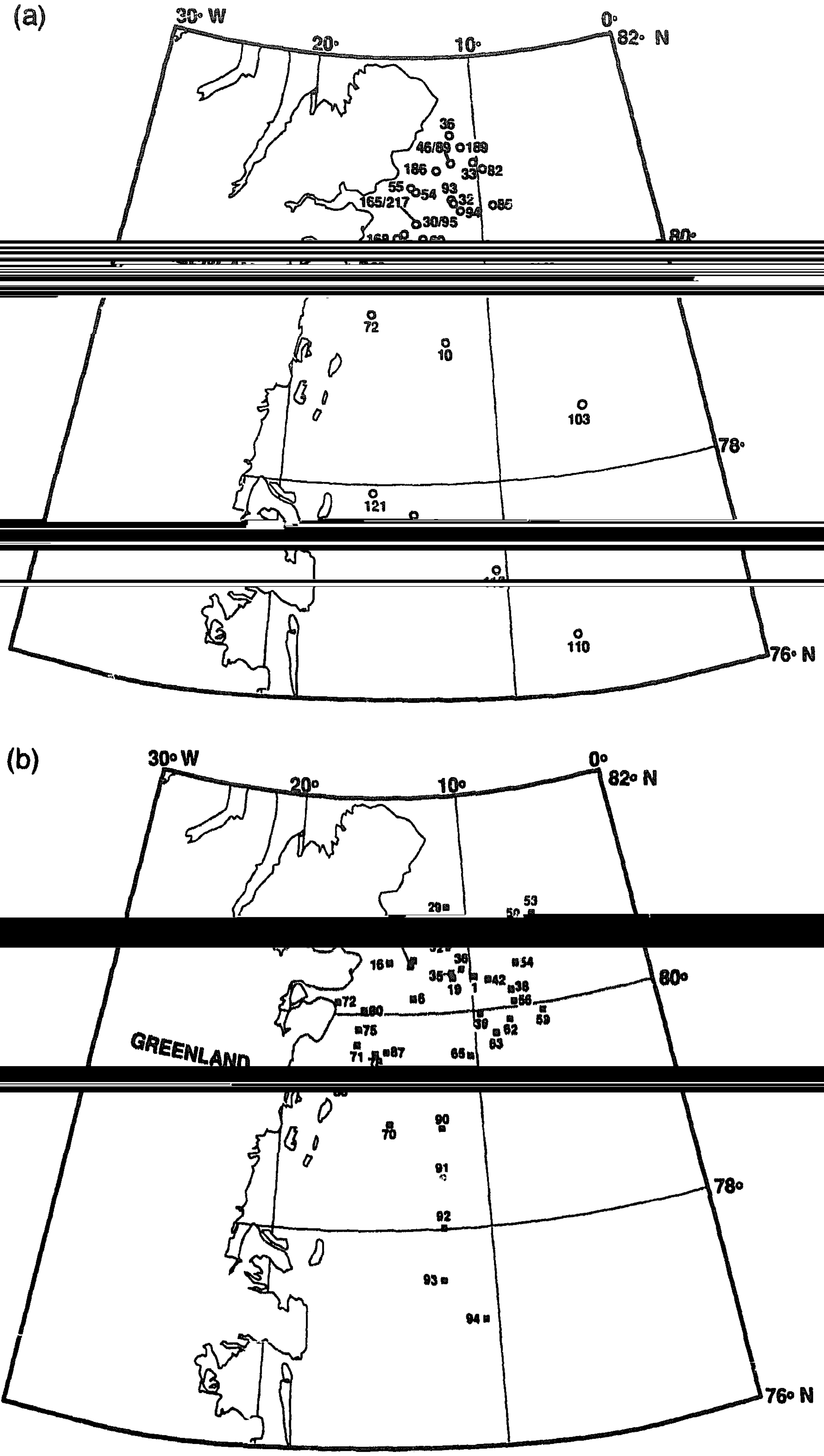


Fig. 1. Map showing the location of the stations where ^{15}N nitrogen uptake was measured during (a) *Polarstern* cruises ARK IX/2 and 3

were calibrated using commercially prepared stan- [illegible] dards (Smith et al., 1993).

Rates of nitrate, ammonium and urea uptake were quantified using stable-isotope tracer techniques and [illegible] ^{15}N-labelled nitrate, ammonium and urea (95–99% carrier free) were prepared from crystalline salts and [illegible] isotopic additions were such to create final concen- [illegible] or 0.05 μM 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 [illegible] less than 0.5 μM, 0.05 μmol l^{-1} were added to [illegible] conducted in 500 ml screw-capped polycarbonate bottles. The simulated in situ incubators were positioned on deck in unshaded locations, and running [illegible] troughs, each of which was wrapped with appropri- [illegible] ate quantities of neutral density screen [illegible] Inc.) to reduce the irradiance to the amounts from [illegible] spectral quality changes with depth, one layer of screen used was a blue filter, which was applied to [illegible] ance.

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. [illegible] and stored for return to the laboratory for analysis. The samples from the *Polarstern* were analyzed using a mass spectrometer (Europa Scientific), and [illegible] bustion. 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 [illegible] of particulate nitrogen and the rates of inorganic nitrogen uptake, the difference between pre- and post-incubation PN concentrations was, on average, [illegible] lated using equation 3 of Dugdale and Wilkerson (1986), and uptake was expressed as hourly rates by [illegible] tions for isotope dilution were made because corrections as calculated by the method of Kanda et al. [illegible] dilution effects calculated from assumed regenera- [illegible] 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 [illegible] rections for uptake of dissolved organic nitrogen [illegible]

3. Results

[illegible] stratification through time, and by mid-summer the [illegible] 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 [illegible] centrations at a location which was repeatedly occupied (ca. 80° 25′N, 13° 40′W) were initially high but decreased through time (Fig. 2); conversely, the stratification at those stations became stronger with [illegible] layer at most stations were ca. 4 μM, which is typical for the local East Greenland Shelf Water.

Phytoplankton biomass was initially low, and did [illegible] served by the *Polarstern* and *Polar Sea* were 9.9 (PSt 223) and 7.4 μg l^{-1} (PS 57), respectively, although the maximum within most stations was less [illegible] Maximum surface productivity during the *Polarstern* survey was 7.08 mg C m^{-3} h^{-1} (Legendre et al.,

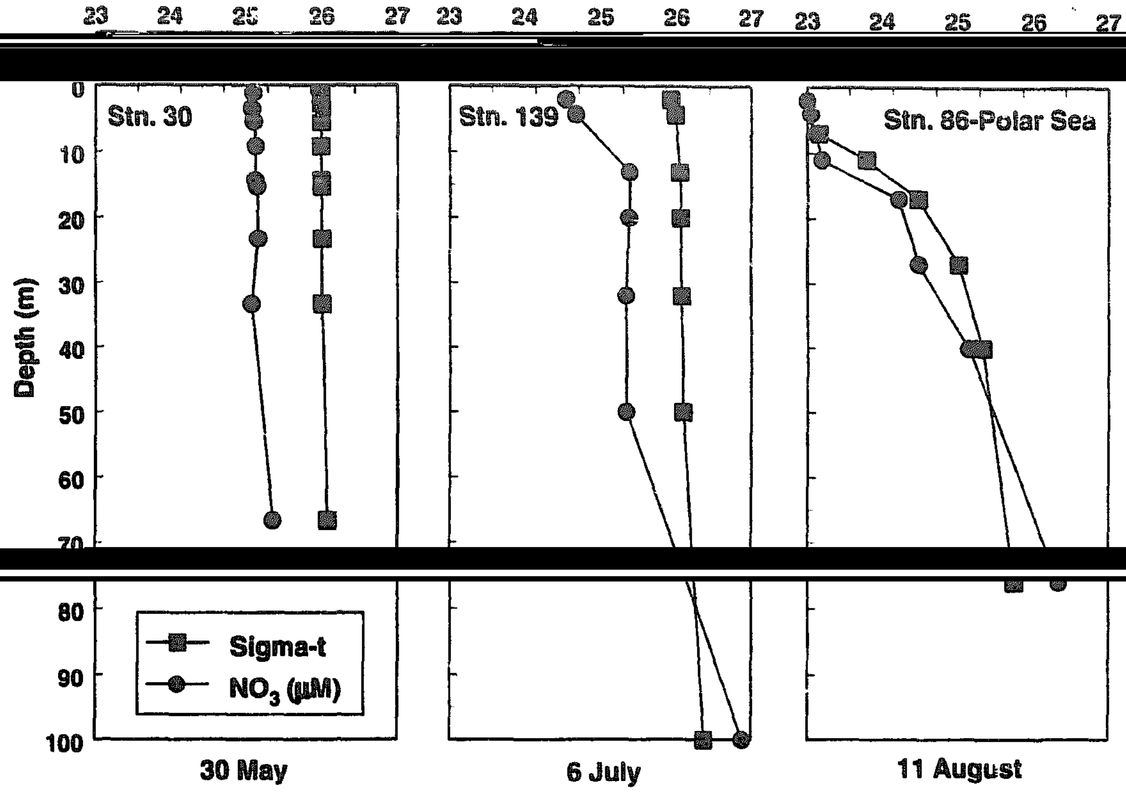


Fig. 2. The vertical distribution of σ_t (a measure of density) and nitrate at selected stations. (left) PSt 30 (80°44′N, 13°20′W). (middle) PSt 139 (80° 27′N, 10°56′W). (right) PS 86 (80°23′N, 13°26′W). The data were collected from stations occupied at intervals of approximately 5 weeks.

1994b) whereas during the *Polar Sea* cruise it was 0.92 mg C m^{-3} h^{-1} (Smith, unpublished; data available from the NSIDC, Boulder, CO). Although the spatial distribution of phytoplankton biomass and [illegible] was proceeding throughout the region, and biogenic [illegible] (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 [illegible] *Polarstern* cruise were 0.097, 0.044 and 0.075 mmol [illegible] *Sea* cruise average rates of nitrate and ammonium uptake were 0.167 and 0.075 mmol m^{-2} h^{-1} (Table [illegible] 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 (±0.24; $n = 11$) whereas those collected from June 21–July 19 from the same cruise averaged 0.49 (±0.22; $n = 11$) indicating a significant ($p < 0.01$) decrease through time in the dependence on nitrate. [illegible] ice concentration present at the time of sampling, [illegible] (Table 2). However, the average integrated water column ni-

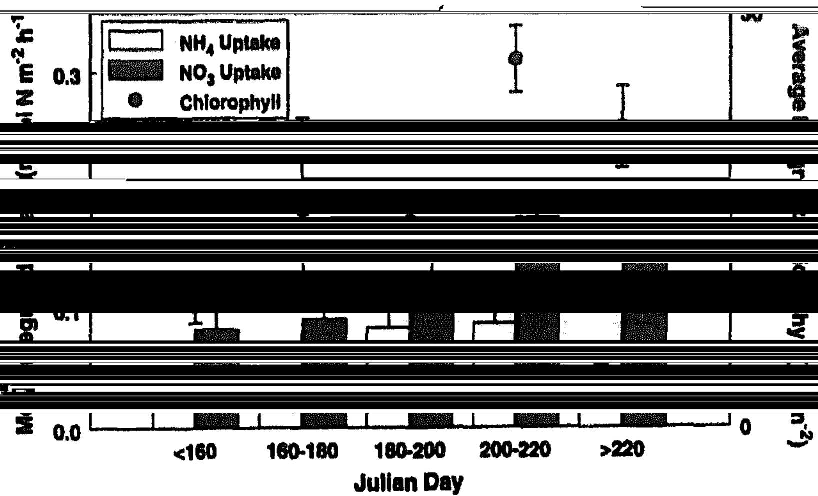


Fig. 3. Average nitrate and ammonium uptake rates during five, 20 day periods during the study. Also included are integrated euphotic zone concentrations of chlorophyll for the same stations and periods. The bars represent the standard error for each interval. Mean *f* ratios for the five periods were: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

[redacted]	[redacted]	[redacted]	[redacted]	[redacted]
		$(\mathrm{mmol\ m^{-2}\ h^{-1}})$	$(\mathrm{mmol\ m^{-2}\ h^{-1}})$	$(\mathrm{mmol\ m^{-2}\ h^{-1}})$
Polarstern	Mean	0.097	0.044	0.038
Polarstern	σ	0.108	0.090	0.055
Polarstern	Maximum	0.439	0.181	0.178
Polarstern	Minimum	0.006	0.0013	0.0007
Polarstern	n	22	23	22
[redacted]	[redacted]	[redacted]	[redacted]	[redacted]
[redacted]	[redacted]	[redacted]	[redacted]	[redacted]
Polar Sea	Maximum	0.622	0.269	ND
Polar Sea	Minimum	0.0049	0.0045	ND
Polar Sea	n	38	38	ND

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 [redacted] appeared to increase in mid-summer, but lack of data during the *Polar Sea* cruise precludes a quantitative [redacted]

[redacted] 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 [redacted]

measured uptake rates (Table 3). At the low nitrate stations, both specific and absolute nitrate uptake rates were significantly ($p < 0.001$) reduced, and [redacted] nificantly reduced (Table 3), with the average f ratio being lowered from 0.71 to 0.39.

[redacted] the complex flow patterns and the magnitude of exchanges within the region (Budéus and Schneider, 1995; Johnson and Niebauer, 1995; Schneider and [redacted]

Table 2
Surface and integrated water column nitrogen uptake rates (means and standard deviations) as a function of ice concentration [redacted]

	0–2/10	3–6/10	7–10/10
[redacted]	[redacted]	[redacted]	[redacted]
Surface nitrate uptake $(\mu\mathrm{mol\ l^{-1}\ h^{-1}})$	0.0056 ± 0.012 (84)	0.0026 ± 0.0025 (20)	0.0045 ± 0.0053 (30)
Integrated nitrate uptake $(\mathrm{mmol\ m^{-2}\ h^{-1}})$	0.162 ± 0.138 (40)	0.131 ± 0.070 (10)	0.072 ± 0.057 (11)
[redacted]	[redacted]	[redacted]	[redacted]
Integrated f ratio	0.67 ± 0.22 (40)	0.63 ± 0.13 (10)	0.79 ± 0.56 (11)

Surface values represent the pooled values from the 100% and 50% isolumes. [redacted] 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

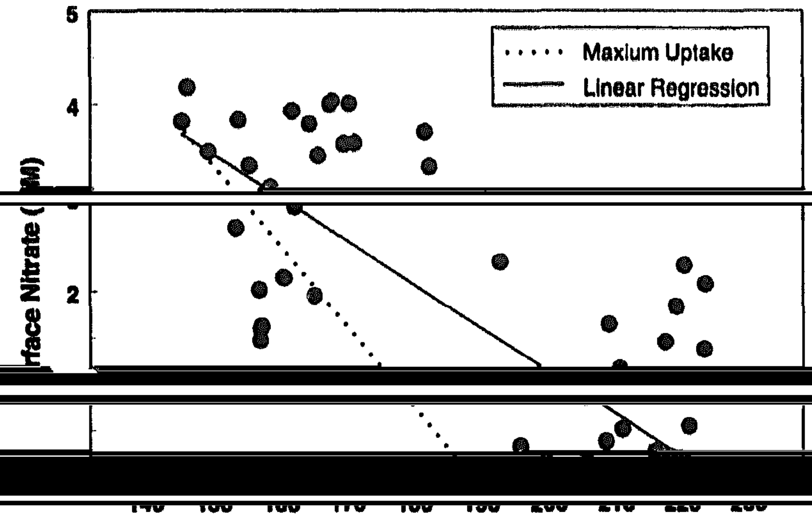
[illegible]	[illegible]	[illegible]
Mean specific rate of nitrate uptake (h^{-1})	0.0018 [a]	0.0078
Standard deviation	0.0019	0.0098
Number of observations	34	33
Mean absolute rate of nitrate uptake (μmol l^{-1} h^{-1})	0.0019 [a]	0.0063
Standard deviation	0.0016	0.0066
Number of observations	34	33
Mean f ratio	0.39 [a]	0.71
Standard deviation	0.24	0.25
Number of observations	34	33

[illegible]

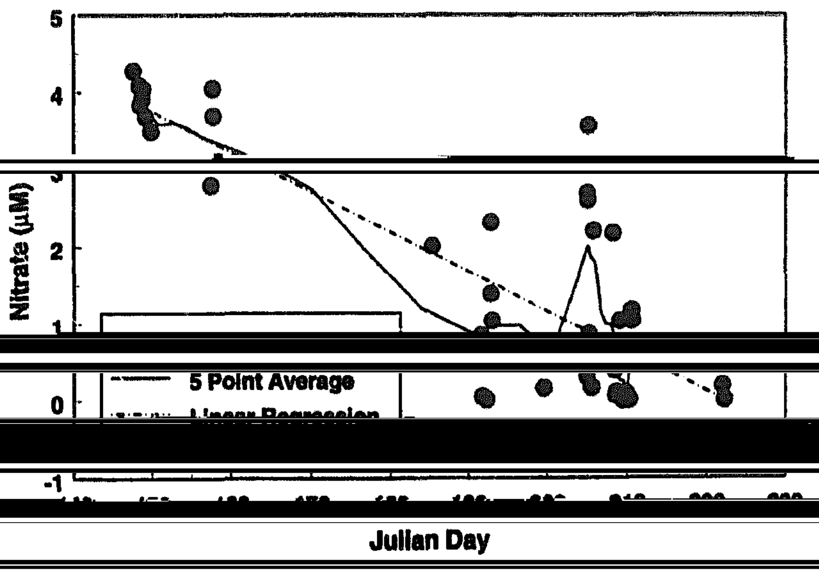
[a] $p < 0.001$.

isolate only those waters that reflect in situ removal [illegible] 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 [$NO_3 = -0.0463DAT + 10.47$ 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% [illegible] isolumes) [illegible] ($n = 134$) 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



[illegible] line represents the linear regression (Model II; Laws and Archie [illegible] water (see text for details).



[illegible] 25′N, 13° 40′W. Only those stations which showed the upper 40 [illegible] solid line connects five-point running means.

correspond with the maximal euphotic zone value observed in the cruise. This procedure resulted in a [redacted] 4).

The second method used to assess net nutrient removal was to analyze surface nitrate concentrations at one location occupied repeatedly during the [redacted] (salinities less than 32.4 p.s.u.) at one location (80° 25′N, 13° 40′W) was assessed (Fig. 5). The nutrient [redacted] location was determined by linear regression (Fig. 5), as was done previously for the entire cruise data set (Fig. 4). Simple regression [$NO_3 = -0.0520DAT + 11.56$; $n = 42$; $r^2 = 0.69$] gave (using a Model II regression; Laws and Archie, 1981) a surface nitrate uptake of 0.063 µmol l^{-1} 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 [redacted] trations also varied temporally.

[redacted]

4. Discussion

Based on extensive summer observations in 1992, the Northeast Water Polynya had been characterized [redacted] 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 [redacted] in July–August, 1993, were similar to those mea- [redacted] 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. [redacted] totrophic 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 [redacted]

The mean integrated nitrate and ammonium up- [redacted] h^{-1}, respectively, similar to those measured in 1993 from the *Polar Sea* during the same months (0.167 [redacted] 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 mmol m^{-2} 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. [redacted] the entire sampling period (0.141 mmol m^{-2} h^{-1}) is converted into daily carbon production using the [redacted] Daly, 1995), new production rates equal 0.361 g C [redacted] that of the Redfield ratio (6.6), and other extreme [redacted] 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 g C m^{-2} d^{-1} (Smith, 1995); hence, the mean new production rates were not markedly different, despite the differences [redacted] 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 production would also be similar. If this were so, then the [illegible] a function of ice cover. Other physical factors might stimulate new production rates by providing inputs of [illegible] (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 [illegible] mmol m^{-2} h^{-1} (Table 1), which is equal to 1.59 g C m^{-2} d^{-1} and was over twice that of the average (0.361 g C m^{-2} d^{-1}). Similarly, the maximum rate of uptake as determined from the disappearance of nitrate in the surface layer was 0.091 μmol l^{-1} d^{-1} [illegible] 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 g C m^{-2} d^{-1}. Using the same relationship, the linear [illegible] g C m^{-2} d^{-1}. New production estimates from the time-series station gave a similar result (0.161 g C m^{-2} d^{-1}). Wallace et al. (1995b) estimated new production in 1992 based on nutrient changes at [illegible] region. The production they estimated from their regression (41.4 mmol C m^{-2} d^{-1}, or 497 mg C m^{-2} d^{-1}) had a standard deviation of 16.1 mmol C m^{-2} d^{-1}, which implies a 'range' of 304–694 mg C m^{-2} d^{-1}. Although our estimates converge on the lower end of the Wallace et al. estimate, they are not greatly different, given the different data used in each analysis [illegible]

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 [illegible] Furthermore, mixing throughout the entire water column is likely in certain locations (Wallace et al., 1995a), and hence surface nitrate concentrations [illegible]

Atlantic Intermediate Water [illegible] photic zone concentrations of ca. 4 μM, indicating that their origin was from Polar Water. We used 4 [illegible] if winter nitrate concentrations were indeed derived from mixing with NADW.

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 [illegible] cesses over the time scale of months) are so close to those measured by direct incubations (seasonal mean of 0.141 mmol m^{-2} h^{-1} or 0.361 g C m^{-2} d^{-1}). This was unexpected because the nitrate concentrations of the surface layer can be influenced by [illegible] low 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 [illegible] tions 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 [illegible] of nitrate observed (nitrate was below 0.5 μM 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). [illegible] 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 g C m^{-2} d^{-1}, respectively (Sambrotto et al., 1986; Smith [illegible] pared to our maximum new production of 1.6 g C m^{-2} d^{-1}. It also emphasizes that the environmental mosaic present in the polynya over long time periods [illegible]

[redacted]

[redacted]

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 [redacted] not significantly, given the variability encountered), [redacted] curred in the late summer (Fig. 2). However, if the [redacted] for samples with nitrate concentrations greater than 0.5 μM, the uptake rate at nitrate-depleted stations is only one-third that of non-limiting nitrate levels and [redacted] 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 calcu- [redacted] for selected stations in the polynya. In general, early [redacted] creased to a small percentage of uptake. For example, at PSt Station 33 in mid-June the diffusive [redacted] of uptake, whereas at PS Station 86 the flux had decreased to less than 10% of uptake (assuming [redacted] limiting phytoplankton growth and yield was greater late in the summer when thermal stratification was [redacted]

[redacted] production of the region. We have shown that the rates of new production in the Northeast Water [redacted]

[redacted] 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 [redacted] The patterns and magnitude of new production may [redacted] structure and function of other continental shelf sys- [redacted]

Acknowledgements

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References

[redacted]

pelagic coupling in the Northeast Water Polynya. J. Geophys. Res., 100: 4411–4422.

[redacted]

Arrigo, K.R. and McLain, C.R., 1994. Spring phytoplankton

[redacted]

mer 1993. J. Mar. Syst., 10: 241–261.

[redacted]

cal fluxes and stoichiometry in an Arctic marine system. Ph.D. Thesis, Univ. Tennessee, 183 pp.

[redacted]

Eppley, R.W., 1972. Temperature and phytoplankton growth in

[redacted]

Holm-Hansen, O., Lorenzen, C.J., Holmes, R.W. and Strickland, J.D.H., 1965. Fluorometric determination of chlorophyll. J.

[redacted]

Johnson, M. and Niebauer, H.J., 1995. The 1992 summer circulation in the Northeast Water Polynya from acoustic Doppler

[redacted]

^{15}N uptake experiments. J. Plankton Res., 9: 79–90.

King, F.D. and Devol, A., 1979. Estimate of vertical eddy diffusion through the thermocline from phytoplankton nitrate uptake rates in the mixed layer of the eastern tropical Pacific. Limnol. Oceanogr., 24: 645–651.

Koroleff, F., 1983. Determination of urea. In: K. Grasshoff, M.

[redacted]

Analysis. Verlag Chemie, Weinheim, pp. 158–162.

Kristiansen, S., Farbrot, T. and Wheeler, P.A., 1994. Nitrogen

[redacted]

regenerated production in the marginal ice zone. Limnol. Oceanogr., 39: 1630–1642.

Lara, R.J., Kattner, G., Tillmann, U. and Hirche, H.-J., 1994. The North East Water Polynya (Greenland Sea). II. Mechanisms of

[redacted]

(Editors), The 1993 Northeast Water Expedition data report of

[redacted]

Legendre, L., Gosselin, M., Pesant, S., Lessard, S., Fraikin, C.,

McGuiness, F. and Bergeron, G., 1994b. Primary production

[redacted]

1986. Relationships among vertical mixing, nitrate uptake, and phytoplankton growth during the spring bloom in the southeast

[redacted]

Sambrotto, R.N., Savidge, G., Robinson, C., Boyd, P., Takahashi, T., Karl, D.M., Langdon, C., Chipman, D., Marra, J. and

[redacted]

Smith, W.O., Jr., 1993. Nitrogen uptake and new production in the Greenland Sea: The spring *Phaeocystis* bloom. J. Geophys. Res., 98: 4681–4688.

Smith, W.O., Jr., 1995. Primary productivity and new production in the Northeast Water (Greenland) polynya during summer 1992. J. Geophys. Res., 100: 4357–4370.

[redacted]

1995. Particulate matter and phytoplankton and bacterial biomass distributions in the Northeast Water Polynya during

[redacted]

Stirling, I. and Cleator, H., 1981. Polynyas in the Canadian Arctic. Can. Wildl. Serv. Occas. Pap., 45: 70 pp.

Wallace, D.W.R., Hopkins, T.S., Behrens, W.J., Bignami, F., Deming, J., Kinder, C., Shi, Y., Smith, W.O., Top, Z. and

[redacted]

Yager, P.L., Wallace, D.W.R., Johnson, K.M., Smith, W.O., Jr.,

[redacted]

hypothesis. J. Geophys. Res., 100: 4389–4398.