

## Ammonium recycling limits nitrate use in the oceanic subarctic Pacific

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### Abstract

Seasonal and diel changes in nutrient concentrations and nitrogen assimilation rates were used to assess the effects of  $\text{NH}_4^+$  on  $\text{NO}_3^-$  assimilation. Surface-water  $\text{NO}_3^-$  concentrations ranged from 6 to 17  $\mu\text{M}$  while  $\text{NH}_4^+$  concentrations ranged from 0 to 0.4  $\mu\text{M}$ . Total N assimilation ranged from 84 to 732  $\text{nM d}^{-1}$  but showed no seasonal trend.  $\text{NH}_4^+$  and urea concentrations were <1% of total dissolved inorganic N, but use of this "regenerated" N still accounted for 44-89% of total N assimilation. Rates of  $\text{NO}_3^-$  assimilation were negatively correlated with ambient  $\text{NH}_4^+$  concentrations, and concentrations of  $\text{NH}_4^+$  between 0.1 and 0.3  $\mu\text{M}$  caused complete inhibition of  $\text{NO}_3^-$  assimilation.  $\text{NO}_3^-$  was more important as a source of N in spring than in summer. We attribute this pattern to a summer increase in turnover rates for  $\text{NH}_4^+$ . Turnover times for the dissolved  $\text{NH}_4^+$  pool were half as long in August as in May. Grazing and recycling in the euphotic zone apparently both play significant roles in preventing depletion of  $\text{NO}_3^-$  in the oceanic subarctic Pacific.

The most frequent forms of N taken up by phytoplankton are  $\text{NO}_3^-$  and  $\text{NH}_4^+$ . Dugdale and Goering (1967) introduced the distinction between "new production" (supported by  $\text{NO}_3^-$  oxidized from organic matter at depth in the water column) and "regenerated production" supported by  $\text{NH}_4^+$  and urea which are produced in the euphotic zone as a result of grazing and other degradation of organic material. The relative use of  $\text{NO}_3^-$  is usually expressed as the *f* ratio, i.e.  $\text{NO}_3^-$  uptake/total N uptake (Eppley and Peterson 1979). Upward fluxes of  $\text{NO}_3^-$  balance downward fluxes of particulate N in steady state systems (Eppley and Peterson 1979). Similarly, any net increase in biomass in the euphotic zone or export of biomass from a particular region requires either net depletion of dissolved  $\text{NO}_3^-$  in the euphotic zone or an equivalent upward flux of dissolved  $\text{NO}_3^-$ .

$\text{NO}_3^-$  assimilation, vertical transport of  $\text{NO}_3^-$  into the euphotic zone, and particulate N (PN) fluxes out of the euphotic zone

should be equivalent if the system being described is in steady state and there is no net transport of dissolved organic N. Consequently, two definitions of new production have arisen in the literature, one based on the form of N being used for primary production and one based on the flux of particulate material out of the euphotic zone. Here, we restrict our attention to the former definition, i.e. the absolute and relative amounts of  $\text{NO}_3^-$  supported production. Results are presented as *f* ratios, but we stress that they are not equivalent to the fraction of primary production that could leave the euphotic zone. The oceanic subarctic Pacific is not a steady state system for time scales <1 yr. Elsewhere (Wheeler et al. in prep.) we will compare various measures of new production and export production in the subarctic Pacific.

Phytoplankton use  $\text{NH}_4^+$ , urea, and  $\text{NO}_3^-$  as sources of N in that order of preference (McCarthy 1980). The physiological preference for  $\text{NH}_4^+$  is presumably derived from an energetic advantage, although this explanation has recently been questioned (Thompson et al. 1989). Reduction of  $\text{NO}_3^-$  to the oxidation level of organic N requires the equivalent of 8 electrons ( $\text{mol NO}_3^-$ )<sup>-1</sup>.  $\text{NH}_4^+$ , on the other hand, is already reduced. In most oceanic regions,  $\text{NO}_3^-$  concentrations are very low in surface water, and vertical transport of  $\text{NO}_3^-$  into the euphotic

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zone controls the availability of new N to phytoplankton. Since assimilation rates of  $\text{NO}_3^-$  in these regions are substrate limited,  $\text{NO}_3^-$  concentrations have been used to estimate the relative contribution of  $\text{NO}_3^-$  to primary production. To get reasonable results, however, Platt and Harrison (1985) had to eliminate stations with  $\text{NH}_4^+$  concentrations  $> 1 \mu\text{M}$  from the data used for their analysis.

A more generally applicable model for predicting  $f$  ratios requires knowledge of functional relationships for the effect of  $\text{NO}_3^-$  availability on uptake rates and the effect of  $\text{NH}_4^+$  on  $\text{NO}_3^-$  uptake. McCarthy (1981) proposed a hyperbolic relationship between  $\text{NH}_4^+$  concentrations and inhibition of  $\text{NO}_3^-$  uptake, and Harrison et al. (1987) assumed a hyperbolic relationship for evaluation of  $f$  ratios from coastal waters. Laboratory studies (Syrett 1981), however, show that  $\text{NH}_4^+$  has multiple effects on  $\text{NO}_3^-$  uptake, including inhibition of membrane transport, inhibition of  $\text{NO}_3^-$  reductase, and repression of  $\text{NO}_3^-$  reductase synthesis. Thus, it is unlikely that kinetics of inhibition follow a simple hyperbolic relationship. The inhibitory effect of  $\text{NH}_4^+$  on  $\text{NO}_3^-$  uptake in the Antarctic is well described by a linear relationship between  $\text{NH}_4^+$  concentration and  $\text{NO}_3^-$  uptake rate (Olson 1980; Glibert et al. 1982), but in the New York Bight an inverse hyperbola provided a good fit to the data (Garside 1981).

Further analysis of these relationships for oceanic waters has been precluded by the difficulty of obtaining accurate estimates of both nutrient concentrations and uptake rates. High nutrient concentrations in the subarctic Pacific are an exception that provides an opportunity to evaluate the effects of  $\text{NH}_4^+$  concentrations on  $\text{NO}_3^-$  assimilation for oceanic waters.  $\text{NO}_3^-$  concentrations in its surface water are high ( $> 6 \mu\text{M}$ ) throughout the year, but phytoplankton standing stocks (Chl levels) are low ( $< 1 \mu\text{g liter}^{-1}$ ) and relatively constant (Miller et al. 1988). The maintenance of low and constant phytoplankton stocks has been attributed to a balance between phytoplankton growth and grazing by copepods and microzooplankton (Frost 1987; Miller et al. 1988). A balance between primary produc-

tion and grazing also implies significant regeneration of reduced N within the euphotic zone.

Several hypotheses can be considered for explanation of the persistently high  $\text{NO}_3^-$  concentrations in the subarctic Pacific: phytoplankton growth is slow due to limitation by some other nutrient, possibly Fe (Martin et al. 1989); frequent or continuous upwelling or wind mixing replenishes the  $\text{NO}_3^-$  supply to the euphotic zone and prevents depletion; nitrification just below the euphotic zone rapidly replenishes  $\text{NO}_3^-$  and prevents depletion; or, grazing by copepods and microzooplankton results in low phytoplankton standing stocks and rapid  $\text{NH}_4^+$  regeneration, with  $\text{NH}_4^+$  recycling, in turn, reducing  $\text{NO}_3^-$  uptake and preventing  $\text{NO}_3^-$  depletion. The goal of this study was to examine the potential role of  $\text{NH}_4^+$  in regulating  $\text{NO}_3^-$  assimilation in this nutrient-rich oceanic region. The validity of alternate hypotheses for the persistently high  $\text{NO}_3^-$  concentrations in the subarctic Pacific is also examined.

The oceanic subarctic Pacific is a gyre system bounded on the south by the Subarctic Current and on the north by the Alaska Current. Nutrient concentrations are maximal at the center of the gyre (Reid 1973). Interannual variations in volumetric flow rates of the major currents of the Pacific Ocean, e.g. ENSO (El Niño southern oscillation) patterns, are apparent as far north as the subarctic Pacific and may cause interannual variations in the exact location of the gyre's center (Emery et al. 1985). Following the 1983 ENSO event the depth of the permanent halocline in 1984 was also apparently shallower (80–90 m) than the 100–150-m depth of more normal years (Denman and Gargett 1988). Most sampling for the SUPER program was at 50°N, 145°W (Canadian Weather Station P) because a large database is available for nutrients and other biological parameters. Additional sampling at 53°N, 145°W was included when possible to allow spatial comparison and to have additional information for waters closer to the gyre center.

Ambient nutrient concentrations and N assimilation rates, measured with  $^{15}\text{N}$  tracers, are presented and examined to deter-

mine if and when NH<sub>4</sub><sup>+</sup> availability influences NO<sub>3</sub><sup>-</sup> uptake rates. Background information on physical parameters were given by Denman and Gargett (1988). An overview of biological parameters and interactions was given by Miller et al. (1988), and estimates of phytoplankton biomass and growth rates were reported by Booth et al. (1988).

### Methods

*Study site*—Sampling was carried out as part of the subarctic Pacific ecosystem research (SUPER) program on six 1-month cruises in 1984 and 1987–1988. Sampling dates at 50°N were 1–21 May and 2–12 August 1984; 3–7, 14–19 June, and 19 September–1 October 1987; and 7–30 May and 10–13, 24–28 August 1988. Sampling dates at 53°N were 13–23 August 1984; 9–13, 24–28 June, and 13–17 September 1987; and 4–8, 15–22 August 1988.

*Water sampling*—Nutrient samples were taken twice daily (0600 and 1800 hours) from 12 depths with 5-liter Niskin bottles on a rosette sampler. Samples were withdrawn immediately from the Niskin bottles and stored in acid-washed polyethylene bottles on ice until analysis (within 1 h). Water for in situ and deck incubation experiments was collected in 20-liter, Teflon-lined GoFlo bottles. For in situ incubations, water was collected between 0300 and 0400 hours, and the in situ array was deployed between 0400 and 0500 hours. Retrieval of the array was ~24 or 48 h after deployment. For deck incubations, water was collected in the same manner between 0500 and 0800 hours, and incubations were started within 1 h.

*Nutrient analyses*—NO<sub>3</sub><sup>-</sup> concentrations were determined by the standard diazo dye formation as modified for autoanalyzers. Coefficients of variation for duplicate NO<sub>3</sub><sup>-</sup> analyses were typically <1.0%. NH<sub>4</sub><sup>+</sup> concentrations were determined either manually or by autoanalyzer with the phenolhypochlorite reaction (Grasshoff et al. 1983). Precision for duplicate manual NH<sub>4</sub><sup>+</sup> analyses was typically ±0.03 μM (SD). Autoanalyzer results were used when comparable precision could be achieved (i.e. 1984 and 1988). Urea was determined manually by

the diacetyl monoxime method (Price and Harrison 1987).

*Isotopic determinations of uptake rates*—NO<sub>3</sub><sup>-</sup> uptake rates were determined by 24- or 48-h “in situ incubations” in 1-liter polycarbonate bottles and 24-h “deck incubations” in 2.7-liter polycarbonate bottles with repeated sampling for time-course measurements. Bottles for deck incubations were screened with neutral density filters to approximate in situ light levels at appropriate depths, and surface seawater was used to cool the incubators. NO<sub>3</sub><sup>-</sup> (98.8 atom% <sup>15</sup>N) was added at concentrations of 1–2 μM (for a 10% enrichment over ambient NO<sub>3</sub><sup>-</sup> levels).

NH<sub>4</sub><sup>+</sup> and urea uptake rates at “trace” 0.1 μM concentrations (99.7 atom% <sup>15</sup>NH<sub>4</sub><sup>+</sup> and 98.0 atom% [<sup>15</sup>N]urea) were determined in separate bottles with repeated sampling for time-course measurements. For all deck incubations, samples were taken at 3–6 h, 7–12 h, and a final point at ~24 h. Particulate material from ~1 liter was collected on GF/F precombusted filters (500°C, 15 min), dried overnight at 60°C, and stored in Vacutainers before isotopic analysis. PN samples were taken at the beginning of each experiment by filtering 1 liter through Whatman GF/F filters. Persulfate digestion and subsequent analysis of NO<sub>3</sub><sup>-</sup> (Grasshoff et al. 1983) was used for analysis of PN collected on the filters. We used this procedure in preference to CHN analysis because we ran parallel samples of material collected on polycarbonate filters (Nuclepore membranes) for fractionation studies.

Isotope dilution of dissolved NH<sub>4</sub><sup>+</sup> was measured during the deck incubation experiments. Dissolved NH<sub>4</sub><sup>+</sup> in GF/F filtrates was recovered at each sampling time by conversion of NH<sub>4</sub><sup>+</sup> to indophenol and recovery of indophenol with solid-phase extraction with a modified elution solvent (Wheeler et al. 1989). Isotopic enrichment of the indophenol was determined in the same manner as for PN (below). Significant isotope dilution occurred in most NH<sub>4</sub><sup>+</sup> incubations, and the weighted mean NH<sub>4</sub><sup>+</sup> enrichment for each time interval was used to calculate uptake rates. The weighted mean NH<sub>4</sub><sup>+</sup> enrichment for each interval was calculated assuming an exponential decrease.

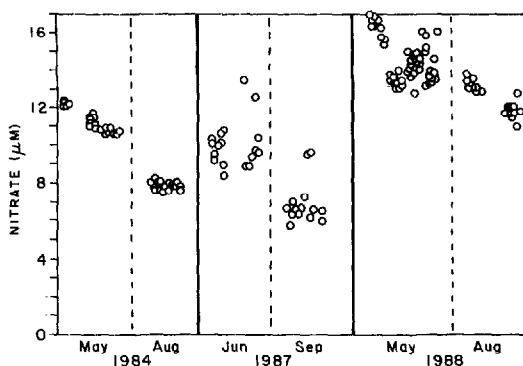


Fig. 1.  $\text{NO}_3^-$  concentrations in surface water at  $50^\circ\text{N}$  plotted as a function of day of month.

Assumption of a linear decrease (unweighted time mean) in enrichment would result in  $<10\%$  difference in calculated  $\text{NH}_4^+$  enrichments and in calculated uptake rates.

**Analysis of  $^{15}\text{N}$  enrichment**—All  $^{15}\text{N}$  samples were analyzed by emission spectrometry as described by Wheeler and Kirchman (1986). At least three peak scans were used for each ratio determination, and commercial isotope standards were used to calibrate the Jasco emission spectrometer. Coefficients of variation for the atom% enrichment values for triplicate combusted samples from a single time point were typically  $<1\%$ . Carrier blanks for the  $\text{NH}_4^+$  isotope dilution measurements were prepared in parallel with samples for each  $\text{NH}_4^+$  regeneration experiment. These carrier values were used to correct for isotope dilution resulting from reagent additions and sample handling.

**Calculations**—Specific uptake rates were

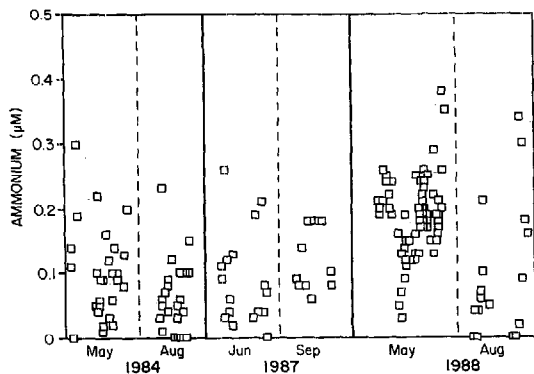


Fig. 2. As Fig. 1, but of  $\text{NH}_4^+$ .

Table 1. Net  $\text{NO}_3^-$  depletion in surface water at  $50^\circ\text{N}$ ,  $145^\circ\text{W}$ .

	Rate $\pm$ SE ( $\text{nM d}^{-1}$ )	<i>n</i>	<i>r</i> <sup>2</sup>
May 84	$98.3 \pm 7.3$	29	0.87
Jun-Jul 84	18.3		
Jul-Aug 87	39.0		
May 88	$412.6 \pm 77.8$	38	0.74
Aug 88	$159.9 \pm 12.7$	15	0.91

calculated as the atom% excess of PN divided by the enrichment of the nutrient source and the length of the incubation. Absolute uptake rates were calculated as the specific uptake rates times the amount of PN. Initial values for PN were used since no detectable changes occurred during incubation periods of  $\leq 48$  h. Values are given as means  $\pm 1$  SD unless otherwise noted. In order to check for possible underestimates of  $\text{NH}_4^+$  uptake, we compared the amount of  $^{15}\text{NH}_4^+$  removed from the medium to the amount recovered in the particulate fraction. Regression parameters for the effect of  $\text{NH}_4^+$  concentrations on  $\text{NO}_3^-$  assimilation were calculated with model 2 regressions.

## Results

**Surface-water concentrations of nitrogenous nutrients**— $\text{NO}_3^-$  concentrations ranged from 5.8 to  $17.0 \mu\text{M}$  and were highest on the earlier cruise for each year (Fig. 1).  $\text{NO}_3^-$  concentrations at  $53^\circ\text{N}$  were 1–3  $\mu\text{M}$  greater than at  $50^\circ\text{N}$ . There were significant decreases in  $\text{NO}_3^-$  concentrations during both May cruises and in August 1988, and between May and August 1984 and June and September 1987 (Table 1).  $\text{NH}_4^+$  concentrations were low and variable, ranging from undetectable ( $<0.03 \mu\text{M}$ ) to  $0.40 \mu\text{M}$  (Fig. 2). Mean  $\text{NH}_4^+$  concentrations for each cruise ranged from 0.10 to  $0.19 \mu\text{M}$ , but there were no significant differences (Student's two-tailed *t*-test,  $P > 0.10$ ) among cruises or between stations. Urea concentrations were generally  $< \text{NH}_4^+$  concentrations. At both stations  $\text{NO}_3^-$  concentrations exceeded  $\text{NH}_4^+$  concentrations by at least one order of magnitude.

**Diel periodicity in  $\text{NH}_4^+$  concentrations**—During calm weather (May 1988) strong diel periodicity in  $\text{NH}_4^+$  concentration was detected.  $\text{NH}_4^+$  concentrations decreased dur-

Table 2. Mean and standard error of ratio of [NH<sub>4</sub><sup>+</sup>]<sub>0600</sub> : [NH<sub>4</sub><sup>+</sup>]<sub>1800</sub> for 5-d periods in 1988.

Sampling	0600:1800		n
	Mean	SE	
7-12 May	1.08	0.06	5
14-18 May	1.96	0.31	5
20-24 May	0.95	0.18	4
25-30 May	0.88	0.16	3
5-8 Aug	1.52	0.16	4
10-15 Aug	1.48	0.18	4
19-22 Aug	1.81	0.37	3

ing the day and increased at night on 9-10 and 15-17 May (Fig. 3A,B). The diel periodicity is less clear for 21-23 May (Fig. 3C). During May and August 1988, NH<sub>4</sub><sup>+</sup> concentrations were measured daily at 0600 and 1800 hours for 5-d sampling sequences. NH<sub>4</sub><sup>+</sup> was significantly greater at 0600 compared to 1800 hours for 4 out of 7 sequences (Table 2). We were unable to detect diel periodicity in NH<sub>4</sub><sup>+</sup> concentrations when net increases or decreases persisted for several days (e.g. Fig. 3C).

Diel changes in ambient NH<sub>4</sub><sup>+</sup> concentrations provide an estimate of net N assimilation during the day and net NH<sub>4</sub><sup>+</sup> remineralization at night. Net in situ NH<sub>4</sub><sup>+</sup> assimilation ranged from 3 to 10 nM h<sup>-1</sup> (Table 3) and are within the range determined during deck incubations with <sup>15</sup>N tracers. Rates of net NH<sub>4</sub><sup>+</sup> remineralization at night ranged from 2 to 19 nM h<sup>-1</sup> (Table 3). The diel patterns in NH<sub>4</sub><sup>+</sup> concentrations clearly illustrate both the rapid recycling of NH<sub>4</sub><sup>+</sup> and the disequilibrium between NH<sub>4</sub><sup>+</sup> uptake and remineralization within 24 h.

*NO<sub>3</sub><sup>-</sup>, NH<sub>4</sub><sup>+</sup>, and urea uptake rates*—Time-courses showed that uptake of NO<sub>3</sub><sup>-</sup> was linear during the day, and that NO<sub>3</sub><sup>-</sup> uptake at night was 2-10% of daytime rates (Table 4). NH<sub>4</sub><sup>+</sup> and urea uptake were both about linear over 24 h. Uptake rates at night were 82 and 69% of the 24-h uptake for NH<sub>4</sub><sup>+</sup> and urea respectively (Table 4). To compare relative use of each form of N on a 24-h basis, we present the uptake rates calculated from the atom% enrichment of PN at 24 h as a representative daily rate. Accuracy of our rate measurements for NH<sub>4</sub><sup>+</sup> uptake are further verified by the high recovery (67-85%) of <sup>15</sup>NH<sub>4</sub><sup>+</sup> in the particu-

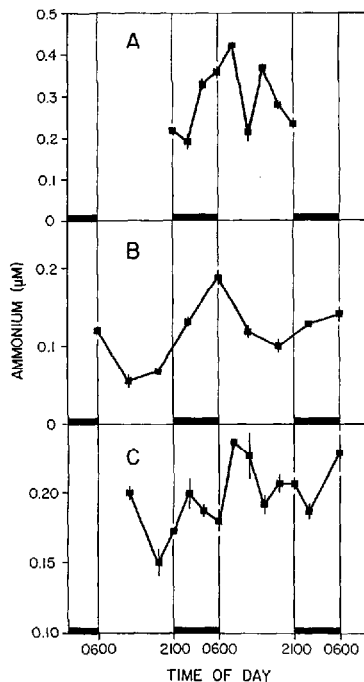


Fig. 3. Diel periodicity in mean ambient NH<sub>4</sub><sup>+</sup> concentrations for 0-30 m in May 1988. Results are aligned with respect to the light-dark cycle for ease of comparison. A. 9-10 May, 24-h sampling. B. 15-17 May, 48-h sampling. C. 21-23 May, 48-h sampling. Bars at bottom indicate dark period. Error bars give SE for mean, n = 3 or 4.

late fraction (Table 5). The label not recovered was probably in the bacterial fraction, a portion of which passes through GF/F filters (Kirchman et al. 1989).

Total N assimilation (NH<sub>4</sub><sup>+</sup> + NO<sub>3</sub><sup>-</sup> + urea) in surface water ranged from 84 to 732 nM d<sup>-1</sup> (Table 6). NH<sub>4</sub><sup>+</sup> uptake rates ranged from 18 to 54% of total uptake with an overall mean value of 39 ± 9%. NO<sub>3</sub><sup>-</sup> uptake rates ranged from 21 to 56% of the total with an overall mean of 37 ± 10% of the total. NO<sub>3</sub><sup>-</sup> uptake rates determined isotopically compared well with rates of net NO<sub>3</sub><sup>-</sup> depletion (Table 1). Urea uptake ranged from 10 to 43% of the total with an overall mean of 24 ± 9% of the total. The mean *f* ratio decreased from 0.41 ± 0.12 during May to 0.25 ± 0.05 during August 1988. There was no significant difference in *f* ratios between June and September 1987. The ranked proportional importance of the three N sources is NH<sub>4</sub><sup>+</sup> ≥ NO<sub>3</sub><sup>-</sup> ≥ urea.

Table 3. Rates ( $\text{nM h}^{-1}$ ) of  $\text{NH}_4^+$  uptake and regeneration calculated from in situ changes in  $\text{NH}_4^+$  concentrations.

	Time (hours)	Uptake rate $\pm$ SE	n	Regeneration rate $\pm$ SE	n
9-10 May	2100-0900			19.3 $\pm$ 4.1	5
	0900-2100	10.3 $\pm$ 9.1	5		
15-17 May	0600-1200	10.0	2		
	1200-0600			2.3 $\pm$ 1.1	4
	0600-1800	7.3 $\pm$ 2.5	3		
	1800-0600			3.3 $\pm$ 0.7	3
21-23 May	1200-1800	8.3	2		
	1800-0900			4.3 $\pm$ 1.5	6
	0900-0000	2.8 $\pm$ 1.0	6		
	0000-1500			6.7	2
Mean		7.7 $\pm$ 3.0		7.2 $\pm$ 7.0	

Turnover times for dissolved  $\text{NH}_4^+ - \text{NH}_4^+$  concentrations were highly variable both within and between cruises. In order to compare relative recycling rates, we divided uptake rates from deck incubations by  $\text{NH}_4^+$  concentrations to estimate  $\text{NH}_4^+$  turnover times (Fig. 4). The overall mean was 1.22 d, but a significant seasonal difference is apparent. Although  $\text{NH}_4^+$  turnover time for May 1988 was  $3.17 \pm 0.80$  d (mean  $\pm$  SE,  $n = 4$ ), the mean for the June, August, and September samples was  $1.48 \pm 0.61$  (mean  $\pm$  SE,  $n = 14$ ).

Inhibition of  $\text{NO}_3^-$  uptake by  $\text{NH}_4^+ - \text{NO}_3^-$  uptake rates decreased as a function of initial ambient  $\text{NH}_4^+$ , but the pooled data for

all deck and in situ experiments showed considerable scatter (Fig. 5). Since ambient  $\text{NH}_4^+$  concentrations can change significantly over a period of several hours, it is obvious that initial  $\text{NH}_4^+$  concentration for incubation experiments is not representative of the mean  $\text{NH}_4^+$  concentration during the incubation. To derive an accurate estimate of the functionality between  $\text{NH}_4^+$  concentrations and daytime  $\text{NO}_3^-$  assimilation rates, we used the  $\text{NH}_4^+$  concentration at the 6-h point and the  $\text{NO}_3^-$  uptake rates for the first 12 h of the 1987 and 1988 deck incubation experiments in model 2 regressions (Fig. 6A,B).  $\text{NO}_3^-$  assimilation rates during each cruise were inversely pro-

Table 4. Regressions for time-course measurements of uptake rates.

	Time period (h)	Coefficient of determination ( $r^2$ ) (mean $\pm$ SD)	Dark uptake (mean $\pm$ SD)
$\text{NO}_3^-$ *			Night/Day
Jun 87	0-7	0.957 $\pm$ 0.044	NA
Sep 87	0-12	0.999	NA
May 88	0-12	0.927 $\pm$ 0.054	0.02 $\pm$ 0.02
Aug 88	0-12	0.996 $\pm$ 0.004	0.10 $\pm$ 0.07
$\text{NH}_4^+$			Night/(Day + Night)
Jun 87	0-24	0.982 $\pm$ 0.036	0.92 $\pm$ 0.13
Sep 87	0-24	0.989 $\pm$ 0.005	0.84 $\pm$ 0.16
May 88	0-24	0.938 $\pm$ 0.104	0.92 $\pm$ 0.07
Aug 88	0-24	0.950 $\pm$ 0.020	0.62 $\pm$ 0.05
Urea			
Jun 87	0-5	0.957 $\pm$ 0.073	NA
Sep 87	0-24	0.971 $\pm$ 0.041	0.87 $\pm$ 0.08
May 88	0-24	0.906 $\pm$ 0.091	0.50 $\pm$ 0.36
Aug 88	0-24	0.964 $\pm$ 0.017	0.70 $\pm$ 0.10

\*  $\text{NO}_3^-$  uptake rates were very low at night, so regressions for time-course cover only the light period.

Table 5. Recovery of  $^{15}N$  during  $NH_4^+$  incubations.

	Mean	SD
	(%)	
Jun 87	77.5	8.1
Sep 87	85.2	17.5
May 88	67.3	19.4
Aug 88	67.2	10.7
Overall mean	75.1	16.0

portional to  $NH_4^+$  concentrations (Table 7). Maximal  $NO_3^-$  assimilation rates (Fig. 6,  $y$ -intercepts) ranged from 5.44 to 9.02  $nM h^{-1}$ , while the  $NH_4^+$  concentration resulting in 50% inhibition ( $k_i$ ) ranged from 0.05 to 0.19  $\mu M$  (Table 7).

*In situ inhibition of  $NO_3^-$  assimilation*—We had sufficient  $NH_4^+$  data from the 1988 cruises to use the regression coefficients in

Table 6. N uptake rates and  $f$  ratio.

	$NH_4^+$	$NO_3^-$	Urea	Total	$f$ ratio
	(nM d <sup>-1</sup> )				
Jun 87					
4	61	52	13	126	0.41
7	31	30	23	84	0.36
10	65	59	48	171	0.34
12	50	144	89	283	0.51
19	60	91	113	264	0.35
22	110	106	103	319	0.33
Mean	63	80	65	208	0.38
SD	24	38	39	86	0.06
Sep 87					
17	84	53	38	175	0.30
24	77	120	36	233	0.52
27	185	101	89	374	0.27
Oct 87					
3	58	72	24	154	0.47
Mean	101	86	47	234	0.39
SD	49	26	25	86	0.11
May 88					
8	61	110	26	198	0.56
14	86	110	31	228	0.48
20	84	59	36	179	0.33
27	70	34	26	130	0.26
Mean	75	78	30	184	0.41
SD	10	33	4	36	0.12
Aug 88					
5		29	53		
11	55	161	221	136	0.21
19	350	67	54	732	0.22
24	92	117	72	213	0.31
Mean	166	93	100	360	0.25
SD	131	50	70	264	0.05

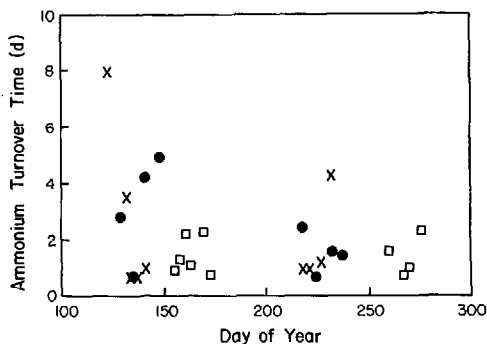


Fig. 4. Ammonium turnover times. Mean rate for each 5-d work cycle in 1984 (●), 1987 (□), and 1988 (×).

Table 4 to obtain daily estimates of inhibition of  $NO_3^-$  assimilation by ambient  $NH_4^+$ .  $NH_4^+$  inhibition decreased from 80 to 30% between 8 and 16 May, then increased continuously from 16 until 29 May, reaching 100% on the last day of sampling (Fig. 7A). During the latter part of May,  $f$  ratios decreased from 0.56 to 0.26. During August 1988, there was a decrease in inhibition by  $NH_4^+$  from 80 to 30% at 53°N and an increase in inhibition from 10 to 80% at 50°N (Fig. 7B).

*Correlation of  $NH_4^+$  inhibition of  $NO_3^-$  uptake with phytoplankton biomass*—The daily to weekly variations in inhibition of  $NO_3^-$  uptake by  $NH_4^+$  are large and could be related to the relative abundance or activity of phytoplankton and microheterotrophs. We examined this possibility by comparing the mean percent inhibition and Chl  $a$  concentrations for each 6-d sampling

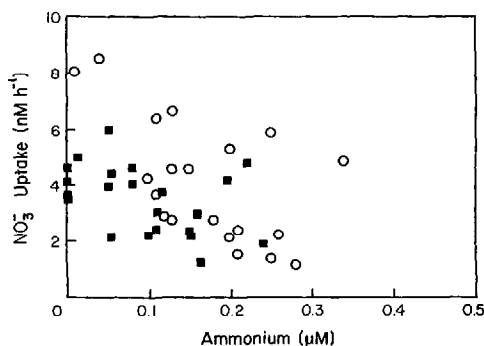


Fig. 5.  $NO_3^-$  uptake as a function of ambient  $NH_4^+$  concentrations. Data from all in situ and deck incubations in 1987 (■) and 1988 (○).

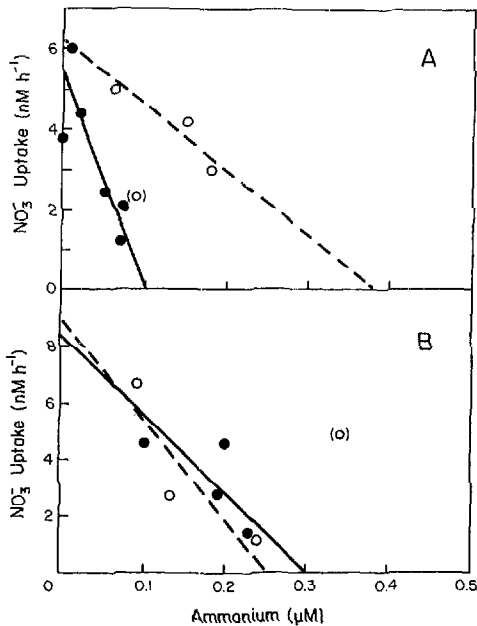


Fig. 6.  $\text{NO}_3^-$  uptake rates as a function of  $\text{NH}_4^+$  concentrations measured at 6 h during deck incubation experiments. A. June (●) and September (○) 1987. B. May (●) and August (○) 1988. Points in parentheses were excluded from regression analysis.

period during the 1988 cruises. The strong negative correlation between percent inhibition and Chl *a* concentration ( $r = 0.70$ ,  $P < 0.05$ , Fig. 8), suggests that when autotrophic biomass is relatively high,  $\text{NH}_4^+$  concentrations and inhibition of  $\text{NO}_3^-$  uptake are low. Conversely, when autotrophic biomass is relatively low,  $\text{NH}_4^+$  concentrations are higher and cause significant inhibition of  $\text{NO}_3^-$  assimilation.

### Discussion

*In situ nutrient concentrations*—The oceanic subarctic Pacific is a relatively stable

Table 7. Regression parameters for  $\text{NH}_4^+$  inhibition of  $\text{NO}_3^-$  uptake. The inhibition constant,  $k_i$ , is the  $\text{NH}_4^+$  concentration causing 50% inhibition.

	Max $\text{NO}_3^-$ uptake (y-intercept) ( $\text{nM h}^{-1}$ )	Slope	$k_i$ ( $\mu\text{M}$ )	$r^2$
Jun 87	5.44	-52.3	0.05	0.83
Sep 87	6.17	-16.2	0.19	0.92
May 88	8.36	-27.8	0.15	0.68
Aug 88	9.02	-36.3	0.12	0.88

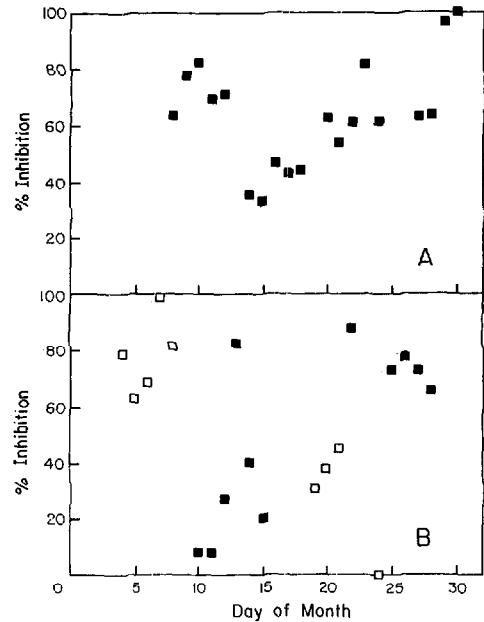


Fig. 7. Inhibition of  $\text{NO}_3^-$  uptake by  $\text{NH}_4^+$ . A. May 1988. B. August 1988. ■—50°N; □—53°N.

region with respect to both vertical mixing and horizontal flows (Miller et al. 1988). As a consequence, regular patterns of changes in nutrient concentrations can be detected and can provide an in situ estimate of net uptake of  $\text{NO}_3^-$  and  $\text{NH}_4^+$ . For  $\text{NO}_3^-$ , significant decreases in surface-water concentrations were detected in May, but decreases were much slower or undetectable in August and September. Although net decreases in surface-water  $\text{NO}_3^-$  could be calculated for some portions of the data, the standard errors of the rates of decrease were rather large.

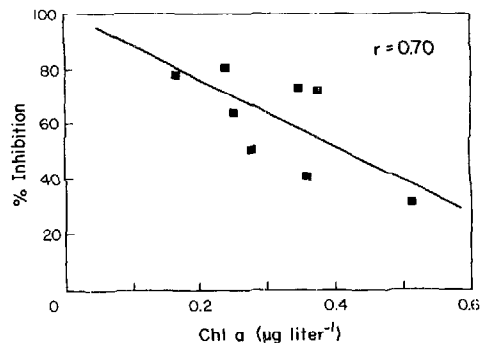


Fig. 8. Inhibition of  $\text{NO}_3^-$  uptake by  $\text{NH}_4^+$  as a function of Chl *a* for May and August 1988.



Similar variability was evident in NO<sub>3</sub><sup>-</sup> concentrations integrated for the upper 80 m of the water column (Wheeler unpubl. data), so we attribute departures from linearity to slight differences in water masses rather than to storm events.

Diel changes in NH<sub>4</sub><sup>+</sup> concentrations indicated net uptake during the day and net remineralization at night. This pattern agrees with our results from microcosm studies in 1987 (Wheeler et al. 1989). Both the small amplitude of changes in NH<sub>4</sub><sup>+</sup> concentration and net fluxes indicated that uptake and regeneration of NH<sub>4</sub><sup>+</sup> are closely compensating over a day. The similarity of assimilation rates determined from net changes in concentration to those determined with <sup>15</sup>N tracers suggests that there were no major incubation artifacts for the experiments reported here. Obviously, however, isotopic measures of uptake rates for a 24-h period would give a higher rate estimate than the net changes in NH<sub>4</sub><sup>+</sup> concentrations.

Although NH<sub>4</sub><sup>+</sup> concentrations in the oceanic subarctic Pacific are higher than in oligotrophic regions such as the Sargasso Sea (Glibert and McCarthy 1984) and the central Pacific gyre (Eppley et al. 1977), they are lower than the 1–4 μM levels reported for the Antarctic (Olson 1980; Glibert et al. 1982; Koike et al. 1986). NH<sub>4</sub><sup>+</sup> has been recognized as the dominant N source for phytoplankton in oligotrophic systems (e.g. Eppley et al. 1977; Glibert and McCarthy 1984) and occasionally in regions with persistently high NO<sub>3</sub><sup>-</sup> concentrations (Glibert et al. 1982; Probyn and Painting 1985; Koike et al. 1986; Probyn 1988). In oligotrophic regions, however, NH<sub>4</sub><sup>+</sup> concentrations are close to detection limits and it is difficult to determine uptake rates accurately with <sup>15</sup>N techniques. Diel changes in NH<sub>4</sub><sup>+</sup> in the oceanic subarctic Pacific demonstrate unequivocally that NH<sub>4</sub><sup>+</sup> is recycled rapidly and that fluxes of NH<sub>4</sub><sup>+</sup> ≥ fluxes of NO<sub>3</sub><sup>-</sup> into phytoplankton in the euphotic zone, despite a 100-fold greater concentration of NO<sub>3</sub><sup>-</sup>.

*Seasonal changes in NO<sub>3</sub><sup>-</sup> uptake*—NO<sub>3</sub><sup>-</sup> assimilation accounts for 21–56% of the total measured N assimilation in the subarctic Pacific, and NO<sub>3</sub><sup>-</sup> assimilation rates normalized to Chl *a* [7–35 nmol (μg Chl *a*)<sup>-1</sup> h<sup>-1</sup>] are comparable to those re-

ported in other waters high in NO<sub>3</sub><sup>-</sup> (Kokinakis and Wheeler 1987). Below ~30 m, NO<sub>3</sub><sup>-</sup> assimilation and photosynthesis appear to be light limited (Miller et al. 1988), but in surface waters photosynthesis and N assimilation are light saturated. Seasonal decreases in NO<sub>3</sub><sup>-</sup> assimilation can usually be attributed to depletion of NO<sub>3</sub><sup>-</sup> in the euphotic zone (e.g. Sambrotto et al. 1986). This explanation, however, clearly does not apply in the subarctic Pacific where NO<sub>3</sub><sup>-</sup> concentrations are always >6 μM.

Martin et al. (1989) postulated that high NO<sub>3</sub><sup>-</sup> concentrations in the subarctic Pacific may be due to Fe limitation of phytoplankton growth. Phytoplankton are growing, however, at close to maximal rates (0.7–1.0 d<sup>-1</sup>) expected for subarctic Pacific temperatures (5°–12°C) during both spring and summer (Booth et al. 1988). Furthermore, NO<sub>3</sub><sup>-</sup> assimilation normalized to Chl *a* is the same in the subarctic Pacific in both spring and summer, despite a significant difference between in situ rates of net NO<sub>3</sub><sup>-</sup> depletion. Thus, it is problematic to attribute continuously high NO<sub>3</sub><sup>-</sup> levels in the subarctic Pacific to Fe-limited phytoplankton growth. It is possible, however, that Fe affects species composition and accumulation of phytoplankton biomass.

*NH<sub>4</sub><sup>+</sup> inhibition of NO<sub>3</sub><sup>-</sup> assimilation*—Phytoplankton preference for NH<sub>4</sub><sup>+</sup> as a source of N is well documented for laboratory cultures (Syrett 1981) and natural populations (McCarthy 1981). For natural populations, the relative preference index introduced by McCarthy has been widely applied and clearly demonstrates that NH<sub>4</sub><sup>+</sup> is used preferentially relative to its availability. Physiological and biochemical processes regulating this preference, however, are not completely understood. NH<sub>4</sub><sup>+</sup> inhibits NO<sub>3</sub><sup>-</sup> reductase activity and represses synthesis of NO<sub>3</sub><sup>-</sup> reductase in phytoplankton (Syrett 1981), but the concentration at which this effect occurs is not clear. McCarthy (1981) suggests nearly complete inhibition of NO<sub>3</sub><sup>-</sup> assimilation at NH<sub>4</sub><sup>+</sup> concentrations of ~1 μM, but also notes that it often occurs at lower NH<sub>4</sub><sup>+</sup> concentrations. Our results indicate that, in the subarctic Pacific, concentrations of 0.1–0.3 μM can completely inhibit NO<sub>3</sub><sup>-</sup> assimilation.

The  $k_i$  (concentration resulting in 50% inhibition) for the subarctic Pacific is an order of magnitude lower than  $k_i$  values reported for coastal regions (Harrison et al. 1987) and for the Antarctic (Olson 1980; Glibert et al. 1982). We do not know what causes this apparent difference in sensitivity to  $\text{NH}_4^+$ .

*Temporal scale for variations in inhibition*—Our results suggest that  $\text{NH}_4^+$  concentrations and turnover times vary significantly on several time scales: diel, weekly, and seasonal. We were unable to detect significant in situ diel variations in  $\text{NH}_4^+$  concentrations during the 1987 cruises but did detect diel variations in  $\text{NH}_4^+$  uptake and regeneration in large-volume (60 liter) microcosm experiments (Wheeler et al. 1989). During rough weather, any diel periodicity in  $\text{NH}_4^+$  concentrations is difficult to detect due to limited frequency of sampling and increased mixing rates. Nonetheless, results presented here for May 1988 indicate that diel changes take place throughout the upper 30 m of the water column during calm weather.  $\text{NO}_3^-$  assimilation is light-dependent and  $\text{NH}_4^+$  concentrations are highest at the end of the dark period, so rates of  $\text{NO}_3^-$  assimilation in the subarctic Pacific will depend on both light intensity and ambient  $\text{NH}_4^+$  concentrations, and both have diel periodicities. At the beginning of the light period, residual  $\text{NH}_4^+$  may cause a lag before onset of  $\text{NO}_3^-$  assimilation.

Variations in  $\text{NH}_4^+$  concentration and inhibition of  $\text{NO}_3^-$  assimilation on temporal scales of days to weeks were negatively correlated with Chl *a* concentrations. We previously used Chl *a* : PN ratios, which ranged from 0.2 to 1.7  $\mu\text{g Chl } a (\mu\text{mol PN})^{-1}$ , as an index of autotrophic vs. heterotrophic biomass in coastal waters off Oregon and Washington (Kokkinakis and Wheeler 1987). For the oceanic subarctic Pacific, Chl *a* : PN ranges from 0.16 to 0.34 (Wheeler unpubl. data) suggesting a relatively low autotrophic biomass. Because PN is nearly constant ( $1.50 \pm 0.11 \mu\text{M}$ , mean  $\pm$  SE,  $n = 18$ ) in the subarctic Pacific, any relationship with Chl *a* : PN is dominated by variations in Chl *a*. Phytoplankton respond to changes in light intensity with a twofold to fivefold variation in cellular Chl *a* (Parsons et al. 1961; Chan 1980). Because light intensity

was not limiting photosynthesis in the upper 30 m during our sampling (Miller et al. 1988), we suggest that changes in Chl *a* reflect variations in the relative abundance of autotrophic and heterotrophic biomass.

The diel to weekly variations in inhibition of  $\text{NO}_3^-$  assimilation by  $\text{NH}_4^+$ , then, may result from changes in the relative abundance and activity of phototrophic and heterotrophic microorganisms. High Chl *a* : PN reflects a plankton community dominated by phytoplankton with relatively low grazing pressure and low recycling rates. Low Chl *a* : PN reflects a community dominated by heterotrophs (or detritus or both) and relatively high grazing pressure. Our results suggest that the relative abundance or activity of the autotrophs and heterotrophs varies significantly on time scales of a few days in the subarctic Pacific.

In situ rates of  $\text{NO}_3^-$  depletion and  $^{15}\text{N}$  measurements of  $\text{NO}_3^-$  uptake clearly decreased over the growing season in the subarctic Pacific.  $\text{NH}_4^+$  concentrations were always relatively low and did not show large seasonal variation.  $\text{NH}_4^+$  turnover rates, however, did vary, and we suggest that increased  $\text{NH}_4^+$  availability is one factor that limits  $\text{NO}_3^-$  depletion in the subarctic Pacific. A similar seasonal decrease in the relative use of  $\text{NO}_3^-$  occurs in the Antarctic, where the *f* ratio decreases from 0.54 in early spring (Olson 1980) to 0.16 in late summer (Koike et al. 1986). In the Antarctic, however, the seasonal decrease in new production is correlated with a significant increase in  $\text{NH}_4^+$  concentrations, i.e. from 0.3  $\mu\text{M}$  in early spring (Olson 1980) to 2.0  $\mu\text{M}$  in late summer (Koike et al. 1986). Koike et al. (1986) also attribute the increased availability and use of  $\text{NH}_4^+$  to an increase in the relative abundance of heterotrophs.

In nutrient-rich regions,  $\text{NO}_3^-$  accounts for a large portion of the N assimilated during primary production, but there is some controversy over the maximal percent new production (*f* ratio). Eppley and Peterson (1979) estimate ~50% new production in upwelling regions, whereas Platt and Harrison (1985) estimate 80% new production for coastal regions. In the subarctic Pacific, grazing pressure (by calanoid copepods and microzooplankton) is sufficient to maintain

low phytoplankton stocks throughout the year. One consequence of this grazing pressure must be significant recycling of NH<sub>4</sub><sup>+</sup>. The biomass of zooplankton equals or exceeds that of phytoplankton (Frost 1987), but most grazing is by microzooplankton (Miller et al. 1988). Standing stocks of heterotrophic flagellates and ciliates is about equal to the standing stock of phytoplankton (Booth unpubl. data); thus one could expect to find a steady state established in which the system is operating primarily on recycled nutrients. Excess inorganic N would remain in the system as NO<sub>3</sub><sup>-</sup>. This type of situation has been modeled previously by Kiefer and Atkinson (1984) but seems not to have received much attention. An important consequence of grazing, NH<sub>4</sub><sup>+</sup> recycling, and the inhibitory effects of NH<sub>4</sub><sup>+</sup> on NO<sub>3</sub><sup>-</sup> utilization is that it sets an upper limit on NO<sub>3</sub><sup>-</sup> uptake in nutrient-rich, grazing-balanced ecosystems.

As argued above, persistently high levels of NO<sub>3</sub><sup>-</sup> in the oceanic subarctic Pacific cannot be attributed to nutrient limitation of phytoplankton growth rates. Simple calculations also indicate that mixing and nitrification do not account for the high NO<sub>3</sub><sup>-</sup> concentrations. The vertical flux of NO<sub>3</sub><sup>-</sup> across the permanent halocline at 90 m in the subarctic Pacific is negligible. Maximal upward flux of NO<sub>3</sub><sup>-</sup> across the halocline is <2 mg N m<sup>-2</sup> d<sup>-1</sup> (T. Powell pers. comm.), and this rate of NO<sub>3</sub><sup>-</sup> input would have insignificant effect on net changes in NO<sub>3</sub><sup>-</sup> concentrations in the euphotic zone seasonally. Rates of nitrification are on the order of 0.04 μM d<sup>-1</sup> at the base of the euphotic zone (Ward et al. 1982). If it occurs in a 10-m layer of the water column, the supply rate of NO<sub>3</sub><sup>-</sup> to the upper 80 m is 5 nM d<sup>-1</sup>. It thus is unlikely that nitrification has any significant effect on either our isotopic rate measurements of NO<sub>3</sub><sup>-</sup> assimilation or on the rate of net NO<sub>3</sub><sup>-</sup> depletion between May and September in the subarctic Pacific.

In conclusion, grazing pressure in the subarctic Pacific has two effects on phytoplankton use of NO<sub>3</sub><sup>-</sup>. Grazing maintains a low standing stock (Frost 1987; Miller et al. 1988), and, since uptake rates are proportional to biomass, it also reduces NO<sub>3</sub><sup>-</sup> uptake. Maintenance of low standing stock,

however, is not sufficient to explain high NO<sub>3</sub><sup>-</sup> concentrations in the subarctic Pacific. As shown by the data presented here, phytoplankton use of N is about 250 nM d<sup>-1</sup>. At these rates (in the absence of any N recycling), phytoplankton would deplete the N supply in 100 d. Our results clearly demonstrate an inverse relationship between NH<sub>4</sub><sup>+</sup> concentrations and rates of NO<sub>3</sub><sup>-</sup> uptake. This regenerated N is used preferentially by phytoplankton and thus leads to a decrease in net NO<sub>3</sub><sup>-</sup> depletion. Although physical factors undoubtedly influence the supply of NO<sub>3</sub><sup>-</sup> to the euphotic zone, it is important to recognize that biological factors (grazing and physiological preferences for NH<sub>4</sub><sup>+</sup>) can have dramatic effects on NO<sub>3</sub><sup>-</sup> uptake rates and relative use of NO<sub>3</sub><sup>-</sup>-N for primary production.

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