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Nitrogen uptake by size-fractionated phytoplankton populations in Antarctic surface waters¹

Abstract—Nitrogen uptake experiments in surface waters off the coast between Cape Ann and Mawson indicate that reduced nitrogen (ammonium and urea) supplied an average of 58% of phytoplankton requirements. Size-fractionation studies provided evidence for nitrogen resource partitioning between the algae of different size classes at three of the five stations. On average, regenerated production amounted to 62% for the nanoplankton and 75% for the picoplankton.

The high inorganic nutrient concentrations typical of waters south of the Antarctic Convergence reduce the likelihood of Antarctic phytoplankton growth rates ever being nutrient-limited (El-Sayed 1984). There is, nevertheless, considerable interest in studies of phytoplankton nitrogen metabolism in this region, especially in terms of the relative role of new and regenerated nitrogen in growth (Dugdale and Goering 1967). The reason for this is that under equilibrium conditions between primary nitrogen assimilation and herbivory the proportion of new production (nitrate-based) is indicative of the amount of primary production that is available for export to higher trophic levels (Eppley and Peterson 1979). Measurements of nitrogen assimilation by phytoplankton in the Antarctic indicate that in spite of the typically high nitrate concentrations (20–30 mg-atoms N m⁻³), ammonium is the principal nitrogen resource utilized. Experiments in the Scotia Sea region have shown that ammonium accounts for about 50–95% of the nitrogen demand by phytoplankton (Olson 1980; Koike et al. 1981; Glibert et al. 1982a; Rönner et al. 1983). Urea uptake was not reported in these studies and ammonium was regarded as the sole source of regenerated nitrogen.

Size-fractionation studies in Antarctic waters have shown that nanoplankton is a very active component of nonbloom phy-

toplankton assemblages. For example, during the austral summer in the Ross Sea area, organisms <10 μm contributed about 54% of primary production, the proportion increasing toward sub-Antarctic waters (El-Sayed and Turner 1977). Bröckel (1981) found that on average, 88% of primary production in the western Antarctic region was attributable to particles <20 μm. Nanoplankton also appears to be more efficient (per unit chlorophyll) than netplankton at nitrogen uptake (Koike et al. 1981; Rönner et al. 1983). In both temperate (Malone 1980; Glibert et al. 1982b; Probyn 1985) and Antarctic waters (Koike et al. 1981), primary production in the nanoplankton size class is based largely on ammonium, with nitrate being relatively more important for netplankton nutrition. Cells in the <1-μm size class, the picoplankton, contribute 20–80% of the total primary production (Gieskes et al. 1979; Li et al. 1983; Joint and Pomroy 1983) and as with nanoplankton, reduced nitrogen is the predominant nitrogen source in picoplankton nutrition (Probyn 1985). The accumulating evidence suggests that for a particular body of water, the amount of new production and the dominant size classes within the phytoplankton community are likely to be closely related. Thus measurements of nitrogen assimilation in natural waters can indirectly provide insight into community structure at the lower trophic levels. Our purpose here was to investigate the relative contributions of nanoplankton and picoplankton to the assimilation of nitrate, ammonium, and urea in Antarctic waters off the coast between Cape Ann and Mawson.

We thank C. M. Weekley for identifying and counting phytoplankton and O. A. M. Lewis for use of his ¹⁵N analyzer.

Surface water samples (ca. 1 m) were collected at 5 of a grid of 46 stations between 65°S–62°S and 52°E–64°E during 26 March–20 April 1984. Experiments were done on the *S. A. Agulhas* in the course of the SIBEX

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Table 1. Ambient nitrate, ammonium, and urea concentrations (mg-atoms N m⁻³) at the surface and particulate organic nitrogen (PON) and carbon (POC) concentrations for <200- μ m size class (mg-atoms N or C m⁻³); nitrogen and carbon values of nanoplankton (<15 μ m) and picoplankton (<1 μ m) are expressed as a percentage of the <200- μ m size class.

Sta.	PON			POC			Nutrient concn		
	<200 μ m	<15 μ m	<1 μ m	<200 μ m	<15 μ m	<1 μ m	NO ₃ ⁻	NH ₄ ⁺	Urea
17	1.048	100.0	37.5	14.222	99.6	34.3	27.5	1.02	0.70
30	0.714	73.4	60.1	7.556	91.2	73.5	25.6	0.34	0.62
42	0.738	80.6	38.8	5.917	93.4	94.3	22.7	0.13	1.33
34	0.667	92.8	40.2	5.611	97.0	79.6	25.9	0.38	0.72
46	0.535	80.2	63.4	4.923	82.9	68.1	23.9	0.24	0.21

I program. Water samples were prescreened through a 200- or 15- μ m plankton mesh or a 1- μ m Nuclepore filter. The <200- μ m fraction was assumed to be representative of the intact phytoplankton community, the <15- μ m fraction, nanoplankton, and the <1- μ m fraction, picoplankton. The <15- μ m size class, although including picoplankton, is treated as the nanoplankton fraction to permit comparison with other studies in which these size classes have not been differentiated. Two liters of surface water were supplemented with 0.2 μ mol ¹⁵NH₄Cl (99.7 atom %), 6.0 μ mol Na¹⁵NO₃ (99.6 atom %), or 0.1 μ mol CO(¹⁵NH₂)₂ (99.1 atom %) and incubated at surface water temperatures in a clear deck box for 5–9 h. Uptake experiments were ended by filtration of particles onto glass-fiber filters (Whatman GF/F) and the filters stored at –18°C for later analysis of ¹⁵N content by emission spectrometry (Fiedler and Proksch 1975). Ammonium concentrations were measured within 0.5 h of filtration by the method of Grasshoff (1976), scaled down to 5-ml samples. Filtrates for nitrate and urea determinations were frozen immediately and analyzed sev-

eral weeks later by the methods of Nydahl (1976) and Grasshoff (1976).

A relative preference index (RPI) was calculated for each nutrient (McCarthy et al. 1977). For example, for ammonium

$$RPI = \frac{\rho NH_4}{\rho \Sigma N} \bigg/ \frac{[NH_4]}{[\Sigma N]}$$

where ρNH_4 and $\rho \Sigma N$ are the uptake rate for ammonium and the sum of the rates for the three nitrogenous nutrients and [NH₄] and [ΣN] their ambient concentrations.

Total particulate nitrogen and carbon in the different size classes and ambient nutrient concentrations are shown in Table 1. Most of the particulate matter (mean 93% as carbon) was in the <15- μ m fraction. Bröckel (1981) reported 13–96% of phytoplankton carbon in the <20- μ m fraction of samples from the western Antarctic region. Our results, however, are overestimates of the relative proportion of nanoplankton and picoplankton in the phytoplankton community because we excluded large specimens of the diatoms *Corethron criophilum* and *Thallassiothrix antarctica* with the 200- μ m mesh. Nevertheless, the number of diatoms in the >200- μ m size class was on average only 17% of that in the 15–200- μ m range. Abundant netplankton species included *Nitzschia seriata*, *Rhizosolenia alata*, *Chaetoceros densus*, *Fragilariopsis antarctica*, and *C. criophilum*. The nanoplankton fraction was comprised mainly of flagellated species although a small *Chaetoceros* spp. was also present. We did not identify picoplankton taxa.

The relative activities of nanoplankton and picoplankton are shown in Table 2. It

Table 2. Mean proportion of total nitrogen (ΣN, mg-atoms N m⁻³ h⁻¹) uptake by the netplankton (15–200 μ m), nanoplankton (<15 μ m), and picoplankton (<1 μ m).

Sta.	ΣN uptake	Relative uptake (%)		
		<200 μ m	<15 μ m	<1 μ m
17	3.62	42.8	57.2	16.0
30	5.91	49.2	50.8	30.6
42	5.16	54.8	45.2	13.6
34	5.45	11.9	88.1	55.0
46	2.16	6.6	93.5	82.0

Table 3. Ammonium, nitrate, and urea uptake rates ($\text{mg-atoms N m}^{-3} \text{ h}^{-1} \times 10$) and relative preference indices (RPI) for the three size fractions.

Sta.	Nutrient	Uptake rate			RPI		
		<200 μm	<15 μm	<1 μm	<200 μm	<15 μm	<1 μm
17	NH_4^+	1.92	0.86	0.32	13.5	11.9	15.8
	NO_3^-	0.88	0.66	*	0.3	0.3	—
	Urea	0.82	0.55	0.26	9.4	11.1	18.7
30	NH_4^+	1.57	1.30	0.85	20.8	33.9	36.7
	NO_3^-	3.65	1.06	0.55	0.6	0.4	0.3
	Urea	0.69	0.64	0.45	5.0	9.2	10.7
42	NH_4^+	0.64	0.46	0.21	22.9	36.6	25.9
	NO_3^-	1.75	0.56	*	0.4	0.3	—
	Urea	2.77	1.31	0.49	9.7	10.2	12.7
34	NH_4^+	1.57	1.33	0.47	20.4	19.7	11.1
	NO_3^-	2.02	1.94	1.24	0.4	0.4	0.4
	Urea	1.86	1.53	1.29	12.8	11.9	16.1
46	NH_4^+	0.75	0.72	0.69	8.5	35.8	39.2
	NO_3^-	1.15	1.20	0.97	0.6	0.6	0.6
	Urea	0.22	0.16	0.12	11.8	9.2	7.8

* Not detectable.

is noteworthy that picoplankton accounted for most of the nitrogen uptake at stations 34 and 46, located about 110 km north of the ice edge and that only about 10% of the activity was due to netplankton. At stations 17, 30, and 42, close to the ice edge, netplankton and nanoplankton contributed about equally to nitrogen uptake.

Nitrogen uptake data for the different size fractions are shown in Table 3. The low relative preference indices (McCarthy et al. 1977) for nitrate indicate discrimination against this nutrient by phytoplankton of all sizes. On the other hand, the relative preference indices well in excess of unity for the reduced nitrogen sources illustrate the marked preference with which they are taken up (Table 3). Preferences for the individual nitrogenous nutrients follow the sequence: ammonium > urea > nitrate. A similar preference for ammonium over nitrate was found in the Scotia Sea (Glibert et al. 1982a). Other studies in which urea uptake has been measured also support its intermediate position (McCarthy et al. 1977, 1982), although departures from this generally observed hierarchy are not infrequent (Furnas 1983; Kaufman et al. 1983; Harrison et al. 1985).

A preference for reduced nitrogen over nitrate, with its sound energetic basis, is often not displayed in absolute terms. Nitrate,

though not preferred, is frequently the major nitrogen resource utilized, especially in regions where upwelling maintains a high ratio of ambient nitrate to ammonium. This does not appear to be the case in Antarctic waters. In spite of the domination of the nitrogenous nutrient pool by nitrate (96%), ammonium and urea were on average the principal nutrients used by phytoplankton (Fig. 1). The mean f -ratio ($f = \text{nitrate uptake}/\text{total nitrogen uptake}$; Eppley and Peterson 1979) for the whole phytoplankton community at all stations was 42%, although at stations 30 and 46 slightly more than half the nitrogen was assimilated as nitrate. These estimates of new production at the surface may be overestimates for the entire euphotic zone, as the f -ratio generally decreases with depth in Antarctic waters (Olson 1980; Koike et al. 1981; Rönner et al. 1983). Depth-integrated f -ratios in these studies range from about 5 to 50% for the whole phytoplankton community. Experiments in the Scotia Sea region suggest a seasonal shift in the f -ratio in response to a changing ambient ammonium concentration. Ammonium appears to be relatively more abundant and more important to phytoplankton nutrition during the austral summer (Koike et al. 1981; Glibert et al. 1982a; Rönner et al. 1983) than in the late winter-early spring (Olson 1980). Biggs

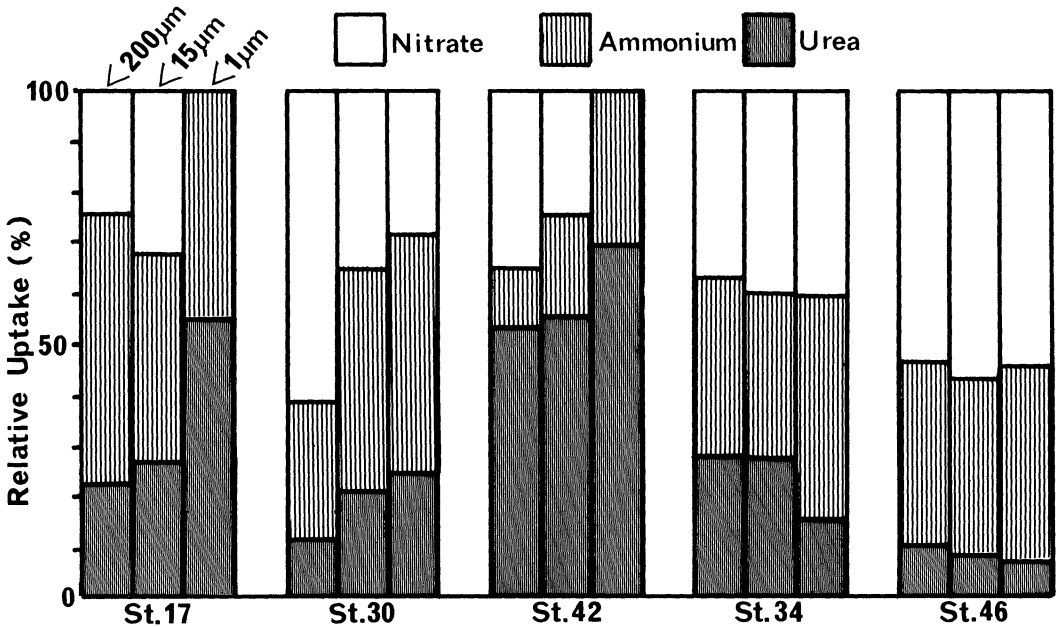


Fig. 1. Relative uptake of the three nitrogenous nutrients by the whole phytoplankton community ($< 200 \mu\text{m}$), nanoplankton ($< 15 \mu\text{m}$), and picoplankton ($< 1 \mu\text{m}$).

(1982) concluded that, of the possible biogenic and nonbiogenic mechanisms of ammonium input to the photic zone in the Ross Sea, the basal melting of the ice shelf is a potentially significant source. The physical injection of ammonium from the melting ice shelf is new to the euphotic zone in the same sense as nitrate and would thus frustrate interpretation of the f -ratio in terms of new production.

The f -value tended to decrease with the screening out of the larger phytoplankton at three of our five stations (Fig. 1). These findings agree with previous measurements in Antarctic (Koike et al. 1981) and temperate (Malone 1980; Probyn 1985) waters, although Furnas (1983) showed that in Narragansett Bay netplankton and nanoplankton use a similar fraction of the nitrogenous nutrient pool. There was no evidence for nitrogen resource partitioning between the different size fractions at our stations 34 and 46, both characterized by a very active picoplankton component (Table 1). On average, regenerated production amounted to 62% for the nanoplankton and 75% for the picoplankton.

The above experimental evidence suggesting a largely ammonium-based nutrition in a vast reservoir of nitrate is even more enigmatic when one considers that we probably underestimated regenerated production by not taking isotope dilution into account. Glibert et al. (1982b) showed that ammonium uptake can be underestimated by a factor of 2–3 under conditions of active ammonium regeneration. Ammonification rates are significant during the summer in the Scotia Sea (Glibert 1982). Another contributing factor is that although urea was not measured in previous investigations in the Southern Ocean, we found it to supply about 27% of the nitrogen requirements for the intact, surface-water community. The proportion of urea taken up by phytoplankton assemblages in Arctic waters (Harrison et al. 1985) and in lower latitude environments is typically variable, but on average is similar to our estimate (McCarthy 1972; Kristiansen 1983). Urea nitrogen, however, can provide the major contribution to the total assimilated in relatively eutrophic areas (Kaufman et al. 1983). Urea uptake by the intact commu-

nity (ρ urea) showed a significant positive correlation ($P < 0.05$) with urea concentration at the five stations in our study [ρ urea = $0.26 + 0.36$ (urea), $r = 0.92$]. Urea could be even more important in regions where supply is enhanced by localized animal activity (e.g. bird aggregations, krill swarms).

In conclusion, the results of this and other studies suggest a proportionally high flux of reduced nitrogen through the nitrogen cycle of Antarctic surface waters during non-bloom periods. As nanoplankton and picoplankton generally use more reduced nitrogen relative to total nitrogen than the larger netplankton species, dominance of these smaller phytoplankters is to be expected. Recent evidence for Antarctic waters indicates that production in the $<20\text{-}\mu\text{m}$ size classes may be high (El-Sayed and Turner 1977; Bröckel 1981) and that it is effectively transferred to higher trophic levels via a microzooplankton link (El-Sayed 1984; Hewes et al. in press). Consequently, the high proportion of regenerated production frequently encountered in near-surface Antarctic waters may be interpreted as evidence for an alternative pathway to the classic diatom-krill food chain, through which a major share of the available energy is flowing.

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References

- BIGGS, D. C. 1982. Zooplankton excretion and NH_4^+ cycling in near-surface waters of the Southern Ocean. 1. Ross Sea, austral summer 1977-1978. *Polar Biol.* **1**: 55-67.
- BRÖCKEL, K. VON. 1981. The importance of nanoplankton within the pelagic Antarctic ecosystem. *Kiel. Meeresforsch. Sonderh.* **5**: 61-67.
- DUGDALE, R. C., AND J. J. GOERING. 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. *Limnol. Oceanogr.* **12**: 196-206.
- EL-SAYED, S. 1984. Productivity of the Antarctic waters—a reappraisal, p. 19-34. *In* Marine phytoplankton and productivity. Lecture Notes on Coastal and Estuarine Studies **8**. Springer.
- , AND J. T. TURNER. 1977. Productivity of the Antarctic and tropical/subtropical regions: A comparative study, p. 463-501. *In* Polar oceans. Proc. Polar Oceans Conf. Montreal.
- EPPLEY, R. W., AND B. J. PETERSON. 1979. Particulate organic matter flux and planktonic new production in the deep ocean. *Nature* **282**: 677-680.
- FIEDLER, R., AND G. PROKSCH. 1975. The determination of nitrogen-15 by emission and mass spectrometry in biochemical analysis: A review. *Anal. Chim. Acta* **78**: 1-62.
- FURNAS, M. J. 1983. Nitrogen dynamics in lower Narragansett Bay, Rhode Island. 1. Uptake by size-fractionated phytoplankton populations. *J. Plankton Res.* **5**: 657-675.
- GIESKES, W. W., G. W. KRAAY, AND M. A. BAARS. 1979. Current ^{14}C methods for measuring primary production: Gross underestimates in oceanic waters. *Neth. J. Sea Res.* **13**: 58-78.
- GLIBERT, P. M. 1982. Regional studies of daily, seasonal and size fraction variability in ammonium remineralization. *Mar. Biol.* **70**: 209-222.
- , D. C. BIGGS, AND J. J. MCCARTHY. 1982a. Utilization of ammonium and nitrate during austral summer in the Scotia Sea. *Deep-Sea Res.* **29**: 837-850.
- , F. LIPSCHULTZ, J. J. MCCARTHY, AND M. M. ALTABET. 1982b. Isotope dilution models of uptake and remineralization of ammonium by marine phytoplankton. *Limnol. Oceanogr.* **27**: 639-650.
- GRASSHOFF, K. 1976. Methods of seawater analysis. Verlag Chemie.
- HARRISON, W. G., E. J. HEAD, R. J. CONOVER, A. R. LONGHURST, AND D. D. SAMEOTO. 1985. The distribution and metabolism of urea in the eastern Canadian Arctic. *Deep-Sea Res.* **32**: 23-42.
- HEWES, C. D., O. HOLM-HANSEN, AND E. SAKSHAUG. In press. Alternate carbon pathways at lower-trophic levels in the Antarctic food web. Proc. 4th Symp. Antarctic Biol., Wilderness, South Africa.
- JOINT, I. R., AND A. J. POMROY. 1983. Production of picoplankton and small nanoplankton in the Celtic Sea. *Mar. Biol.* **77**: 19-27.
- KAUFMAN, Z. G., J. S. LIVELY, AND E. J. CARPENTER. 1983. Uptake of nitrogenous nutrients in a barrier island estuary: Great South Bay, New York. *Estuarine Coastal Shelf Sci.* **17**: 483-493.
- KOIKE, I., U. RÖNNER, AND O. HOLM-HANSEN. 1981. Microbial nitrogen metabolism in the Scotia Sea. *Antarctic J.* **16**: 165-166.
- KRISTIANSEN, S. 1983. Urea as a nitrogen source for the phytoplankton in the Oslofjord. *Mar. Biol.* **74**: 17-24.
- LI, W. K., AND OTHERS. 1983. Autotrophic picoplankton in the tropical ocean. *Science* **219**: 292-295.
- MCCARTHY, J. J. 1972. The uptake of urea by natural

- populations of marine phytoplankton. *Limnol. Oceanogr.* **17**: 738–748.
- , W. R. TAYLOR, AND J. L. TAFT. 1977. Nitrogenous nutrition of the plankton in the Chesapeake Bay. 1. Nutrient availability and phytoplankton preferences. *Limnol. Oceanogr.* **22**: 996–1011.
- , D. WYNNE, AND T. BERMAN. 1982. The uptake of dissolved nitrogenous nutrients by Lake Kinneret (Israel) microplankton. *Limnol. Oceanogr.* **27**: 673–680.
- MALONE, T. C. 1980. Size-fractionated primary productivity of marine phytoplankton. *Brookhaven Symp. Biol.* **31**, p. 301–319. Plenum.
- NYDAHL, F. 1976. On the optimum conditions for the reduction of nitrate to nitrite by cadmium. *Talanta* **23**: 349–357.
- OLSON, R. J. 1980. Nitrate and ammonium uptake in Antarctic waters. *Limnol. Oceanogr.* **25**: 1064–1074.
- PROBYN, T. A. 1985. Nitrogen uptake by size-fractionated phytoplankton populations in the southern Benguela upwelling system. *Mar. Ecol. Prog. Ser.*: In press.
- RÖNNER, U., F. SÖRENSON, AND O. HOLM-HANSEN. 1983. Nitrogen assimilation by phytoplankton in the Scotia Sea. *Polar Biol.* **2**: 137–147.

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Eutrophication and the rate of denitrification and N_2O production in coastal marine sediments

Abstract—Large (13 m³, 5 m deep) microcosms with coupled pelagic and benthic components were used to measure the effect of nutrient loading and eutrophication in coastal marine ecosystems on the rates of benthic denitrification (N_2) and N_2O production. After 3 months of daily nutrient addition, average denitrification rates ranged from about 300 $\mu\text{mol N m}^{-2} \text{h}^{-1}$ in the sediments of the control microcosm to 880 in the most enriched microcosm, which received 65 times the nutrient input of the control. Increases in the production of N_2O were more dramatic and increased by a factor of about 100, from 0.56 $\mu\text{mol N m}^{-2} \text{h}^{-1}$ in the control to 51 in the most enriched microcosm. Although there was a clear increase in the denitrification rate in the more eutrophic systems, the amount of fixed nitrogen removed was a constant or progressively smaller fraction of the nitrogen input. Even in the most enriched microcosm, at least 16% of the N input was removed by denitrification.

Many estuaries and other coastal marine ecosystems are receiving increased nitrogen from sewage, industrial wastes, and agricultural runoff (Walsh et al. 1981; Meybeck 1982; U.S. EPA 1982). In some cases these anthropogenic sources have come to dominate natural inputs from the watershed, the atmosphere, and coastal seawater. For example, sewage inputs alone account for 50% or more of the inorganic nitrogen loading

in Long Island Sound, New York Bay, Raritan Bay, Delaware Bay, and San Francisco Bay (Nixon and Pilson 1983). Similar situations no doubt exist elsewhere.

The ecological consequences of increasing nitrogen inputs in coastal marine ecosystems are not as well known as the impact of phosphorus loading on lakes (Schindler 1981; Nixon and Pilson 1983). The fate of the increased nitrogen input to coastal systems is even more poorly known. Increasing amounts of nitrogen may be buried in sediments, transported in various forms to nearshore ocean waters, or lost to the atmosphere as a result of denitrification (N_2) and N_2O production. In Narragansett Bay, R.I., denitrification is an important sink for fixed nitrogen and is removing, as N_2 , an amount of N equal to half of the inorganic nitrogen loading to that estuary each year from urban sewage (Seitzinger et al. 1980, 1984; Seitzinger 1982). N_2O is also produced in coastal sediments, although its production does not appear to be a major mechanism of removal of nitrogen loading (Seitzinger et al. 1983). The production of N_2O is of global geochemical interest, however, because of the role of this trace gas in the destruction of stratospheric ozone