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RACER: Uptake rates of ammonium and nitrate by phytoplankton populations during the 1989 austral spring bloom

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The southern ocean is characterized by much vertical mixing and, hence, nutrient concentrations are generally not considered to be a limiting factor for phytoplankton production. Despite this, primary production in this region has been found to be generally low (El-Sayed 1987) with exceptions, however, such as coastal areas near the Antarctic Peninsula (Holm-Hansen, Letelier, and Mitchell 1987). The Research on Antarctic Coastal Ecosystem Rates (RACER) program (Huntley et al., *Antarctic Journal*, this issue) is aimed at understanding the dynamics of such highly productive areas with one component focusing on phytoplankton-nutrient processes.

As part of this program, the uptake of ammonium and nitrate was examined to assess nitrogen utilization and mineralization by the planktonic population at different depths within the euphotic zone, as well as by size fractionated portions of the surface planktonic population. We present here preliminary information on the rates of these processes and discuss the implications of our results on new and recycled production and the regeneration of nitrogen in the RACER area.

Depth profile water samples were collected by Niskin bottles attached to a conductivity-temperature-depth (CTD) system (Amos, Jacobs, and Hu, *Antarctic Journal*, this issue) and surface seawater samples for size fractionation studies were collected by a bucket. Samples for depth profile uptake experiments were dispensed into 1 liter, clear polycarbonate bottles. Nitrogen-15 ammonium or nitrate (99.5 percent) was added (15 to 30 percent of ambient concentration) to a pair of bottles, respectively. One bottle from each pair was immediately filtered through a glass-fiber filter (Whatman, GF/F) and the filter and some filtrate frozen for initial time measurements. The second bottle from each pair was incubated on the ship's deck under simulated light and temperature conditions or *in situ*. After incubation, water samples were filtered through GF/F filters, and the filter and a sample of the filtrate were stored at −20 °C before preparation for mass spectrometric analysis of particulate organic nitrogen and nitrogen-15 components (Tupas, Koike, and Holm-Hansen, *Antarctic Journal*, this issue).

Surface-water samples for size fractionation experiments were dispensed into 4-liter polycarbonate containers, enriched with nitrogen-15 ammonium and nitrate, sampled for initial measurements as above, and incubated on deck for 24 hours. After incubation, portions of each water sample were filtered through

nylon nets having pore sizes of 20, and 10 micrometers, and through GF/C glass fiber filters which retain particles of approximately 1-micrometer diameter. Filtrates from each fraction and the original unfractionated water sample were filtered onto GF/F filters and analyzed as above. Uptake rates for ammonium and nitrate were calculated following the equations of Dugdale and Goering (1967) and normalized to a 24-hour day.

Chlorophyll-*a*, ammonium, and nitrate concentrations and estimates of ammonium and nitrate uptake at station A during 3 weeks in November are presented in table 1. Ammonium and nitrate uptake rates in the upper 5 meters of the water column were generally high, ranging from 0.065 to 0.6 micromoles of nitrogen per liter per day and 0.079 to 2.48 micromoles nitrogen per liter per day for ammonium and nitrate respectively, with total uptake rates from 0.144 to 2.891 micromoles of nitrogen per liter per day. Three different stages of the bloom can be distinguished during the course of the study. The phytoplankton population sampled on 2 November appeared to be in a pre-bloom stage with chlorophyll *a* concentrations from 1 to 2 micrograms per liter and low ammonium concentrations. On 7 November, both chlorophyll *a* and ammonium increased by approximately 10 times but nitrate concentrations remained about the same. This early-bloom stage was still present at the next experimental date (13 November) with a slight decrease in surface ammonium concentrations. During this time, the phytoplankton population at the upper layers (upper 20 meters) of station A was predominantly subsisting on nitrate with the lower layers (deeper than 20 meters) assimilating more ammonium. The almost tenfold increase in chlorophyll *a* from 2 to 7 November increased the uptake rates of ammonium and nitrate but did not change the pattern of nitrogen assimilation.

As the bloom continued to develop, a third stage evolved characterized by high chlorophyll *a* and low nitrate concentrations in the upper 10 meters. This upper mixed layer contained predominantly ammonium utilizers in contrast to previous periods when nitrate assimilation was more important. This shift may have been caused by a change in the composition of the phytoplankton population.

From the early bloom and its successive stages, ammonium accumulation occurred which shows larger production of ammonium than consumption within the planktonic food web. Fluctuations in ammonium concentrations at this station reflect variations in the regeneration of ammonium, and/or possible changes in water masses from vertical and horizontal transport during the bloom.

Chlorophyll *a* and particulate organic nitrogen concentrations and the estimates of nitrogen uptake by the different fractions of the surface planktonic population at station A with the percentage of these fractions to their respective total values are presented in table 2. Size fractionation of the planktonic population showed a shift in the dominant sized organisms from >20 micrometers at pre-and early-bloom stages to <20 micrometers during progress of the bloom. This shift in the phytoplankton population was consistent with the shift from predominantly nitrate utilization to ammonium utilization stated before.

Previous studies on nitrogen uptake by phytoplankton in the southern ocean have shown variations in the uptake of ammonium and nitrate. Olson (1980) reported an almost equal utilization of ammonium and nitrate in the Scotia Sea in spring whereas later in the season assimilation of ammonia has been reported to dominate (Glibert, Biggs, and McCarthy 1982; Rönner, Sörensson, and Holm-Hansen 1983; Koike, Holm-Hansen, and Biggs 1986). Our data show a similar trend, with concom-

Table 1. Chlorophyll *a*, nutrient concentrations, and nitrogen uptake rates at various depths and times at station A. Ammonium (N_4^+) and nitrate (NO_3^-) concentrations include the enrichment of nitrogen-15 labeled nitrogen tracers (0.2 micromoles per liter NH_4^+, 1 to 2 micromoles per liter NO_3^-).

Station/date	Depth[a]	Chlorophyll *a*	NH_4^+[b]	NO_3^-[b]	pNH_4^+[c]	pNO_3^-[c]	Σ pN[c]	pNH_4^+/Σ pN (%)
A107	1	1.81	0.32	20.1	0.065	0.079	0.144	45.1
Nov. 2	5	1.06	0.41	20.0	0.132	0.138	0.270	48.9
	10	1.31	0.32	20.0	0.119	0.187	0.306	38.9
	20	1.54	0.31	20.1	0.127	0.229	0.356	35.7
	30	1.83	0.32	20.0	0.164	0.139	0.303	54.1
	50	1.20	0.21	20.0	0.087	0.035	0.122	71.3
A205	1	10.50	1.22	20.8	0.508	1.143	1.651	30.8
Nov. 7	5	11.00	1.12	25.5	0.313	1.423	1.736	18.0
	10	12.08	0.82	24.5	0.324	1.405	1.729	18.7
	20	6.90	0.82	25.0	0.234	0.441	0.675	34.7
A301	1	13.44	0.64	25.0	0.411	2.480	2.891	14.2
Nov. 13	5	14.86	0.72	23.1	0.455	2.070	2.525	18.0
	10	14.78	0.72	21.7	0.436	0.464	0.900	48.4
	20	14.78	0.72	23.9	0.099	0.083	0.182	54.4
	30	11.00	0.72	23.1	0.072	0.042	0.114	63.2
A407	5	15.02	1.11	3.8	0.599	0.402	1.001	59.8
Nov. 20	10	14.86	1.50	4.3	0.551	0.069	0.620	88.9
	15	5.75	1.90	14.3	0.109	0.078	0.187	58.3
	25	0.75	1.31	16.6	0.091	0.175	0.266	34.2

[a] In meters.
[b] In micromoles per liter.
[c] In micromoles per liter per day.

Table 2. Chlorophyll *a* (Chl *a*), particulate organic nitrogen (PON), nitrogen uptake rates, and their proportion to total values of each size fraction of surface water at station A collected at different times. (NH_4^+ denotes ammonium. NO_3^- denotes nitrate.)

Station/date	Fraction[a]	Chl *a*[b]	PON[c]	pNH_4^{+}[d]	pNO_3^{-}[d]	Σ pN[d]	pNH_4^+/Σ pN (%)
A205	Total	11.68 (100)	8.514 (100)	0.550 (100)	1.573 (100)	2.123 (100)	26.0
Nov 7	<20	1.28 (11.0)	1.761 (20.7)	0.132 (24.0)	0.144 (9.2)	0.276 (13.0)	47.8
	<10	0.99 (8.5)	1.237 (14.5)	0.092 (16.7)	0.077 (4.0)	0.169 (8.0)	54.4
	<1	0.08 (0.7)	0.640 (7.5)	0.033 (6.0)	0.005 (0.3)	0.038 (1.8)	86.8
A213	Total	11.52 (100)	7.877 (100)	0.676 (100)	1.200 (100)	1.876 (100)	36.0
Nov 8	<20	1.96 (17.0)	2.155 (27.4)	0.161 (23.8)	0.136 (11.3)	0.297 (15.8)	54.2
	<10	1.50 (13.0)	1.908 (24.2)	0.121 (17.9)	0.087 (7.3)	0.208 (11.1)	58.2
	<1	.05 (0.5)	0.390 (5.0)	0.044 (6.5)	0.003 (0.3)	0.047 (2.5)	93.6
A301	Total	11.25 (100)	11.537 (100)	0.292 (100)	1.982 (100)	2.274 (100)	14.7
Nov 13	<20	1.71 (15.2)	5.550 (48.1)	0.273 (93.5)	0.528 (26.6)	0.801 (35.2)	34.1
	<10	1.69 (15.0)	5.368 (46.5)	0.256 (87.7)	0.451 (22.8)	0.707 (31.1)	36.2
	<1	0.11 (1.0)	0.792 (6.9)	0.022 (7.5)	0.005 (0.3)	0.027 (1.2)	81.5
A407	Total	11.84 (100)	7.357 (100)	0.366 (100)	0.372 (100)	0.738 (100)	49.6
Nov 20	<20	7.03 (59.3)	5.262 (71.5)	0.198 (54.1)	0.130 (34.9)	0.328 (44.4)	60.4
	<10	4.34 (36.7)	3.653 (48.4)	0.108 (29.5)	0.095 (25.5)	0.203 (27.5)	53.2
	<1	0.55 (4.7)	0.548 (7.4)	0.056 (15.3)	— (—)	0.056 (7.5)	100

[a] In micrometers.
[b] In micrograms per liter.
[c] In micromoles of nitrogen per liters.
[d] In micromoles per liter per day.

itant changes in the size spectrum of the phytoplankton. Nutrient regeneration in the euphotic zone thus appears to be of major importance in regard to dynamics of the microbial food web at station A. Additional data at representative stations indicate that the entire RACER area is similarly characterized by relatively high rates of nitrogen cycling.

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