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Nitrate use by plankton in the eastern subtropical North Atlantic, March–April 1989

Abstract—Nitrate concentration was measured in seawater samples from the euphotic zone at the beginning and end of 12-h, daytime, in situ incubations. The changes in concentration are considered to be measurements of new production. During periods of 2–3 weeks in March–April 1989, important time scales for NO_3^- input to the euphotic zone (i.e. residence times) and new production were ~26 d at 18°N, 31°W and ~10 d near 33°N, 21°W. The average rate of NO_3^- use in the two areas was 2.63 and 0.62 mmol N m^{-2} $(12\ h)^{-1}$, or, in carbon equivalents 209 and 49 mg C m^{-2} d^{-1}, respectively. These values bracket the large-scale estimate by Jenkins of new production in the nearby beta triangle of 150 mg C m^{-2} d^{-1}.

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Ten years ago there was renewed controversy over the magnitude of photosynthetic production in the ocean. New observations, based on seasonal and annual integrations of organic matter production or its proxies, exceeded those based on historical ^{14}C bottle experiments. One of those new observations was Jenkins's (1982) estimate of annual oxygen utilization rate (OUR) beneath the euphotic zone in the eastern subtropical Atlantic. The OUR was an estimate of the rate of new or export production and did not include the production of organic matter that was recycled in the euphotic zone. It exceeded by severalfold the rate of new production expected for the subtropical gyres of the central oceans from summaries of ^{14}C measurements. There were no measurements of new production at the location of his study, however. This report offers some new production measurements, based on short-term bottle incubations analogous to ^{14}C production experiments, for two other locations in the eastern subtropical Atlantic. We compare the results with the annual

OUR of Jenkins. New production rates in various parts of the ocean were recently reviewed (Eppley 1989).

This work reports the new production measurements during *Meteor* cruise 10/1, the first leg of the Centennial Cruise of the Hensen Plankton Expedition, and the southernmost part of the Joint Global Ocean Flux Study (JGOFS) of the North Atlantic Bloom Experiment of 1989. New production in the euphotic zone is usually measured with $^{15}NO_3^-$ (Dugdale and Goering 1967). In these subtropical waters, however, NO_3^- concentrations were low and the tracer addition, typically 50–100 nM, would be large compared to ambient levels and perturb (increase) the NO_3^- utilization rates. Also, any concurrent nitrification, leading to formation of NO_3^- during the measurement, would dilute the ^{15}N label and confound measurement of NO_3^- use (Ward et al. 1989). Measurement of net changes in NO_3^- concentration was therefore both expedient, scientifically justified, and perhaps even preferred for these low-NO_3^- waters. The net change will underestimate NO_3^- use, however, if there is concurrent NO_3^- production by nitrification.

The cruise included two 3-week segments, the first near 18°N, 31°W (area 1) and the second near 33°N, 21°W (area 2). Both areas are in the North Atlantic subtropical gyre (Stramma and Siedler 1988). These areas are south and northeast, respectively, of the beta triangle (apices 26.5°N, 38.5W; 32.5°N, 30.0°W; 22.5°N, 28.5°W) where Jenkins (1982) studied export production from the euphotic zone in terms of oxygen consumption in the underlying waters. His annual rate (±1 SD), expressed as organic C consumption, was 55 ± 5 g C m^{-2} yr^{-1} or ~150 mg C m^{-2} d^{-1}. To our knowledge there are no other measurements in the region of new production or export production from the euphotic zone, apart from the sediment trap studies carried out on this cruise.

Water samples were collected at ~0600 hours each morning with a CTD-rosette system with 10-liter Niskin water bottles fitted with silicone rubber tubing as closing springs. Samples were taken at 5–10-m intervals in the upper 100 m. Subsamples were drawn into 250-ml polycarbonate bottles, cleaned between uses with 10% HCl. No airspace was left in the bottles in order to suspend them in situ during the day. Other subsamples were analyzed directly for NO_3^-, and sometimes NO_2^-, with a chemiluminescence analyzer (Garside 1982). At the end of the day the in situ incubated samples were retrieved and analyzed directly for NO_3^-.

The sampling was done over several days while following the drift of a sediment trap array. Thus we anticipated that each morning cast would essentially replicate that of the previous and subsequent days.

A second cast was made at ~1800 hours. Water samples were sometimes taken in area 2 from this evening cast for overnight incubation in the ship's constant-temperature room, ~18°–20°C, in the dark. NO_3^- concentration was determined at the beginning and end of the incubations as before. In situ changes in NO_3^- concentration were <20 nM between morning and evening samples from the upper 20 m, indicating NO_3^- consumption during the day that agreed well with the incubation results (Eppley et al. 1990). Sixteen daytime and four overnight experiments yielded successful depth profiles of net changes in NO_3^- concentration. The measurements understimate NO_3^- utilization when NO_3^- production takes place at the same time.

The size class of the organisms effecting change in NO_3^- concentration was examined by passing water samples through Nuclepore filters before incubation. Plastic apparatus, cleaned with 10% HCl, was used for these manipulations. These samples were incubated in a small deck incubator shaded from direct sunlight or in darkness in the ship's constant-temperature room.

Each sample taken for NO_3^- analysis was analyzed ≥2 times, until replicates agreed within 2 nM or 1% at the highest concentrations observed. The mean difference between replicates of 102 samples containing 20 nM NO_3^- was 1.17 nM (SD 1.00 nM). Rates of NO_3^- utilization were the difference between the final average values and the initial ones. Some estimate of the error in measurement can be had by taking the range of the analytical differences, i.e. sub-

tracting the lowest final value from the highest initial value and the highest final value from the lowest initial value. In the data presented the value from the former is here called the maximal rate, and the latter the minimal rate of NO_3^- use. Sometimes NO_3^- concentration increased during incubation. The NO_3^- utilization rate (net nitrification rate) is then expressed as a negative value. We made replicate incubations in the size-fractionation experiments as a further check on analytical error. The maximal difference in NO_3^- use among seven pairs of replicates was 4.9 nM with ambient concentrations between 60 and 110 nM.

$^{15}NO_3^-$ was added to samples from deep in the euphotic zone where the probability of encountering NO_3^- above nanomolar levels was greatest. For this work, 4-liter polycarbonate bottles were filled at the 0600-hour cast and incubated in situ over the day. On recovery, this water was filtered through precombusted GF/F glass-fiber filters. The filters with the particulate matter were dried overnight at 60°C and the dry filters returned to the home laboratory in a desiccator. The $^{15}N:^{14}N$ ratio of the particulate matter was determined with a JASCO model N-150 ^{15}N analyzer as described by Harrison (1983). The final NO_3^- concentration of these samples was measured directly after incubation on the ship. Relatively large additions of $^{15}NO_3^-$ were required because of the low precision of our ^{15}N analyzer. It should be noted, however, that true tracer experiments have been carried out recently, even with ambient NO_3^- at nanomolar levels (J. McCarthy et al. pers. comm.).

Sources of error in the chemiluminescence NO_3^- measurements were examined in detail earlier (Eppley et al. 1990) and will not be repeated here. That report considered contamination problems and their avoidance, interfering substances, nitrification, and comparisons of NO_3^- changes in situ with the bottle incubations.

In area 1, near 18°N, 31°W, depth distributions of NO_3^- were of two different types. About two-thirds of the stations showed a NO_3^--depleted surface layer, with NO_3^- concentration 10–20 nM at 0600 hours and increasing with depth (Fig. 1). NO_3^- use at such stations showed a maximum within the depth range of NO_3^- increase, the latter hereafter called the nitracline.

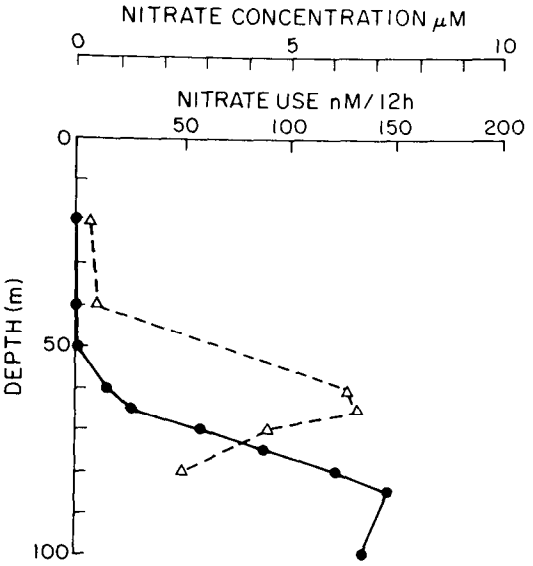

Fig. 1. NO_3^- concentration (●) and rate of utilization (△) at station 260 in area 1. NO_3^- concentration at 20-m depth was 14 nM.

The other stations in area 1 showed a subsurface NO_3^- maximum within the euphotic zone (Fig. 2). In the example shown, station 249, the depth profile of NO_3^- utilization showed two maxima, one at the chlorophyll fluorescence maximum near 45-m depth and a second one associated with the NO_3^- concentration maximum (Fig. 2). (This NO_3^- intrusion feature was new to us. Because of its novelty and possible significance for new production it will be treated elsewhere). The mean rate of NO_3^- use in the 12-h daytime incubations (Table 1) was 2.63 ± 2.02 mmol N m^{-2} (12 h) $^{-1}$.

Several stations in area 2, near 33°N, 21°W, showed nearly uniform NO_3^- concentrations in the euphotic zone below the layer of surface depletion, rather than a monotonic increase with depth, with concentrations in the range 200–500 nM (Fig. 3). NO_3^- use showed a single peak near the top of this NO_3^- distribution at these stations (Fig. 3). In spite of the presence of NO_3^- in the lower euphotic zone, overall NO_3^- concentrations were lower in this second area as were rates of NO_3^- utilization (Table 1).

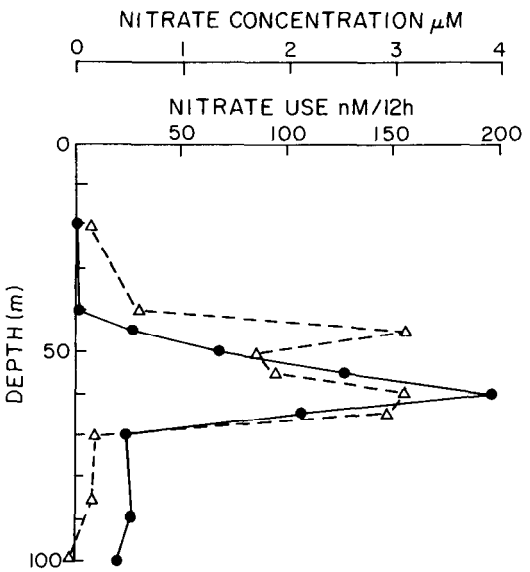

Fig. 2. NO_3^- concentration and rate of utilization at station 249 in area 1. Symbols as in Fig. 1. NO_3^- concentration at 20-m depth was 11 nM.

Surface concentrations of NO_3^- were elevated (40–50 nM) at station 366 (Fig. 4), with a minimal NO_3^- concentration at 60 m. The rate of NO_3^- use measured with $^{15}NO_3^-$ was greater than the rate of NO_3^- disappearance from solution. Either the added 100 nM $^{15}NO_3^-$ increased the rate of NO_3^- use at the 60- and 70-m depths at that station, where the NO_3^- added was twice the ambient concentration, or the difference between the two measurements of NO_3^- represented the production of NO_3^- (nitrification), detected only by measuring the net change of NO_3^- concentration (Fig. 4). Other examples of apparent nitrification during this cruise were reported earlier (Eppley et al. 1990).

Fortuitously, the night incubations at area 2 involved water with low NO_3^- concentration. NO_3^- clearly disappeared from solution during the night (Table 2), as well as in daytime, but the range of NO_3^- concentrations observed and the rates themselves were limited in scope and we were unable to distinguish nighttime incubation results from daytime results.

Effects of removing larger particles and of adding mercuric chloride to stop metabolic processes were examined briefly while the

Table 1. NO_3^- utilization in the eastern subtropical Atlantic Ocean, March–April 1989. Area 1 is at 18°N, 31°W; area 2 is at 33°N, 21°W. Daytime incubations in situ over the depth indicated. Explanation of maximum, minimum, and mean estimate of NO_3^- utilization given in text. Negative values for station 292 indicate net NO_3^- production.

Sta.	NO_3^- use [mmol m^{-2} (12 h)$^{-1}$] Max	Min	Mean	NO_3^- content (mmol m^{-2})	Integration depth (m)
18°N, 31°W					
241	2.19	1.75	1.97	47.6	100
249	4.48	3.35	3.91	64.5	90
254	6.15	3.47	4.81	196	100
260	6.51	3.06	4.79	132	90
266	0.53	0.47	0.50	7.7	80
273	3.71	1.63	2.67	80.7	90
292	−0.05	−0.47	−0.26	12.2	100
33°N, 21°W					
361	0.71	0.64	0.68	2.7	55
366	1.49	1.39	1.44	2.1	50
370	0.35	0.18	0.27	2.6	50
376	2.09	1.87	1.98	18.4	70
382	0.20	0.18	0.19	0.65	70
387	0.39	0.22	0.31	4.3	80
392	0.15	0.08	0.11	7.0	77
398	0.27	0.21	0.24	1.8	70
403	0.42	0.32	0.37	12.4	80

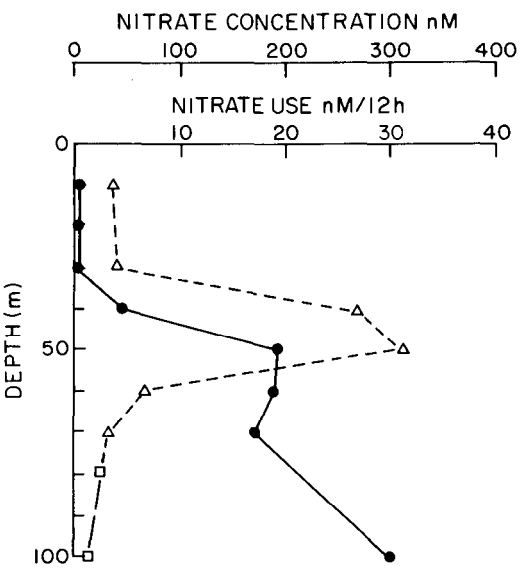

Fig. 3. NO_3^- concentration (●) and rate of utilization at station 361 in area 2. NO_3^- use measured as NO_3^- disappearance from solution—△; NO_3^- incorporation into particles measured with $^{15}NO_3^-$—□. NO_3^- concentration at 10–30-m depth was 7.9 nM.

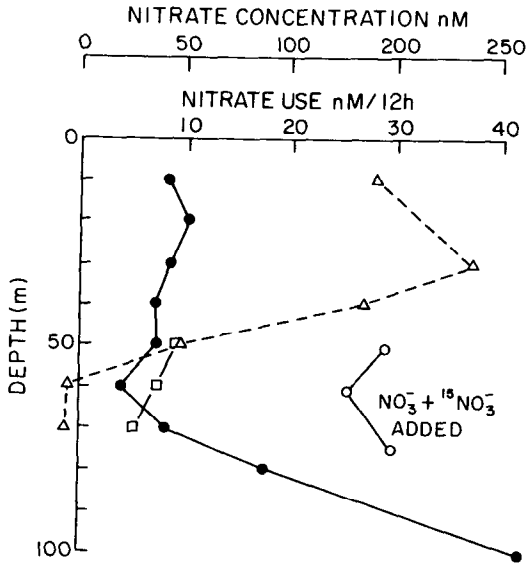

Fig. 4. NO_3^- concentration and rate of utilization at station 366 in area 2. Symbols as in Fig. 3 except: O—the sum of ambient NO_3^- and added $^{15}NO_3^-$ concentrations.

ship transited from area 1 to area 2. The experiments are incomplete as no daytime, euphotic zone experiment was included. Results with the 150-m water in daytime incubation may not be applicable to the euphotic zone, but they are the only daytime results available.

As expected, the addition of 2 mM Hg to a seawater sample stopped NO_3^- uptake (Table 3). The effects of prefiltering water through 1- and 0.4-μm sieves (Nuclepore filters) was interesting because, in both experiments, uptake was greatest in the sample passed through the 1-μm sieve and slightly less in the unfiltered water. Most of the NO_3^- utilization was removed by passing the water through the 0.4-μm sieve. Some activity remained, however, implying the presence of NO_3^- utilizing, very small picoplankton (Table 3).

In this study the NO_3^- utilization rate per unit of volume was a linear function of NO_3^- concentration for concentrations below about 40 nM in both areas 1 and 2 (Eppley et al. 1990), and this relation accounted for most of the variability in NO_3^- use in the upper euphotic zone where NO_3^- concentrations were low. The depth-integrated rates

Table 2. NO_3^- utilization at night, area 2. Samples incubated 12 h overnight in ship's constant-temperature room. T—20°C. Negative values for station 385 indicate net NO_3^- production.

Sta.	NO_3^- use [mmol m^{-2} (12 h)$^{-1}$] Max	Min	Mean	NO_3^- content (mmol m^{-2})	Integration depth (m)
33°N, 21°W					
368	0.19	0.26	0.22	0.75	75
380	0.73	0.58	0.66	11.4	75
385	−0.48	−0.64	−0.56	8.0	75
389	0.27	0.21	0.24	2.7	75

of NO_3^- use also increased with the NO_3^- content of the euphotic zone in area 1 (Fig. 5, upper panel). In area 2 NO_3^- contents were low, and there was no clear dependence of depth-integrated rate of NO_3^- use on depth-integrated NO_3^- content, nor was there a difference between day and night results (Fig. 5, lower panel).

The chlorophyll content of the euphotic zone of area 1 also varied with NO_3^- content, and the depth-integrated NO_3^- use was a linear function of chlorophyll content.

$$\underset{\text{mmol m}^{-2}\,(12\text{ h}^{-1})}{\text{NO}_3^-\text{ use}} = 0.29\underset{\text{mg m}^{-2}}{(\text{Chl } a)} - 6.05$$

with $r = 0.87$, $P < 0.01$. Area 2 did not show these relationships of NO_3^- use to NO_3^- content or chlorophyll.

The quotient of the NO_3^- content of the euphotic zone and its rate of utilization has units of time. It represents the time required to deplete the available NO_3^- at the observed rate of utilization. Although the

Table 3. Utilization of NO_3^- by organisms passing 1- and 0.4-μm sieves, compared with that in unfiltered water and in water poisoned with 2 mM mercuric chloride. Filtration was done before incubation.

Treatment	NO_3^- use (mM)
Exp. 1: 80-m water from 30°17'N, 23°15'W incubated 13 h in the dark	
Unfiltered water	7.2
1-μm filtered water	8.5
0.4-μm filtered water	2.0
Unfiltered + Hg	−1.6
Exp. 2: 150-m water from 25°14'N, 26°45'W incubated 8 h in daylight	
Unfiltered water	14.9
1-μm filtered water	17.2
0.4-μm filtered water	2.3

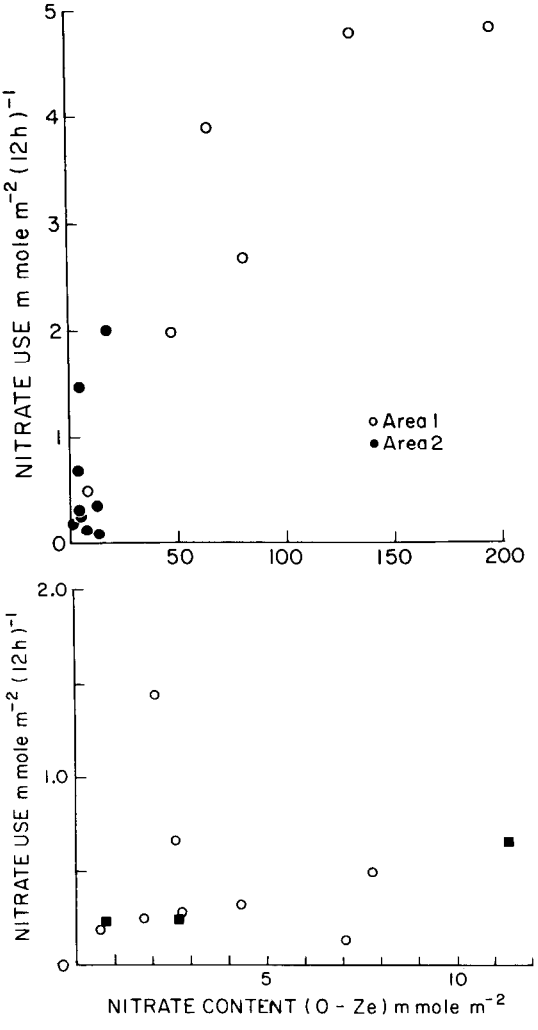

Fig. 5. Depth-integrated rate of NO_3^- utilization vs. depth-integrated NO_3^- content of the euphotic zone. Depths of integration (Z_e) given in Table 1. Lower panel is a blow-up of upper panel emphasizing stations with low NO_3^- content of the euphotic zone (O). All but one are from area 2. Also shown are area 2 stations where samples were incubated overnight in the dark (■). Note change in scale.

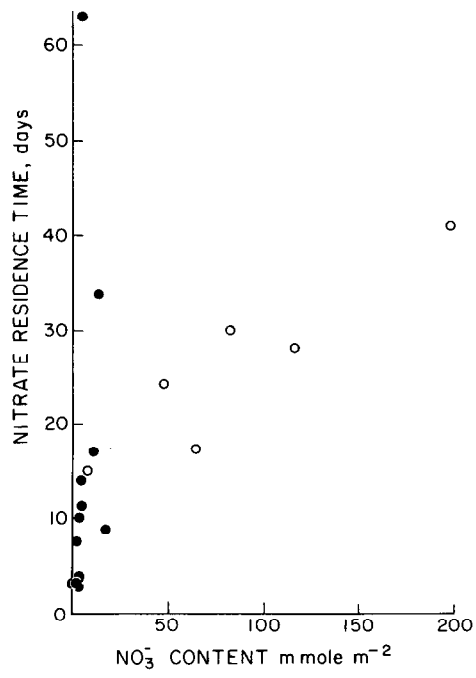

Fig. 6. Variation in NO_3^- residence time in the euphotic zone with NO_3^- content of the euphotic zone. Area 1—O area 2—●.

times were quite variable, the median residence time in area 1 was 26 d but only 10 d in area 2. The range was 15–41 d for area 1 (omitting station 292 where there was net NO_3^- production) and 1.5–63 d for area 2 (Fig. 6).

The rate of NO_3^- utilization per square meter varied by an order of magnitude in each of the two areas studied and by nearly 50-fold considering the two areas together (Table 1). Much of this extreme variability in area 1 was due to large changes in the NO_3^- and chlorophyll contents of the euphotic zone (Fig. 5), rather than to the methodology. Given such large variations in the NO_3^- distributions we encountered, it is clear that undersampling can be a serious problem for the eastern subtropical North Atlantic when discrete water sampling and bottle incubation methods are used. Platt et al. (1989) proposed that much of the difference in new production estimates between shipboard incubation methods and in situ methods (e.g. Jenkins 1982) that integrate over larger time and space scales was likely due to undersampling. Our results reinforce that view.

We are hesitant to express an average result for these two areas in the face of the large variability or especially to use them to compute an annual average. Besides the variability in daytime rates, there is additional uncertainty concerning NO_3^- use at night—a process studied even less comprehensively than the daytime rates. It should be noted, however, that several of the day-

time NO_3^- utilization rates (Table 1) approached or exceeded the OUR below the euphotic zone (equivalent to ~150 mg C m^{-2} d^{-1} or 1.9 mmol N m^{-2} d^{-1}) in the nearby beta triangle region (Jenkins 1982). Jenkins used oxygen data and transport calculations over a large area to compute oxygen consumption rates and thereby integrated over large time and space scales. Such methods are to be encouraged. Process studies, such as described here, are more concerned with mechanisms.

The relation in area 1 between NO_3^- utilization in the euphotic zone and the NO_3^- content of the euphotic zone as seen in the upper panel of Fig. 5 was new to us. The relationship did not extend to area 2, which showed the lowest rates and NO_3^- contents (Fig. 5, lower panel). The relationship is easy to understand because depth-integrated NO_3^- use and Chl *a* content were well correlated. On the basis of the "rule of thumb" that 1 mg of Chl *a* is equivalent to 1 mmol of phytoplankton N, the slope of the relationship of NO_3^- use to Chl *a* approximates the specific rate of NO_3^- use, 0.29 d^{-1}. Phytoplankton specific growth rates in oceanic waters approach the maximal rates expected from the ambient temperature (Herbland and LeBouteiller 1983; Laws et al. 1987), as predicted by Goldman et al. (1979), with depth-integrated rates of ~1 d^{-1}. This finding suggests that ~30% of phytoplankton production in area 1 took place at the expense of NO_3^- and ~70% was on recycled N.

Results of the size-distribution experiments are reminiscent of those of Hansell and Goering (1989). In the Bering Sea they found a discrepancy between the urea-N removed from solution and that recovered in particles. Passing water through a 20-μm screen resolved most of this difference. The screen removed only ~4% of the phytoplankton chlorophyll, but apparently most of the grazers. Here passing the water through a 1-μm sieve increased NO_3^- utilization ~15% (Table 3), possibly because the sieve removed some of the animals that graze on the microorganisms utilizing NO_3^-.

Based on $^{15}NO_3^-$ incorporation into particles, Harrison and Wood (1988) found that picoplankton passing a 1-μm sieve incorporated a variable fraction of the total NO_3^- taken up (from 11 to 63%; mean, 27%) in oceanic waters of the NW Atlantic. NO_3^- utilization by picoplankton (that passing the 1-μm sieve) in our experiments was high compared with the unfiltered water, however. The discrepancy could lie in differences in time and place, but also in method: $^{15}NO_3^-$ incorporation into particles in their work vs. NO_3^- removed from solution as measured here.

The residence times of NO_3^- in the euphotic zone (Fig. 6) suggest that important scales for NO_3^- input at the time of measurement were shorter in area 2 (avg 10 d) than in area 1 (avg 26 d). Ten days is near the event time scale, characteristic of weather-related processes. Twenty-six days approaches the mesoscale typical of eddies and fronts (Haury et al. 1978). Area 2 is south of the subtropical front observed in March–April 1982 cruises. The front generated mesoscale eddies on both sides, however (Käse and Siedler 1982). Mesoscale features were also seen in chlorophyll distributions near the subtropical front west of the present study area (Fasham et al. 1985). The complexity imposed by the large variability observed on time scales of days to weeks impresses on us once more the need to parameterize new production rates in order that basin-scale, seasonal, and annual summaries can be achieved, as required by JGOFS.

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Nitrogenase activity of *Microcoleus lyngbyaceus* mat communities in a eutrophic, tropical marine environment

Abstract—Floating and attached cyanobacterial mats consisting primarily of *Microcoleus lyngbyaceus,* a nonheterocystous, filamentous cyanobacterium, are a permanent feature of the nearshore marine environment at La Parguera, Puerto Rico. Nitrogenase activity in these mat communities, as determined by acetylene reduction, exhibited a diel cycle with daytime inhibition and enhanced nocturnal activity. Contrary to reports regarding benthic cyanobacterial mats adapted to oligotrophic conditions, nitrogenase activity in *M. lyngbyaceus* mats is closely regulated by concentrations of NH_4^+ and NO_3^- within the range of values common to their environment. The opportunistic strategy of N utilization used by *M. lyngbyaceus,* whereby molecular N is primarily consumed only in the absence of significant concentrations of alternate inorganic N sources, assures the success of these cyanobacterial mat communities.

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Inshore waters at La Parguera, on the southwestern coast of Puerto Rico, are subjected to chronic sewage discharges resulting in incipient nearshore eutrophication (Corredor et al. 1985). Blooms of *Microcoleus lyngbyaceus,* a nonheterocystous, filamentous cyanobacterium, grow over the bottom of the inshore channel, on seagrass beds, attached to buoys, and as floating mats associated with these discharges. The occurrence of floating cyanobacterial mats