

Nitrate uptake and diffusive nitrate supply in the Central Atlantic

*Dolors Planas*¹

GEOTOP, Department of Biological Sciences, University of Quebec, C.P. Box 8888 Centre Ville, Montreal, Quebec H3C 3P8, Canada

Susana Agustí, Carlos M. Duarte, and Tim C. Granata

Centro de Estudios Avanzados de Blanes, CSIC, Camí de Santa Bàrbara s/n, 17300 Blanes, Spain

Martín Merino

Instituto de Ciencias del Mar y Limnología, UNAM, Apdo. Postal 70-305, Mexico City, DF 04510, Mexico

Abstract

The latitudinal variation (35°S to 28°N) in the rate of diffusive nitrate supply across the thermocline and the associated variation in the uptake rate of nitrate and ammonium in the Central Atlantic was studied. The calculated diffusive nitrate flux showed a sharp latitudinal gradient, with the lowest nitrate supply ($0.00037 \mu\text{mol m}^{-3} \text{d}^{-1}$) in the South Atlantic subtropical gyre and the highest values ($23.5 \mu\text{mol m}^{-3} \text{d}^{-1}$) between the Equator and 15°N. The uptake rate of nitrate was inhibited at high irradiance at most stations. Both nitrate and ammonium uptake rates were lowest (about 3 and $10 \mu\text{mol m}^{-3} \text{d}^{-1}$, respectively) at the southern end of the transect and increased (about 20 and $55 \mu\text{mol m}^{-3} \text{d}^{-1}$, respectively) towards the Equator, with this increase being much greater for ammonium than for nitrate uptake. The *f*-ratio was highest (≈ 0.4) just south of the Equator and lowest (≈ 0.03) at the southern end of the transect. The slope between total uptake rate of dissolved inorganic nitrogen and gross primary production, calculated from O₂-based measurements, in surface waters (4.72 ± 1.54) was somewhat lower, but not significantly so, than the expected C/N ratio of 6.6. The average uptake rate of nitrate did not differ significantly from the average estimated diffusive supply of nitrate to the biogenic layer over the Central Atlantic. However, the nitrate uptake rate increased as the $\frac{1}{2}$ power of the diffusive nitrate flux to the biogenic layer. As a result, nitrate uptake far exceeded (by up to 100-fold) the nitrate flux to the biogenic layer in the stations where the supply of nitrate was lowest. The excess nitrate uptake averaged $0.65 \pm 0.24 \text{ mmol NO}_3 \text{ m}^{-2} \text{d}^{-1}$ (range, 0.05–1.9 $\text{mmol NO}_3 \text{ m}^{-2} \text{d}^{-1}$), which must be supplied through atmospheric deposition and other perturbation events. This excess nitrate uptake is relatively large compared to the diffusive supply in the most unproductive areas, where external nitrate inputs fuel the new production. In contrast, these sources of nitrate are far less significant where high diffusive fluxes suffice to maintain high nitrate uptake rates.

In the open ocean, under equilibrium conditions the nitrogen needed to support primary production is believed to be mostly supplied from the nutrient-rich deeper waters via advective fluxes of nitrate during upwelling or vertical mixing or diffusive fluxes driven by the nitrogen gradient across the thermocline (Lewis et al. 1986). Advective nitrate fluxes in the open ocean tend to be higher at high latitudes, where convective mixing favors high levels of primary production.

In contrast, fluxes are low in the permanently stratified tropical ocean, where a permanent thermocline limits the fluxes to those associated with the slow process of diffusive supply. The supply of nitrogen is lowest in the middle oceanic gyres, where a deep thermocline and smooth nutrient gradients determine slow rates of nutrient supply to the biogenic zone (Sverdrup 1955; Dugdale et al. 1990). However, nitrogen fluxes are enhanced in the equatorial zone of the Pacific and Atlantic Oceans, where equatorial divergence leads to doming of the pycnoclines at the Equator, bringing nitrate-rich waters in closer contact with surface waters. This process accounts for the higher phytoplankton biomass and primary production observed in the equatorial ocean (Murray et al. 1989; Peña et al. 1992; Carr et al. 1995). Hence, there should be strong latitudinal patterns in the nitrogen supply and, therefore, in primary production in the tropical ocean.

The link between the rates of nitrogen supply and new production have been studied extensively in the Central Pacific (e.g., Peña et al. 1992; Carr et al. 1995). Studies in the Atlantic Ocean are largely restricted to the North Atlantic (Lewis et al. 1986; Glibert et al. 1988; Eckman 1994; Harrison et al. 1996), and there is a remarkable paucity of information on the Central and South Atlantic (Le Bouteiller 1986; Metzler et al. 1997). These studies have provided some evidence of imbalances between the diffusive nitrogen

¹ Corresponding author, e-mail: planas.dolores@uqam.ca.

Acknowledgments

This is a contribution to the “Latitude” project (grant # AMB94-0739) funded by the Spanish Interministerial Commission of Science and Technology (CICYT). D. Planas was supported by the Natural Sciences and Engineering Research Council (NSERC) of Canada and a grant from the Université du Québec à Montréal (UQAM). We also thank the financial aid of the “Acciones Integradas” between Quebec-Catalonia programme of the General Direction of Research of the government of Catalonia. We thank Mario Manriquez and Pedro Jornet for assistance with CTD profiling, Paola Satta, Gustavo Carreras and Aimé Rodriguez for help with gross production determinations, Patricia Wickham for isotope analyses, the commander and crew of the BIO-Hesperides for help during the cruise, and two anonymous reviewers and D. Kirchman for helpful comments on the manuscript.

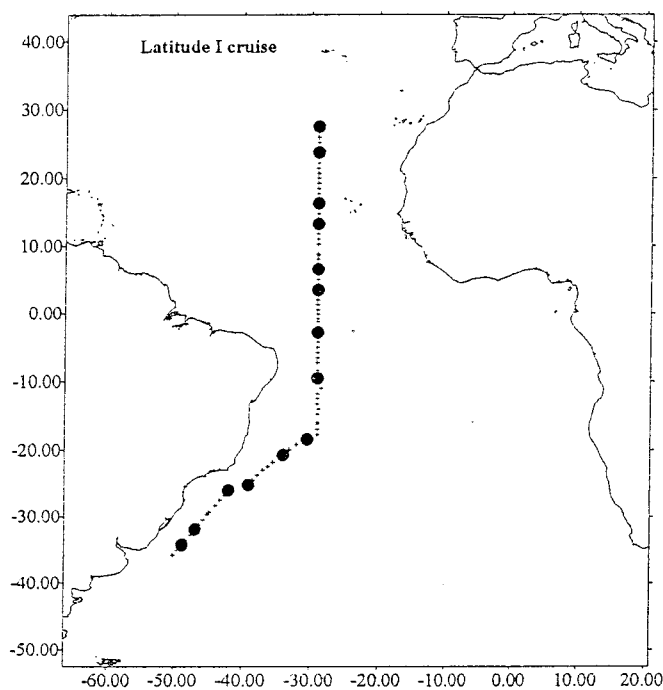


Fig. 1. Track of the "Latitude I" cruise across the Central Atlantic, showing the position of the stations studied (●).

supply and new production (McGillicuddy et al. 1998; Oschlies and Garçon 1998). However, the present empirical information on nitrate uptake and supply in the Central and South Atlantic is too meager to reliably test the existence, magnitude, and distribution of such imbalances.

The goal of this study was to test the balance between nitrate uptake and diffusive supply in the Central Atlantic, using data acquired during a meridional study (35°S–28°N) across the Central Atlantic. We first calculated the vertical turbulent diffusion coefficient and the nitrate gradient across the thermocline, thereby allowing the calculation of upward diffusive nitrate supply rates. We then used ^{15}N tracer additions to estimate nitrate and ammonium uptake rates and to test their possible light dependence. The estimated nitrogen uptake was then compared with gross primary production and estimates of diffusive nitrate supply to the biogenic layer.

Methods

This study was conducted as part of the LATITUDE I cruise, aimed at elucidating latitudinal patterns in the structure and functioning of the biogenic zone across the Central Atlantic Ocean (Fig. 1). The cruise was conducted between 17 March and 15 April 1995 on board the RV *BIO-Hesperides*. The physical structure of the water column was profiled at 87 stations along the transect, with a vertical resolution of 10 cm, using a MARK V or MARK III conductivity-temperature-depth (CTD) fitted with a fluorometer and a Rosette sampler system. Salinity and temperature estimates derived from both CTDs were calibrated from salinity samples and a highly accurate reversible thermometer,

respectively. Salinity measurements were made on a Guildline Autosol salinometer calibrated with IAPSO standard seawater (34.993 ppt). Horizontal velocity was measured continuously along the transect using a VM150 narrow-band acoustic Doppler current profiler (RD Instruments) mounted in midhull of the ship. The two horizontal velocity components, E–W (u , m s^{-1}) and N–S (v , m s^{-1}), were taken every 1.2 s in 8-m bins from the subsurface (16 m) down to 400 m. The calibration of the average velocities was done as recommended by Joyce (1989). The estimates were averaged to 5-min intervals and scanned for errors due to changes in ship position and speed (King and Cooper 1993; Saunders and King 1995).

Nitrogen uptake—Nitrate and ammonium uptake rates were estimated in surface (5 m depth) waters and those at the deep chlorophyll maximum (DCM), as determined from the profiles obtained from the fluorometer mounted on the CTD, at 14 of the stations using ^{15}N tracer (as $^{15}\text{NO}_3^-$ and $^{15}\text{NH}_4^+$; modified from Dugdale and Goering [1967] as recommended by McCarthy et al. [1992]). The use of $^{15}\text{NH}_4^+$ as a tracer should provide conservative estimates of recycled production because urea and amino acids, although often below detection limit, may support a significant fraction of the N uptake in the Central Atlantic (Metzler et al. 1997). The water samples for these experiments were collected from the 12-liter Rosette sampling system between 0900 and 1100 h (local time). All the containers used for subsampling and incubation were of cleaned polycarbonate (Fitzwater et al. 1982). Once cleaned, the bottles were soaked with seawater for 24 h before use and rinsed with the sample before pouring the water. Water samples were screened through a 150- μm Nyltex mesh and transferred to dark 20-liter carboys. Four 20-ml subsamples, filtered through precombusted (460°C for 4 h) GF/F, were drawn to analyze initial NH_4^+ and NO_3^- . The carboys were then spiked with the adequate tracer [$(^{15}\text{NH}_4)_2\text{SO}_4$ or K^{15}NO_3 99 atom%] and mixed, and an aliquot was filtered onto a precombusted GF/F filter and kept frozen for later analysis of the initial particulate organic nitrogen (PON) (Glibert et al. 1991). The filtrate was also used to measure the initial ^{15}N atom% enrichment of the substrate. The $^{15}\text{NO}_3^-$ additions did not exceed 10% of ambient NO_3^- concentrations. Whenever NO_3^- concentrations were below the detection limit and for $^{15}\text{NH}_4^+$ experiments, where estimates of the in situ ammonium concentrations were not available before spiking the sample with the tracer, the additions were 0.025 μM for NO_3^- and NH_4^+ .

Incubation of the ^{15}N -enriched samples was initiated within 1 h of sample collection in 2-liter polycarbonate bottles fitted with neutral density screens to adjust the incident light levels to 100%, 50%, 10%, and 1% of the incident irradiance for surface waters and to 50%, 10%, 6%, and 1% of the incident irradiance for waters at the deep chlorophyll *a* maximum. We assumed low diel periodicity in the low-nitrogen regions studied, comparable to findings elsewhere (Sahlsten 1987; Glibert et al. 1988). Thus, the incubation period, generally between 1000 to 1400 h local time, was short (2–3 h) to minimize isotopic dilution (Glibert et al. 1985) and ammonification, which can be particularly important in oligotrophic waters (Garside 1984). The bottles were incubated

in a deck incubator and cooled with a continuous flow of seawater.

At the end of the incubation, the bottle contents were filtered through precombusted GF/F filters and immediately frozen for isotope analysis. The sample nitrogen was converted to pure N_2 based on the Dumas combustion technique (Handley et al. 1991). The isotopic composition of the gas samples was analyzed on a dual-inlet, triple-collector Prism Series II ratio mass spectrometer (VG Isotech), which yielded a standard deviation of 0.0006 atom% ^{15}N for a mean of 0.3673 atom% ^{15}N (coefficient of variation = 0.17%). The equations used to calculate the specific uptake and uptake rates for both forms of inorganic nitrogen were those recommended by Dugdale and Wilkerson (1986), because our survey encompassed a broad trophic range. Uptake rates ($\mu\text{mol m}^{-3} \text{h}^{-1}$) were calculated by multiplying the specific uptake rates, V (h^{-1}), by PON (measured in the same sample during the mass spectrometer analysis) at the end of the incubation. The V parameter was determined as the mean of V_i (the percentage of ^{15}N atoms in the sample adjusted by subtracting the natural abundance of ^{15}N) and V_o , based on the measured initial value of PON (Dugdale and Wilkerson 1986). The NH_4^+ uptake rates must be considered as minimum estimates because no corrections for the isotopic dilution were made. The f -ratio was calculated as the ratio between the NO_3^- uptake rate and the sum of the NO_3^- and NH_4^+ uptake rates (Eppley and Peterson 1979). These estimates of NO_3^- uptake involved a ≤ 2 -fold uncertainty, resulting from the possible inclusion of detritus in PON, diel periodicity in NO_3^- uptake, and uncertainties in the initial NO_3^- concentrations.

Water column characteristics—Profiles of underwater spectral irradiance were obtained at the stations using a spectroradiometer (LiCor LI-1800UW) and integrated over the 400–700 nm to estimate the irradiance within the photosynthetically active radiation (PAR) band. Mean (\pm SE) PAR at 5 m depth, from where the surface water samples were collected, was $53.7\% \pm 2.7\%$ of that at the surface and at the depth of the deep chlorophyll a maximum (average depth = 90.2 m; range, 50–139 m) was $3\% \pm 0.5\%$ of that incident at the surface.

Gross oxygen production rates in surface waters were calculated from oxygen variations after incubation of samples in light and dark bottles. Water samples were filtered through a 150- μm mesh (to exclude larger zooplankton) and carefully siphoned into 125-ml narrow-mouth Winkler bottles. The initial oxygen concentration was immediately determined in replicate bottles, and dark and light bottles were incubated at surface sea temperature in an incubator for 17–22 h, similar to incubation times used for other plankton-poor waters (e.g., Williams and Jenkinson 1982). Light bottles were incubated at 600 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, which represented an average of 65% of the incident light level. Dissolved oxygen concentration was measured using high-precision Winkler titration (Carrit and Carpenter 1966), using a Metrohm-682 Autotitrator for the potentiometric (redox electrode) end-point detection (Oudot et al. 1988). Despite the high sensitivity of this technique, gross primary production rates at the southern end of the transect (at the

southern subtropical gyre) could not be reliably measured. We therefore increased the number of replicate bottles from five to eight, resulting in an improved capability to detect low gross production rates, yielding a precision of about 0.17 $\text{mmol O}_2 \text{m}^{-3}$ and a coefficient of variation of the dissolved oxygen concentration of 0.12%. As a result of these difficulties, estimates of gross primary production in surface waters are not available for all of the stations where ^{15}N tracer addition experiments were conducted. Gross primary production was calculated as the sum of the rate of change in oxygen concentration in light bottles and that of oxygen consumption in dark bottles and was converted to daily (24 h) estimates by considering the length of the day and night at each station. Estimates of gross primary production, based on O_2 production, were converted to carbon-based primary production, using a photosynthetic quotient of 1.1, as recommended under a dominance of recycled production (Laws 1991).

Water samples taken for nutrient analysis at each station (down to 400 m depth) and subsamples drawn from the ^{15}N incubation bottles were immediately filtered using a 0.45- μm membrane filter and analyzed for NH_4^+ and NO_3^- within 2 h of collection. When quick analysis was not possible, samples were deep-frozen (-20°C) until analyzed. Standard analytical procedures for analysis of nutrients in seawater (i.e., Grashoff 1983) were conducted using a four-channel SKALAR San-plus autoanalyzer, and accounting for the suggestions made by Mee (1986) for automated analysis of nutrients. The detection limits with these methodologies were 0.15 μM for NH_4^+ and 0.1 μM for NO_3^- . Particulate organic C and N concentrations were measured using a Carlo-Erba CHN analyzer after collecting the particles in 2–3 liters of water onto precombusted Whatman GF/F filters. The coefficient of variation of these measurements was 5%.

Diffusive nitrate flux and integrated nitrate uptake—Vertical profiles of salinity and temperature derived from the (corrected) CTD data were screened for errors. The density anomaly, σ_t , was then calculated from temperature and salinity following the algorithms of Fofonoff and Millard (1981), and data were averaged to 1-m intervals. The vertical gradient in σ_t ($\Delta\rho/\Delta z$) was then used to calculate the squared Brunt-Väisälä or buoyancy frequency (N^2) according to the equation

$$N^2 = \frac{-g \Delta\rho}{\rho \Delta z}, \quad (1)$$

where g is the gravitational acceleration and ρ is the mean density averaged over Δz depth interval.

The estimates of velocity obtained during sampling at the stations contained faulty data, so that only those obtained during navigation at a uniform speed had sufficient quality to provide adequate velocity estimates. Vertical shear was calculated following the formula:

$$\left[\frac{\partial U}{\partial z}\right]^2 = \left[\left(\frac{\Delta u}{\Delta z}\right)^2 + \left(\frac{\Delta v}{\Delta z}\right)^2\right]. \quad (2)$$

Buoyancy frequencies were depth averaged to intervals corresponding to those used in the calculation of vertical shear,

and both estimates were combined to derive an estimate of the vertical diffusivity across the thermocline (following Granata et al. [1995] after Gregg [1989]):

$$K_{\rho}(z) = K_0 \left\langle \frac{S^4}{S_{GM}^4} \right\rangle, \quad (3)$$

where $K_{\rho}(z)$ is a parametrization of turbulent diffusivity in a thermocline, z is depth, K_0 is the background diffusivity and was set to $5 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$ (Gregg and Kunze 1991), S_{GM} is the Garrett-Munk shear, which was set to $1.66 \times 10^{-10} [(N^2/N_0)]$, N_0 was $5.2 \times 10^{-3} \text{ s}^{-1}$ (Gregg 1989), and S was the shear measured over 8 m (broad band). Vertical nitrate fluxes across the thermocline (units $\mu\text{mol m}^{-2} \text{ d}^{-1}$) were then calculated from the product of the (geometric) mean turbulent diffusivity across the thermocline (units $\text{m}^2 \text{ d}^{-1}$) and the NO_3^- concentration gradient (units $\mu\text{mol m}^{-4}$) across the thermocline, determined using linear regression analysis. The (geometric) mean turbulent diffusivity and the NO_3^- concentration gradient (units $\mu\text{mol m}^{-4}$) across the thermocline were calculated for the same depth ranges, because the nitracline was located within the thermocline at all stations.

Rates of nitrate uptake obtained from the ^{15}N experiments were derived from samples collected at only two depths but incubated under a range of irradiances. To allow comparison of the rate of upward diffusive nitrate supply to the biogenic zone (units $\text{mmol m}^{-2} \text{ d}^{-1}$) with the rates of nitrate uptake (units of $\mu\text{mol m}^{-3} \text{ d}^{-1}$), we estimated the integrated rate of nitrate uptake within the biogenic zone (units $\text{mmol m}^{-2} \text{ d}^{-1}$). The relationship between nitrate uptake (whether volumetric or per unit chlorophyll a) and changes in incident irradiance with depth did not follow a simple or consistent trend. To calculate the integrated nitrate uptake rate, we first separated the biogenic layer into (1) the upper layer of water where phytoplankton communities were vertical mixed, as indicated by examination of chlorophyll a and in situ induced fluorescence profiles, and the nitrate uptake rates measured for the surface communities were assumed to apply and (2) the deeper layer containing the deep chlorophyll a maximum, where the nitrate uptake rates measured for the communities at the deep chlorophyll a maximum were assumed to apply. Because there was no simple relationship between uptake and irradiance, we used the depth of the midpoints between the irradiances where nitrate uptake was assayed for each of the two communities (i.e., 75%, 30%, and 8%, and 30%, 8%, and 3.5% of surface irradiance for the surface and deep chlorophyll a maximum communities, respectively) to separate each of the two water layers into depth layers where the different uptake rates applied (e.g., the nitrate uptake rate measured at 1% of the incident light for the deep chlorophyll a maximum community was applied to the water layer located between the depth receiving 3.5% of surface irradiance and the bottom of the biogenic layer). This procedure resulted in the partitioning of the biogenic layer into three to five contiguous water layers (i.e., the upper and deep layers never reached $<8\%$ and $>30\%$ of the surface irradiance, respectively), to which different experimental nitrate uptake rates were assigned. These uptake rates were then integrated to yield the estimated areal nitrate uptake. Although the accuracy of these estimates cannot be

evaluated here, their precision is similar to that in previous studies, which also derived integrated rates from the integration of estimates derived at two to seven depths (e.g., Le Bouteiller 1986; McCarthy et al. 1992, 1996). Nitrate uptake rates typically vary with depth by a factor of <4 -fold (e.g., MacIsaac and Dugale 1972; Murray et al. 1989; McCarthy et al. 1992; Dickson and Wheeler 1995; Metzler et al. 1997), which represents, therefore, an upper limit to the possible error in integrating these rates. This resolution is, however, adequate for the comparison between areal nitrate uptake rates and diffusive fluxes, because the parametrization of $K_{\rho}(z)$ used, the main source of uncertainty in the calculation of the diffusive nitrate flux, involves an uncertainty of about 5-fold (Gregg 1989). Hence, estimates of areal nitrate uptake rates and diffusive fluxes in agreement within a factor of <5 -fold cannot be considered here as significantly different.

Results

Water column structure—The cruise tract spanned the western portion of the South Atlantic subtropical gyre, between 35°S and 15°S , the Intertropical Convergence Zone, between 15°S and 10°N , and the southeastern extreme of the North Atlantic subtropical gyre, at 25°N . A two-layer system occurs between 30°S and 15°N , with the pycnocline located between 40 and 60 m depth (Fig. 2). North of 15°N , however, convective mixing deepens the surface mixed layer and promotes weak pycnocline formation. The isopycnal surfaces in the lower layer abruptly slope downward in the southern section of the transect (30°S to 12°S). The doming of isopycnals between 5°S and about 3°N marks the upwelling (divergent) region of the Southern Equator Current (SEC) and the Equatorial Counter Current (ECC). North of the SEC and ECC, at approximately 10°N , a second upwelling region occurs with the divergence of the Equator Counter Current and the North Equatorial Current. Maxima in fluid stability (e.g., N^2) were coincident with surface divergent features (Fig. 2), with the largest gradient, that of the pycnocline, located near the surface (40 m) at the Equator. Similarly, $(dU/dz)^2$, the squared vertical shear of horizontal current, was also elevated in the convergent/divergent zones, with a maximum near 55 m at the Equator (Fig. 2).

The vertical turbulent diffusion coefficient [$K_{\rho}(z)$] increased from south to north across the Central Atlantic, reaching a maximum around 15°N and declining thereafter (Table 1). The nitrate gradient across the thermocline, which together with the vertical coefficient of turbulent diffusivity sets the magnitude of the diffusive nitrate flux, reflected the strength of the thermocline, with sharp thermocline (as reflected in high maximal Brunt-Väisälä frequencies; Fig. 2) resulting in strong concentration gradients. The nitrate gradient across the thermocline was strongest towards the Equator and declined with increasing distance from the Equator (Table 1).

Nitrogen uptake—The examination of the uptake rates of nitrate and ammonium at different irradiance levels revealed no consistent pattern across the transect (Table 1). There was however a tendency (about 50% of the experiments) for maximal uptake rates to be observed under 50% of surface

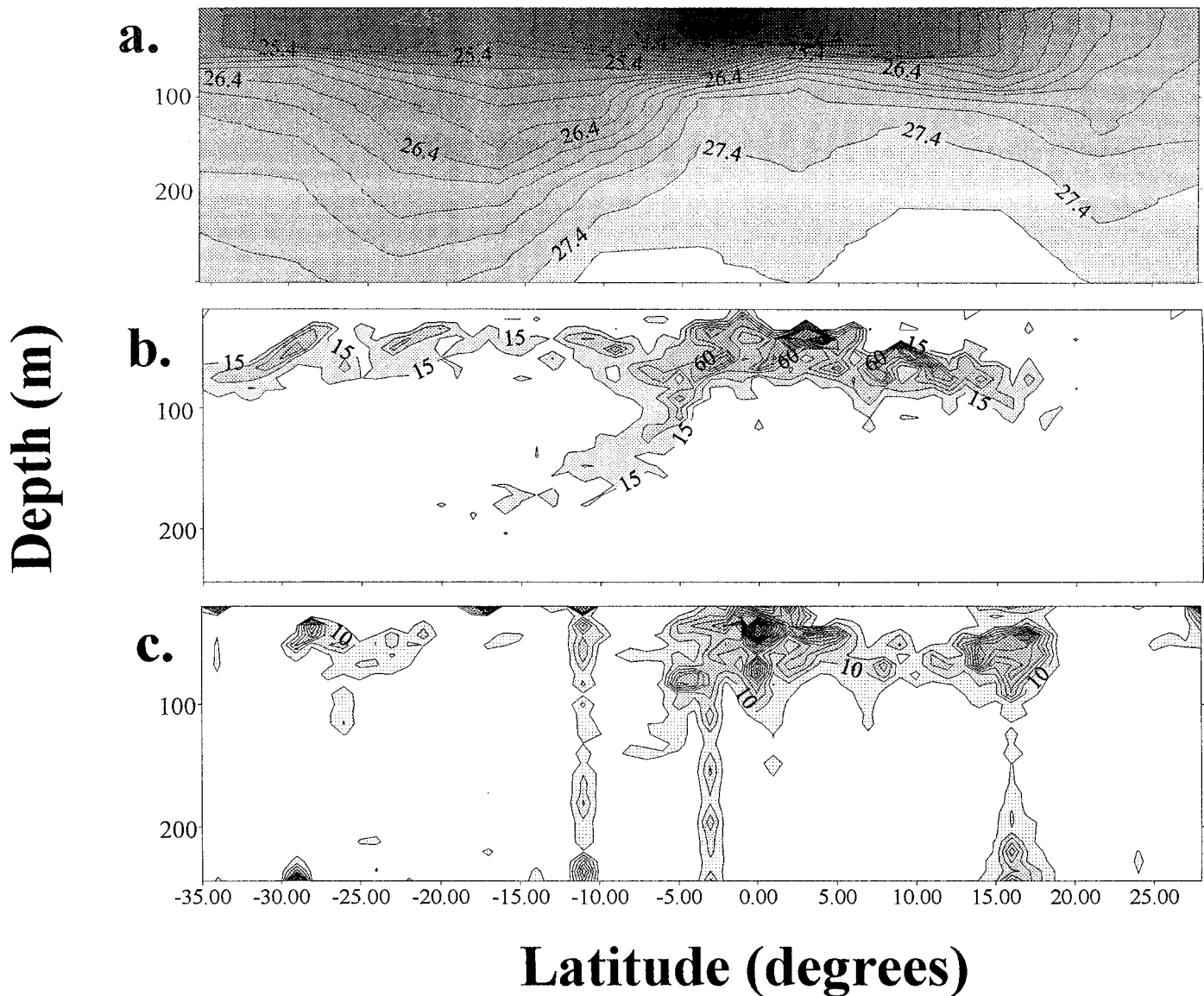


Fig. 2. Meridional distributions of (a) the anomaly density, σ_t (kg m^{-3}), (b) square of the buoyancy frequency, N^2 ($\times 10^5 \text{ s}^{-2}$), and (c) square of the vertical shear, $[dU/dz]^2$ ($\times 10^5 \text{ s}^{-2}$) in the Central Atlantic.

irradiance, with declining uptake rates at either lower or higher irradiances (Table 1). The uptake rate of ammonium tended to exceed that of nitrate at all of the irradiances tested, with nitrate uptake generally comprising about 10–30% of the combined uptake of nitrate and ammonium both in surface and DCM waters. As a consequence, the specific uptake rate was greater for ammonium than it was for nitrate (Wilcoxon signed rank test, $P < 0.0001$), suggesting a higher affinity for ammonium uptake. The turnover times of particulate nitrogen estimated from these specific rates ranged from 6 to 4 months if based on nitrate uptake down to about 2 weeks if based on ammonium uptake. The estimated rates of nitrogen uptake were poorly correlated ($r < 0.4$, $P > 0.05$) with the chlorophyll *a* concentration of the waters.

The latitudinal changes in nitrogen uptake rate were, however, far greater than the differences attributable to differences in the community (surface or DCM waters) or any

possible light dependence of the uptake rate (Fig. 3). Both nitrate and ammonium uptake rates were lowest at the southern end of the transect and increased towards the Equator, and this increase was much greater for ammonium than for nitrate uptake (Fig. 3). As a consequence, the *f*-ratio showed a clear latitudinal pattern, with the highest values reached just south of the Equator and the lowest values observed at the southern end of the transect.

The gross production (P , $\mu\text{mol C m}^{-3} \text{ d}^{-1}$) measured in surface waters was strongly correlated (Fig. 4) with the total uptake rate of dissolved inorganic nitrogen (U , $\mu\text{mol N m}^{-3} \text{ d}^{-1}$), as described by the regression equation

$$P = 332.8 (\pm 85.9) + 4.72 (\pm 1.54) U \quad (4)$$

($R^2 = 0.65$, $F = 10.31$, $P = 0.032$). The slope of the relationship (4.72) is somewhat lower, but not significantly so,

Table 1. The latitude, vertical diffusivity across the thermocline ($K_p(z)$), nitrate concentration gradient across the thermocline, chlorophyll *a* (Chl *a*) concentration, and nitrate and ammonium uptake rates measured at different irradiances (as percentage of subsurface irradiance) and depths (surface and deep Chl *a* maximum) at stations along the Central Atlantic. Missing uptake rates indicate assays were not performed or that the rates were below detection limits.

Latitude (decimal)*	Depth (m)	$K_p(z)$ ($\text{m}^2 \text{d}^{-1}$)	NO_3 gradient (mmol m^{-4})	Chl <i>a</i> ($\mu\text{g/liter}$)	NO_3 uptake ($\mu\text{mol m}^{-3} \text{d}^{-1}$)					NH_4 uptake ($\mu\text{mol m}^{-3} \text{d}^{-1}$)				
					100%	50%	10%	6%	1%	100%	50%	10%	6%	1%
-34.25	5	0.097	0.0005	0.16	9.6	1.2	0.48		0.12	20.3	19.2	18.1		18.6
	64			0.56										
-31.95	5	0.015	0.0025	0.14	0.24	0.12				12.4	5.0	10.9		5.0
	100			0.31										
-25.99	5	0.491	0.0168	0.23	1.92	2.52	1.44		1.68	13.4	10.2	10.6		8.8
	100			0.36										
-25.24	5	0.417	0.0365	0.13	14.0	14.3	16.2		22.7	49.9	40.3	49.7		38.8
	93													
-20.75	5	0.796	0.0017	0.17	3.72	3.96	2.4		4.2	23.9	38.5	28.3		27.4
	84			0.25										
-18.5	5	1.13	0.049	0.05	9.6	21.5	22.8		21.5	8.3	16.2	25.8		21.0
	110			0.24										
-9.5	5	0.266	0.109	0.02	8.04	11.8	8.4		10.2	7.4	13.2	12.0		6.4
	139			0.23										
-2.84	5	1.45	0.159	0.07		21.6	21.2		71.4		69.5	55.2		53.9
	70			0.84										
3.41	5	1.76	0.225	0.22	10.2	15.5	11.5		20.4	51.1	51	64.6		56.8
	50			0.88										
6.50	5	5.84	0.268	0.11	12.7	24.6	0		4.92	55.6	57	40.7		36.6
	75			0.80										
13.25	5	4.15	0.202	0.15	3.24	14.8	4.8		5.88	46.2	52.7	38.5		38.5
	68			0.71										
16.25	5	14.43	0.146	0.12	7.2	6.6	5.64		32.8		41.5	32.4		25.1
	90			0.60										
23.75	5	1.14	0.038	0.04		9.6	4.32		9.6	14.3	21.8	20.3		24.4
	105			0.33										
27.50	5	2.59	0.030	0.02	4.8	8.04	3.48		2.16	18.4	21.2	15.3		15.8
	115			0.50										

* Negative values are S; positive values are N.

than the expected Redfield C/N ratio of 6.6 (Redfield 1958). However, the intercept of the relationship was significantly greater than 0 (t -test, $P = 0.028$), suggesting the existence of other sources of nitrogen for phytoplankton uptake than those investigated here, and/or the release of dissolved organic nitrogen (Bronk et al. 1994).

The relationship between uptake and diffusive flux of nitrogen—The latitudinal pattern in the calculated upward diffusive nitrate supply to the biogenic layer was roughly similar to that in the integrated nitrate uptake rate. However, the average integrated nitrate uptake rate over the study area ($0.86 \pm 0.19 \text{ mmol NO}_3 \text{ m}^{-2} \text{ d}^{-1}$) exceeded by a factor of 2 the average diffusive nitrate supply to the biogenic layer ($0.38 \pm 0.18 \text{ mmol NO}_3 \text{ m}^{-2} \text{ d}^{-1}$), although these regional estimates cannot be considered statistically different because of the 5-fold uncertainty about both estimates. The stoichiometry between the total uptake rate and gross primary production was close to the expected Redfield value, and nitrate uptake and supply were roughly in agreement at the regional scale. This suggests that the average f -ratio should be similar when calculated from the ^{15}N tracer experiments and when estimated as the average ratio between the new production supported from the diffusive nitrate flux and the measured

gross production. This similarity in f -ratios was indeed confirmed by our results (t -test, $P = 0.23$).

Closer examination of the relationship between the integrated nitrate uptake ($\text{NO}_{3\text{uptake}}$, $\text{mmol NO}_3 \text{ m}^{-2} \text{ d}^{-1}$) and the upward diffusive supply ($\text{NO}_{3\text{flux}}$, $\text{mmol NO}_3 \text{ m}^{-2} \text{ d}^{-1}$) revealed a significant tendency for the uptake rates to exceed the diffusive supply rates at the stations with low diffusive supply, suggesting this relationship to be nonlinear (Fig. 5). This relationship was confirmed by the examination of the scaling between these two variables, as described by the allometric equation

$$\text{NO}_{3\text{uptake}} = 1.5\text{NO}_{3\text{flux}}^{0.31(\pm 0.05)} \quad (R^2 = 0.75, F = 38.4, P = 0.00004), \quad (6)$$

which shows nitrate uptake to increase as the $\frac{1}{3}$ power of the upward diffusive nitrate flux to the biogenic layer. As a result, the uptake of nitrate exceeded its diffusive supply by nearly three orders of magnitude at the most oligotrophic sites investigated, whereas these rates were comparable at the most productive ones (Fig. 5). Even considering the 5-fold uncertainty about the areal estimates of nitrate supply and uptake, the uptake exceeded the upward diffusive flux when this was $<0.1 \text{ mmol NO}_3 \text{ m}^{-2} \text{ d}^{-1}$. The excess nitrate

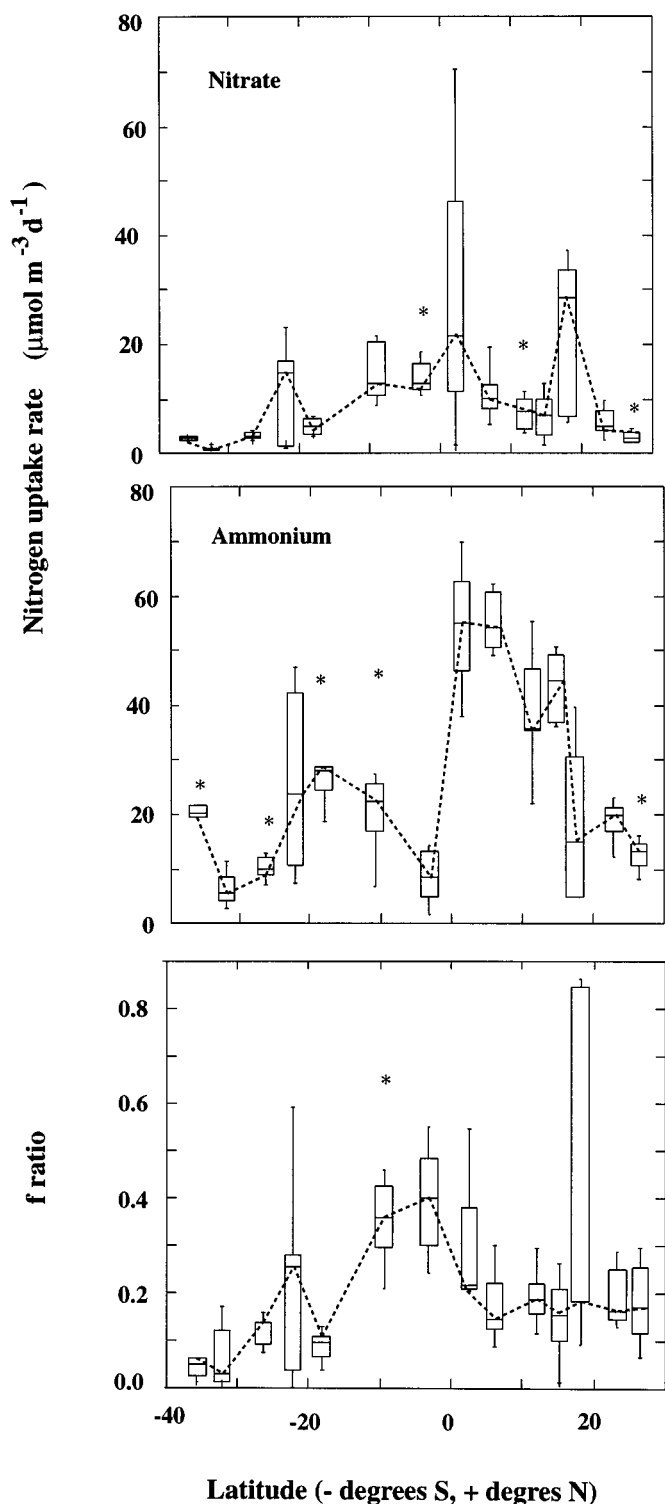


Fig. 3. Box plots describing the latitudinal variation in uptake rates of nitrate and ammonium and the resulting f -ratio, measured at different irradiance levels in surface and DCM waters along the Central Atlantic. Boxes encompass 50% of the data, the central line represents the median, the bars encompass the range of 90% of the values, and asterisks represent observations beyond the 90% percentile of the data.

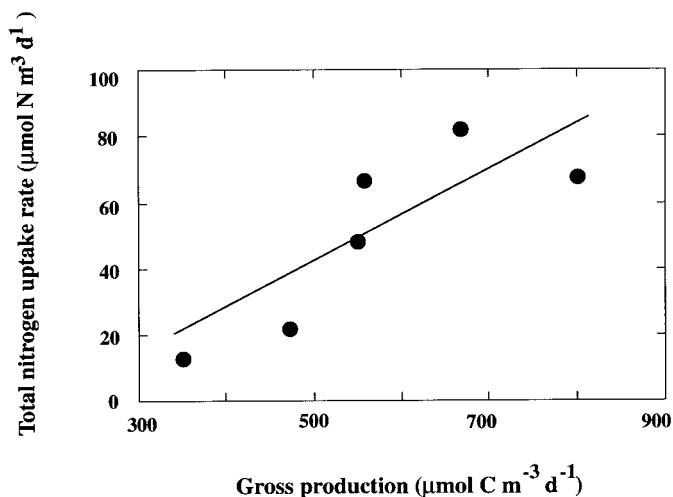


Fig. 4. The relationship between gross primary production and total dissolved inorganic nitrogen uptake rates in surface waters of the Central Atlantic. The solid line describes the fitted regression equation (Eq. 4).

uptake in the region of low upward diffusive flux averaged $0.65 \pm 0.24 \text{ mmol NO}_3 \text{ m}^{-2} \text{ d}^{-1}$ (range, $0.05\text{--}1.9 \text{ mmol NO}_3 \text{ m}^{-2} \text{ d}^{-1}$), which must be supplied through atmospheric deposition.

Discussion

The results described demonstrate the existence of significant latitudinal variations in nitrogen uptake rates across the Central Atlantic. As expected, uptake rates were enhanced towards the Equator and were reduced in the gyre areas, being particularly low in the South Atlantic subtropical gyre. Meridional changes were much more important in accounting for the variation in uptake rates than were differences between communities growing in the surface waters or in the deep chlorophyll maximum. There was no consistent relationship between nitrate or ammonium uptake rates and incident light, except for a tendency for the rates at 50% of the irradiance incident in the surface waters, which corresponds to that reaching down to 5 m depth, to be higher than rates observed at either higher or lower irradiances. In addition, the results provide evidence of a strong inhibition of nitrogen uptake rates under high irradiance at most of the stations, supporting past claims that irradiance is an important determinant of nitrogen uptake rates (e.g., Collos and Slawyk 1980; Dugdale et al. 1990).

The uptake of nitrate comprised 10–40% of the total uptake rate of dissolved inorganic nitrogen (overall f -ratio mean \pm SE = 0.21 ± 0.02), being highest (mean f -ratio ≈ 0.4) around the Equator. Both the total uptake rate of dissolved inorganic nitrogen and that of nitrate were low compared with recently published estimates for stations located west of those reported here (Metzler et al. 1997), and in the gyre areas they reached values among the lowest yet recorded in the ocean (Table 2). These slow rates resulted in slow turnover rates of the particulate organic nitrogen (weeks to months). The specific nitrate uptake was on the order of

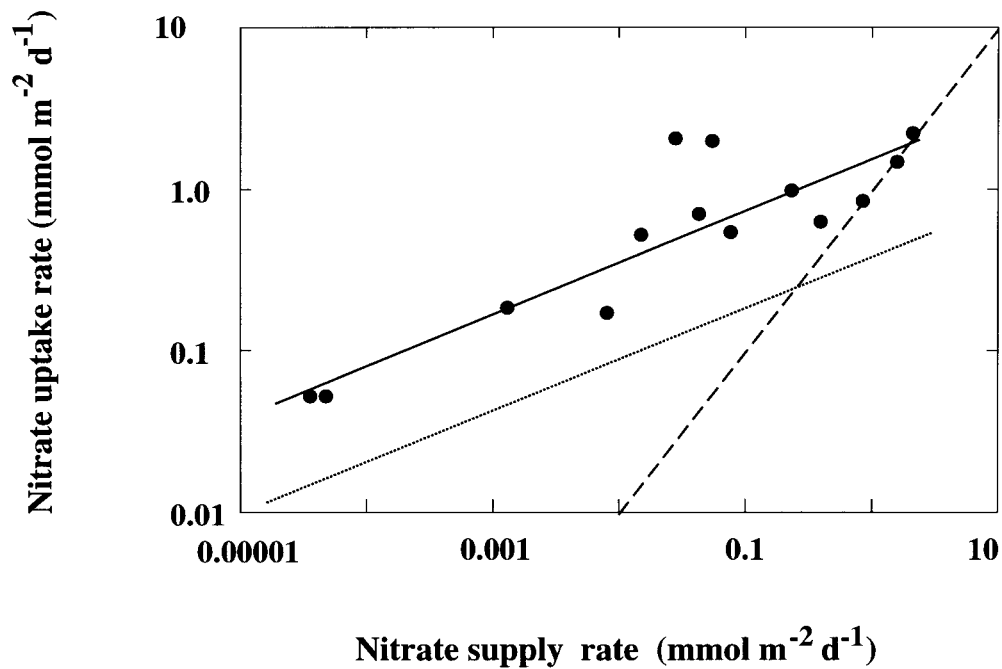


Fig. 5. The relationship between the integrated nitrate uptake rate within the biogenic layer and the supply rate of nitrate from diffusion across the thermocline. The solid and dotted lines represents the fitted regression equation (Eq. 6) and its lower 95% confidence limit, and the broken line represents the 1-to-1 line.

Table 2. Compilation of nitrate and ammonium uptake rates and the corresponding f -ratios observed in the tropical ocean.

Region	Nitrate		Ammonium		f -ratio	Source
	Uptake rate ($\mu\text{mol m}^{-3} \text{d}^{-1}$)	Specific uptake (d^{-1})*	Uptake rate ($\mu\text{mol m}^{-3} \text{d}^{-1}$)	Specific uptake (d^{-1})*		
Tropical Pacific						
32°N, 127°W	4.20	0.011			0.09	Dugdale and Wilkerson 1992
30°N–0°S	3.8–14.9†		17.3–77.7†		0.17–0.25‡	Kanda et al. 1985
28°N, 155°W	10.8–14.4	0.100	36.0–74.4	0.19–0.26	0.22–0.16‡	Sahlsten 1987
20°N–10°S, 80–115°W	31	0.09	30	0.12	0.51‡	MacIsaac and Dugdale 1972
15°N–15°S	1.6–14.5†		1.4–24.4†		0.05–0.84	Peña et al. 1992
15°N–15°S, 150°W	1.2 ± 36†		6–96†		0.02–0.40‡	Dugdale et al. 1992
15°N–15°S, 150°W	7.5–17.7		31.2–50.0		0.06–0.14	McCarthy et al. 1996§
8°N–2°S, 84–90°W	<12–76.8†		<48–115.2†		0.23	Murray et al. 1989
Tropical Atlantic						
Gulf Stream	1.2–13.2†		4.8–62.4†		0.17–0.2	Glibert et al. 1998
Sargasso Sea	1.2–2.4†		14.4–42.0†		0.04–0.08	Glibert et al. 1998
30–47°S, 48.8–38°W	12.0†		121†		0.16–0.24	Metzler et al. 1997
28°30'N, 23°W	4.8–14.4†		19.2–34.8†		0.21–0.30‡	Lewis et al. 1986
0–4°W	3–96†	0.48	6–66†	0.04–0.12	0.33–0.45‡	LeBouteiller 1986
N. Atlantic subtropical gyre, 27–10°N, 29°W	5.7 (2.16–37.7)	0.02 (0.001–0.12)	23.04 (5.6–52.4)	0.08 (0.01–0.16)	0.18 (0.01–0.88)	This study¶
Equatorial Atlantic, 10°N–15°S, 29–50°W	10.4 (1.1–71.4)	0.03 (0.005–0.4)	49.8 (6.5–69.6)	0.12 (0.03–0.74)	0.24 (0.09–0.57)	This study¶
S. Atlantic subtropical gyre, 15–35°S, 29°W	1.2 (0.12–22.8)	0.011 (<0.001–0.12)	18.8 (3.1–49.9)	0.07 (0.01–0.22)	0.12 (0.03–0.66)	This study¶

* Hourly transport rates $\times 12$ h.

† Hourly rates $\times 24$ h.

‡ Estimated from their nitrate and ammonium transport rates.

§ Data obtained during El Niño event.

|| From stratified data.

¶ Median (range) values.

0.001 h⁻¹ (overall mean \pm SE = 0.0013 \pm 0.0002 h⁻¹), three times slower than that for ammonium uptake (overall mean \pm SE = 0.0038 \pm 0.0002 h⁻¹). The dominance of ammonium over nitrate uptake is indicative of a system dominated by recycled production, as described for other similarly oligotrophic regions of the tropical ocean (Eppley 1981; Murray et al. 1989; Dugdale et al. 1992; Peña et al. 1992; Harrison et al. 1996). The dominance of ammonium uptake was associated with a major contribution of picoautotrophs to the photosynthetic production in the area (Agustí unpubl. data), as well as with a high biomass of pico- and microheterotrophs (Vaqué et al. unpubl. data).

Both nitrate and ammonium concentrations were low, often close to the detection limit of the methods used, yet our results suggest a relatively high uptake of nitrogen. The latitudinal variation in nitrate and ammonium uptake rates was associated with the water column dynamics that regulate the diffusive nitrogen fluxes in this permanently stratified area of the ocean. The doming of the pycnoclines towards the Equator, which is a conspicuous feature of the Central Atlantic particularly along its Eastern margin (Voituriez and Dandonneau 1974), leads to sharp thermoclines located close to the ocean surface. These thermoclines in turn result in steep nitrate gradients across the thermoclines and a high volumetric diffusive supply of nitrate due to the relatively thin biogenic layer over which the diffused nitrate is distributed. Moreover, shear induced by the subequatorial counter-current leads to a high turbulence at the thermocline and a high vertical diffusion coefficient around the Equator. All these factors result in a clear meridional gradient in diffusive nitrate supply across the Central Atlantic and a parallel pattern in the observed nitrogen uptake rates.

The average estimated fraction of the primary production that can be supported by the calculated diffusive nitrate supply was close to the average *f*-ratio observed experimentally. The significant correlation between the total nitrogen uptake and that of nitrate and the average *f*-ratio observed (0.21) indicate that each nitrogen molecule supplied is, assuming steady state conditions, recycled about four times before being lost. This finding suggests that the residence time of nitrogen in the biogenic layer should be about five times longer than the turnover time of the particulate organic nitrogen, which ranges from weeks to months. Ammonium residence times of 190–350 days have been reported for the equatorial Pacific (McCarthy et al. 1996), suggesting that these long residence times are characteristic of the tropical open ocean. Moreover, these results suggest that, on average, the nitrogen loss rate should be comparable to the diffusive nitrate supply, implying a sinking flux of about 20% of the gross primary production, similar to that reported for the equatorial Pacific (14–38%, Murray et al. 1989).

The nitrate and ammonium uptake rates measured in the Central Atlantic are within the range of values reported for a station within the Guinea Gulf by Le Bouteiller (1986) and the NO₃ uptake rates reported by Metzger et al. (1997) off the Brazilian coast, although the ammonium uptake rates they reported are almost 2-fold higher than ours. The maximum nitrate uptake rate observed in the Guinea Gulf was somewhat higher than what we observed (Table 2), probably because of enhanced nitrate diffusion within the Guinea

Dome (cf. Herbland and Voituriez 1979). Data on nitrogen uptake rates in the gyre areas of the North Atlantic are few (Table 2), but the results we obtained in the northern end of our transect were similar to those reported in a station nearby by Lewis et al. (1986). The uptake rates reported by Glibert et al. (1988) in the Sargasso Sea were, however, even lower than those we report here for the gyre areas.

A comparison of the rates of nitrate uptake observed in the tropical Atlantic with those observed in the tropical Pacific, which has been studied in greater detail, suggests close similarities between these two oceanic provinces (Table 2). Both areas show an increased uptake rate of nitrogen from the ultraoligotrophic gyre areas (nitrate uptake rates of 1.2–14.4 and 0.12–22.7 $\mu\text{mol N m}^{-3} \text{d}^{-1}$ in the Pacific and Atlantic gyres, respectively) to the equatorial region (nitrate uptake rates up to 76 and 71.4 $\mu\text{mol N m}^{-3} \text{d}^{-1}$ in the Pacific and Atlantic equatorial regions, respectively). The rates of ammonium uptake were also similar both in the gyre and equatorial regions of both oceans, both showing a fast turnover rate of particulate nitrogen in the equatorial region (Table 2). Our results indicate that the rates of nitrate uptake and the *f*-ratios in the gyre areas of the tropical Atlantic ocean are among the lowest yet reported (Table 2).

The similarity in the rates of nitrate uptake in the tropical Atlantic and Pacific Oceans is paralleled by a comparable vertical diffusive nitrate supply in the two areas. Although there are no previous estimates of the diffusive vertical nitrate flux in the equatorial Atlantic, the values we obtained (0.23–1.56 $\text{mmol N m}^{-2} \text{d}^{-1}$) for this region are similar to those reported for the equatorial Pacific (0.57–1.3 $\text{mmol N m}^{-2} \text{d}^{-1}$, Carr et al. 1995). In addition, Lewis et al. (1986) reported the diffusive vertical nitrate flux in a station positioned at 28°N, 20°W to be 0.14 $\text{mmol N m}^{-2} \text{d}^{-1}$, reasonably close to that we obtained (0.08 $\text{mmol N m}^{-2} \text{d}^{-1}$) in the northernmost stations investigated (27°30'N, 29°W), which were only a few kilometers away. The overall agreement between both the uptake rates and the rates of diffusive nitrate supply to the biogenic layer suggests that the relationship reported here may reflect a broader, more general pattern applicable to the tropical ocean.

The results presented showed that the relationship between nitrate uptake and upward diffusive supply was strongly nonlinear. Nitrate uptake far exceeded (by 2–3 orders of magnitude) the upward diffusive nitrate supply in the most unproductive waters, but these rates were in good agreement in the more productive region. A possible explanation is that the ¹⁵N method overestimates uptake in the most oligotrophic waters, where nitrate is below detection limit. The uncertainty about uptake rates in areas where nitrate concentrations (three of the stations investigated here) are below detection limit is of a factor of 2 (McCarthy et al. 1992), well below the large (2 orders of magnitude) differences between nitrate uptake and diffusional flux at the most oligotrophic stations. The addition of tracer may have also influenced N uptake in these oligotrophic waters. However, this effect would have resulted in *f*-ratios imposed by the ratios of ¹⁵NH₄⁺ and ¹⁵NO₃⁻ added, which was not the case, because the experimental *f*-ratio was independent of what would have resulted if the uptake was controlled by the tracer added ($r = -0.10$, $P > 0.05$). Substantially enhanced

nitrogen uptake would not necessarily lead to increased particulate organic nitrogen concentrations, which was not the case here, because there was no significant increase in particulate organic nitrogen (t -test, $P > 0.05$) during the incubations. Hence, our results are robust against these sources of error, because the differences between nitrate uptake and supply we describe are >5 -fold.

That the nitrate uptake rate exceeds the upward diffusive nitrate supply to the biogenic layer of the oligotrophic Central Atlantic suggests that the nitrate required to support uptake rates measured in the most oligotrophic waters are delivered by perturbations, such as atmospheric inputs (Gruber and Sarmiento 1997) or episodic inputs such as those resulting from mesoscale eddy dynamics (cf. McGillicuddy et al. 1998; Oschlies and Garçon 1998). Gruber and Sarmiento (1997 fig. 12) reported an excess N concentration in the Central Atlantic (north of the Equator) that can only be accounted for by significant atmospheric inputs. In agreement with this hypothesis, the absolute magnitude of the excess nitrate uptake averaged $0.23 \text{ mol NO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ in the tropical Atlantic, well within the range of the available estimates of atmospheric deposition there ($0\text{--}1.3 \text{ mol m}^{-2} \text{ yr}^{-1}$; Roos and Gravenhorst 1984; Smethie et al. 1985; Andrié et al. 1986; Schlitzer 1989). This excess nitrate uptake is relatively large compared with the diffusive supply in the most unproductive areas, where external sources of nitrate (e.g., atmospheric deposition) fuel new production (e.g., Owens et al. 1992). In contrast, these sources of nitrate are far less significant where high volumetric diffusive fluxes suffice to maintain high nitrate uptake rates.

In summary, nitrate and ammonium uptake rates within the Central Atlantic were within the lowest rates reported by other studies and displayed a maximum toward the waters at the equatorial upwelling. These patterns were driven by the forces that control the meridional differences in diffuse nitrate supply rates, which were on average in agreement with the measured uptake rates at the regional scale. Yet, the nitrate uptake rate in the most unproductive waters examined far exceeded the diffusive supply of nitrate. The excess nitrate taken up must be derived from atmospheric deposition, which fuels the new production of the unproductive gyre waters studied here, whereas diffusive nitrate fluxes suffice to maintain the new production of the more productive areas.

References

- ANDRIÉ, C., C. OUDOT, C. GENTHON, AND L. MERLIVAT. 1986. CO_2 fluxes in the tropical Atlantic during FOCAL cruises. *J. Geophys. Res.* **91**: 11741–11755.
- BRONK, D. A., P. M. GLIBERT, AND B. B. WARD. 1994. Nitrogen uptake, dissolved organic nitrogen release, and new production. *Science* **265**: 1843–1846.
- CARR, M.-H., M. R. LEWIS, AND D. KELLY. 1995. A physical estimate of new production in the equatorial Pacific along 150°W . *Limnol. Oceanogr.* **40**: 138–147.
- CARRIT, D. E., AND J. H. CARPENTER. 1966. Comparison and evaluation of currently employed modifications of the Winkler method for determining dissolved oxygen in sea water. A NASCO Report. *J. Mar. Res.* **24**: 286–318.
- COLLOS, Y., AND G. SLAWYK. 1980. Nitrogen uptake and assimilation by marine phytoplankton, p. 195–211. *In* P. Falkowski [ed.], *Primary production in the sea*. Plenum.
- DICKSON, M.-L., AND P. A. WHEELER. 1995. Nitrate uptake rates in a coastal upwelling regime: A comparison of PN-specific, absolute, and Chl a -specific rates. *Limnol. Oceanogr.* **40**: 533–543.
- DUGDALE, R. C., AND J. J. GOERING. 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. *Limnol. Oceanogr.* **12**: 196–206.
- , AND F. P. WILKERSON. 1986. The use of ^{15}N to measure nitrogen uptake in eutrophic oceans: Experimental considerations. *Limnol. Oceanogr.* **31**: 673–689.
- , AND ———. 1992. Nutrient limitation of new production in the sea, p. 107–122. *In* P. G. Falkowski and A. D. Woodhead [eds.], *Primary productivity and biogeochemical cycles in the sea*. Plenum.
- , ———, R. T. BARBER, AND F. D. CHAVEZ. 1992. Estimating new production in the equatorial Pacific Ocean at 150°W . *J. Geophys. Res.* **97**: 681–686.
- , ———, AND A. MOREL. 1990. Realization of new production in coastal upwelling systems: A means to compare relative performance. *Limnol. Oceanogr.* **35**: 822–829.
- ECKMAN, J. E. 1994. Modelling physical-biological coupling in the ocean: The U.S. GLOBEC Program. *Deep-Sea Res.* **41**: 1–5.
- EPPLEY, R. W. 1981. Autotrophic production of particulate matter, p. 342–366. *In* A. R. Longhurst [ed.], *Analysis of marine ecosystems*. Academic.
- , AND B. J. PETERSON. 1979. Particulate organic matter flux and planktonic new production in the deep ocean. *Nature* **282**: 677–680.
- FITZWATER, S. E., G. A. KNAUER, AND J. H. MARTIN. 1982. Metal contamination and its effect on primary production measurements. *Limnol. Oceanogr.* **27**: 544–551.
- FOFONOFF, N. P., AND R. C. MILLARD. 1981. Algorithms for computation of fundamental properties of seawater. UNESCO Tech. Pap. **44**: 160.
- GARSDIE, C. 1984. Apparent ^{15}N uptake kinetics and re-mineralisation experiment. *Limnol. Oceanogr.* **29**: 204–210.
- GLIBERT, P. M., M. R. DENNETT, AND D. A. CARON. 1988. Nitrogen uptake and NH_4 regeneration by pelagic microplankton and marine snow from the North Atlantic. *J. Mar. Res.* **46**: 837–852.
- , C. GARSDIE, J. A. FUHRMAN, AND M. R. ROMAN. 1991. Time-dependent coupling of inorganic and organic nitrogen uptake and regeneration in the plume of the Chesapeake Bay estuary and its regulation by large heterotrophs. *Limnol. Oceanogr.* **36**: 895–909.
- , F. LIPSCHULTZ, J. J. MCCARTHY, AND M. A. ALBATET. 1985. Has the mystery of the vanishing ^{15}N in isotope dilution experiments been resolved? *Limnol. Oceanogr.* **30**: 444–447.
- GRANATA, T. C., J. WIGGERT, AND T. DICKEY. 1995. Trapped, near-inertial waves and enhanced chlorophyll distributions. *J. Geophys. Res.* **100**: 20793–20804.
- GREGG, M. A., AND E. KUNZE. 1991. Shear and strain in Santa Monica Basin. *J. Geophys. Res.* **96**: 16709–16719.
- GREGG, M. C. 1989. Scaling turbulent dissipation in the thermocline. *J. Geophys. Res.* **94**: 9686–9698.
- GRUBER, N., AND J. L. SARMIENTO. 1997. Global patterns of marine nitrogen fixation and denitrification. *Global Biogeochem. Cycles* **11**: 235–266.
- HANDLEY, L. L., C. M. SCRIMGEOUR, S. F. THORNTON, AND J. J. SPRENT. 1991. Determination of the natural abundances of the stable isotopes of ^{15}N and ^{13}C by mass spectrometry: A simplified manual method for the preparation of N_2 and CO_2 . *Funct. Ecol.* **5**: 119–124.
- HANSEN, H. P., AND K. GRASSHOFF. 1983. Automated chemical

- analysis, p. 347–379. *In* K. Grasshoff, M. Ehrhardt, and K. Kremling [eds.], *Methods of seawater analysis*, 2nd ed. Verlag Chemier.
- HARRISON, W. G., L. R. HARRIS, AND B. D. IRWIN. 1996. The kinetics of nitrogen utilization in the oceanic mixed layer: Nitrate and ammonium interactions and nanomolar concentrations. *Limnol. Oceanogr.* **41**: 16–32.
- HERBLAND, A., AND B. VOITURIEZ. 1979. Hydrological structure analysis for estimating the primary production in the tropical Atlantic Ocean. *J. Mar. Res.* **37**: 87–101.
- JOYCE, T. M. 1989. On in situ “calibration” of shipboard ADCPs. *J. Atmos. Ocean. Technol.* **6**: 169–172.
- KANDA, J., T. SAINO, AND A. HATTORI. 1985. Nitrogen uptake by natural populations of phytoplankton and primary production in the Pacific Ocean: Regional variability of uptake capacity. *Limnol. Oceanogr.* **30**: 987–999.
- KING, B. A., AND E. B. COOPER. 1993. Comparison of ship’s heading determined from an array GPS antennas with heading from conventional gyrocompass measurements. *Deep-Sea Res.* **40**: 2207–2216.
- LAWS, E. A. 1991. Photosynthetic quotients, new production and net community production in the open ocean. *Deep-Sea Res.* **38**: 143–167.
- LE BOUTELLER, A. 1986. Environment control of nitrate and ammonium uptake by phytoplankton in the Equatorial Atlantic Ocean. *Mar. Ecol. Prog. Ser.* **30**: 167–179.
- LEWIS, M. R., W. G. HARRISON, N. S. OAKEY, D. HEBERT, AND T. PLATT. 1986. Vertical nitrate fluxes in the oligotrophic ocean. *Science* **234**: 870–873.
- MACISAAC, J. J., AND R. C. DUGDALE. 1972. Interactions of light and inorganic nitrogen in controlling nitrogen uptake in the sea. *Deep-Sea Res.* **19**: 209–232.
- MCCARTHY, J. J., C. GARSIDE, AND J. L. NEVINS. 1992. Nitrate supply and phytoplankton uptake kinetics in the euphotic layer of a Gulf stream warm-core ring. *Deep-Sea Res.* **39**: S393–S403.
- , ———, J. L. NEVINS, AND R. T. BARBER. 1996. New production along 140°W in the equatorial Pacific during and following the 1992 El Niño event. *Deep-Sea Res.* **43**: 1065–1093.
- MCGILLICUDDY, D. J., JR., AND OTHERS. 1998. Influence of meso-scale eddies on new production in the Sargasso Sea. *Nature* **394**: 263–266.
- MEE, L. D. 1986. Continuous flow analysis in chemical oceanography: Principles, applications and perspectives. *Sci. Total Environ.* **49**: 27–87.
- METZLER, P. M., P. M. GLIBERT, S. A. GAETA, AND M. LUDLAM. 1997. New and regenerated production in the South Atlantic off Brazil. *Deep-Sea Res.* **44**: 363–384.
- MURRAY, J., J. DOWNS, S. STROM, C. WEI, AND H. JANNASCH. 1989. Nutrient assimilation, export production, and ²³⁴Th scavenging in the eastern equatorial Pacific. *Deep-Sea Res.* **36**: 1471–1489.
- OSCHLIES, A., AND V. GARÇON. 1998. Eddy-induced enhancement of primary production in a model of the North Atlantic Ocean. *Nature* **394**: 266–269.
- LOUDOT, C. R., R. GERARD, P. MORIN, AND I. GNINGUE. 1988. Precise shipboard determination of dissolved oxygen (Winkler procedure) for productivity studies with a commercial system. *Limnol. Oceanogr.* **33**: 146–150.
- OWENS, N. J. P., J. N. GALLOWAY, AND R. A. DUCE. 1992. Episodic atmospheric nitrogen deposition to oligotrophic oceans. *Nature* **357**: 397–399.
- PEÑA, M. A., W. G., HARRISON, AND M. R. LEWIS. 1992. New production in the central equatorial Pacific. *Mar. Ecol. Prog. Ser.* **80**: 265–274.
- REDFIELD, A. C. 1958. The biological control of chemical factors in the environment. *Am. Sci.* **46**: 202–221.
- ROOS, M., AND G. GRAVENHORST. 1984. The increase in oceanic carbon dioxide and the net CO₂ flux into the North Atlantic. *J. Geophys. Res.* **89**: 8181–8193.
- SAHLSTEN, E. 1987. Nitrogenous nutrition in the euphotic zone of the Central North Pacific gyre. *Mar. Biol.* **96**: 433–439.
- SAUNDERS, P. M., AND B. A. KING. 1995. Bottom currents derived from a shipborne ADCP on WOCE cruise A11 in the South Atlantic. *J. Phys. Oceanogr.* **25**: 329–347.
- SCHLITZER, R. 1989. Modeling the nutrient and carbon cycles of the North Atlantic. 2. New production, particle fluxes, CO₂ gas exchange, and the role of organic nutrients. *J. Geophys. Res.* **94**: 12781–12794.
- SMETHIE, W. M., T. TAKAHASHI, D. W. CHIPMAN, AND J. R. LEDWELL. 1985. Gas exchange and CO₂ flux in the tropical Atlantic Ocean determined from ²²²Rn and pCO₂ measurements. *J. Geophys. Res.* **90**: 7005–7022.
- SVERDRUP, H. J. 1955. The place of physical oceanography in oceanographic research. *J. Mar. Res.* **14**: 287.
- VOITURIEZ, B., AND Y. DANDONNEAU. 1974. Relations entre la structure thermique, la production primaire et la régénération des sels nutritifs dans le Dôme de Guinée. *Cah. ORSTOM Sér. Océanogr.* **12**: 241–255.
- WILLIAMS, P. J., AND N. W. JENKINSON. 1982. A transportable microprocessor-controlled Winkler titration suitable for field and shipboard use. *Limnol. Oceanogr.* **27**: 576–584.

Received: 16 October 1997

Accepted: 5 August 1998

Amended: 17 September 1998