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A comparison of isotopic and chemiluminescent methods of estimating microalgal nitrate uptake in the NE Atlantic

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ABSTRACT: Microalgal nitrate uptake rates derived from measurements using incorporation of isotopic ^{15}N tracer were compared with those estimated from the disappearance of nitrate measured by the chemiluminescent technique during 2 cruises investigating phytoplanktonic processes in the NE Atlantic. Nitrate uptake was assessed during the development of the spring bloom in May 1990 and also shortly after the decline of a mesoscale coccolithophore bloom in July 1991. In May 1990, surface ambient nitrate concentrations ranged from 6 µmol l^{-1} to 20 nmol l^{-1}, while concentrations of < 1 µmol l^{-1} were recorded during July 1991. Regression analysis of all data from both years reveals a significant correlation between the 2 techniques ($p < 0.005$; $r^2 > 0.67$, $n = 28$). This significant correlation suggested the absence of potential artifacts noted for these techniques such as nitrification. Thus, in the majority of our comparisons, the observed near 1:1 relationship between these 2 independent methods of estimating nitrate uptake gives us confidence in our current ability to estimate 'new production' over a wide range of ambient nitrate and chlorophyll concentrations in the NE Atlantic.

KEY WORDS: Nitrate uptake · Phytoplankton · Methods intercomparison · NE Atlantic

INTRODUCTION

The export of organic carbon from the surface layers of the sea is the primary means by which the ocean can serve as a sink for atmospheric CO_2 (Lewis et al. 1986). In this context, 'new production' (as defined by Dugdale & Goering 1967) has provided a useful conceptual model of the relationship between primary production and the rate of export of biogenic particles out of the surface layer of the ocean (Eppley & Renger 1986). Indeed, modelling the ocean carbon cycle to include 'new production' is a major theme in several international science plans such as the Joint Global Ocean Flux Study programme (Sarmiento et al. 1987). In addition, one of the current objectives in biological oceanography is to achieve accurate measurements of 'new production' in order to obtain reliable and sufficiently synoptic measurements in tandem or as a prelude to remote sensing (Sathyendranath et al. 1991).

In the majority of studies, 'new production' in the euphotic zone has been measured using the ^{15}N-NO_3 technique (Eppley & Koeve 1990). Considerable debate has taken place over the limitations of this technique including the potential for the perturbation of nitrate utilization rates, particularly in oligotrophic waters where ambient nitrate concentrations are low and when the detection limit of the method of ^{15}N analysis used is not low enough to permit the accurate measurement of low % ^{15}N values (Eppley & Koeve 1990). Recently, the problem of poor precision at low

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tracer enrichment associated with the ^{15}N technique has been largely overcome through the use of continuous flow IRMS (Isotope Ratio Mass Spectrometry) as opposed to emission spectrometry or previous mass spectrometry techniques. The introduction of a high resolution chemiluminescence technique for the analysis of nitrate concentrations (Garside 1982) has enabled the detection of nanomolar nitrate concentrations. The sensitivity attained by this method has permitted the estimation of 'new production' whereby nitrate uptake is calculated by difference — the change in ambient nitrate concentration over a preselected incubation period (NOx method) (Eppley & Renger 1986, Eppley et al. 1990). As no addition of nitrate to the incubation vessel is required using the NOx method, this technique overcomes the potential problem of perturbation of uptake rates associated with the ^{15}N technique.

The pelagic nitrogen cycle of ocean waters provides outstanding examples of simultaneous, interrelated reactions (Ward et al. 1989). These nitrogen transformations may make the interpretation of data obtained using these 2 techniques difficult: the use of ^{15}N tracer estimates assimilation of nitrate into particles while the NOx method examines the disappearance of nitrate. Therefore, the ^{15}N technique may potentially underestimate 'new production' if significant labelled DON is synthesized and then released extracellularly (Bronk & Glibert 1994), or if bacteria, that will pass through a GF/F filter, utilize nitrate (Eppley & Renger 1992). The chemiluminescence method may also underestimate new production: the production of nitrate by nitrification has been detected by tracer methods even when a decrease in nitrate concentration was observed over the incubation period using the NOx method (Ward et al. 1989). Thus it is desirable to compare the methods in different oceanographic provinces to assess the reliability of the methods.

No previous study has compared these 2 methods over a wide range of ambient nitrate and chlorophyll concentrations. A number of other studies have compared uptake rates calculated from tracer and chemiluminescence methods in oligotrophic waters (Eppley & Renger 1986, Ward et al. 1989), in equatorial waters (Eppley & Renger 1992) and using data from tracer and chemical methods in eutrophic waters (Dugdale & Wilkerson 1986). As the occurrence of sharp gradients in surface nitrate concentration of 6 to <0.5 µmol l^{-1} has been recorded over 10 km during surveys carried out in the NE Atlantic (P. Boyd unpubl.), this oceanic region provided a valuable location for the comparison of nitrate uptake rates derived from measurements using isotopic and chemiluminescence methods over a range of conditions.

STUDY AREA AND METHODS

The data described were obtained during Biogeochemical Ocean Flux Study (BOFS) cruises in the NE Atlantic in May 1990 and July 1991. In May, the specific objectives of the cruise were to monitor intensively the changes in a wide range of physical, chemical and biological variables in the water column over the expected course of the spring phytoplankton bloom. The initial hydrographical, chemical and biological conditions prior to the deployment of the main drogue at 48° N, 19° W and the resultant drogue track within the mesoscale eddy field are reported by Savidge et al. (1992). In July 1991, the aim of the cruise was the characterization of the upper water column biology after the decline of a mesoscale coccolithophore bloom. This study was centred on 61° N, 20° W (Harris et al. unpubl.). During both cruises, nitrate uptake rates were determined from measurements made using ^{15}N isotopic (Dugdale & Goering 1967, Preston & Owens 1983) and NOx chemiluminescence techniques (Eppley & Koeve 1990). Water was obtained before dawn using clean 30 l Go-Flo bottles on Kevlar line activated by teflon messenger (Fitzwater et al. 1982). Water was sampled from 6 depths from 2 to 35 m in May 1990 and from 2 m only in July 1991. In 1990, bottles were deployed just prior to dawn for 24 h on 2 free-floating productivity rigs (Joint & Pomroy 1983) with the ^{15}N and NOx rigs being released in series, joined by a 100 m surface line. The depth of deployment of samples matched the depth of sample collection in each experiment. In 1991, samples were incubated for 24 h in a deck incubator with continuously flowing seawater and covered with 50% incident irradiance neutral density screening.

Incorporation of ^{15}N-NO_3: experimental and analytical details. At each depth sampled, water was transferred to 2 replicate 2.4 l polycarbonate bottles to which spikes of ^{15}N-$NaNO_3$ (enriched to 99.7% ^{15}N) were added. The amount of ^{15}N added was calculated, where possible, to be 10% or less of the ambient nitrate concentration at the time of sample collection. Additions throughout the study ranged from 0.02 to 0.68 µmol NO_3-N l^{-1}. After 24 h the rig was recovered and the contents of the bottles were filtered immediately through ashed Whatman GF/F filters, always commencing with the surface samples. Samples pending filtration were stored in the dark at ambient seawater temperatures. Particulate material collected on the filters was washed with 0.2 µm filtered seawater prior to frozen storage. On return to the laboratory the filters were dried and analysed for total N and ^{15}N enrichment using an automated 'Roboprep' Dumas combustion elemental analyser interfaced to a 'Tracermass' triple collector mass spectrometer (Europa Sci-

entific) (Preston & Owens 1983, Owens & Rees 1989). Using a modification of Owens & Rees (1989), conditions of combustion and detection were set up to allow for the detection of samples of low nitrogen content (0.3 to 1.5 µmol NO_3-N). Under these conditions total N can be analysed with an accuracy of < 5% error and a precision of ± 0.06 µmol NO_3-N and atom % values can be measured with an accuracy of < 0.3% error and a precision of ± 0.004 atom %. Nitrogen assimilation rates were calculated using the method outlined in Goering et al. (1966) and Dugdale & Goering (1967) using the following equation (Owens et al. 1986)

$$dN = N_f(C_p - C_0)/(C_d - C_0)$$

where dN is the uptake of nitrate during the incubation; N_f is the particulate nitrogen concentration at the end of the incubation; C_p is the atom % ^{15}N in the particulate fraction after the incubation; C_0 is the initial atom % ^{15}N in the particulate fraction at the start of the incubation; and C_d is the atom % ^{15}N in dissolved nitrogen at the start of the incubation.

Disappearance of nitrate method: analytical and experimental details. At each depth sampled, seawater was added to 6 clean 60 ml polycarbonate bottles such that no air space remained in the bottles. Three of the bottles were placed in a perspex frame and attached to the *in situ* rig whilst the 3 remaining 'initial' bottles were placed in darkness at ambient seawater temperatures for a maximum of 1 h prior to analysis of nitrate concentration using the method of Garside (1982). After the 24 h incubation period, the 'final' bottles were removed from the rig and sampled (1 to 10 ml aliquots) as for the 'initial' bottles. All samples were analysed using a Dasibi 2108 (Dasibi Environmental Corporation, Glendale, CA, USA) NOx chemiluminescence analyser. Nitrate uptake rates were calculated from the net change in concentration: initial – final nitrate concentration over 24 h in the sample bottles. Replicate nitrate samples were analysed with an accuracy of ±4% in the micromolar range and ±6% in the nanomolar range. In order to estimate the error in the calculation of rates of 'new production', maximal and minimal rates of nitrate utilization were calculated after Eppley & Koeve (1990). Where a net increase in nitrate concentration over the incubation period was observed, the nitrate uptake rates generated from these data are expressed as negative rates.

RESULTS

The background physical, chemical and biological methodologies and data recorded during the May 1990 cruise are in Savidge et al. (1992); details of the July 1991 cruise will also be published. From May 1 to 20, 1990, the surface nitrate concentrations decreased from 6.0 ± 0.25 µmol l^{-1} to 9 ± 2 nmol l^{-1} (Savidge et al. 1992). During this period water temperature increased from 12.64 to 13.68°C (Fig. 1a) whilst surface chlorophyll increased from < 1.5 to > 3.5 µg l^{-1} (Fig. 1b). The depth profiles of chlorophyll (Fig. 1b) showed no evidence of the presence of a subsurface maxima. Nitrate uptake profiles obtained from both ^{15}N and NOx measurements were obtained concurrently on 4 occasions during this period (Fig. 2a to d). In general, nitrate uptake rates were highest at the surface and decreased with depth, however the profile obtained for May 19 showed a subsurface peak in nitrate uptake at 15 m (Fig. 2d). On this date, ambient nitrate concentrations, within a secondary thermal structure (Fig. 1a), in the surface 10 m were < 25 nmol l^{-1} (Boyd & Savidge

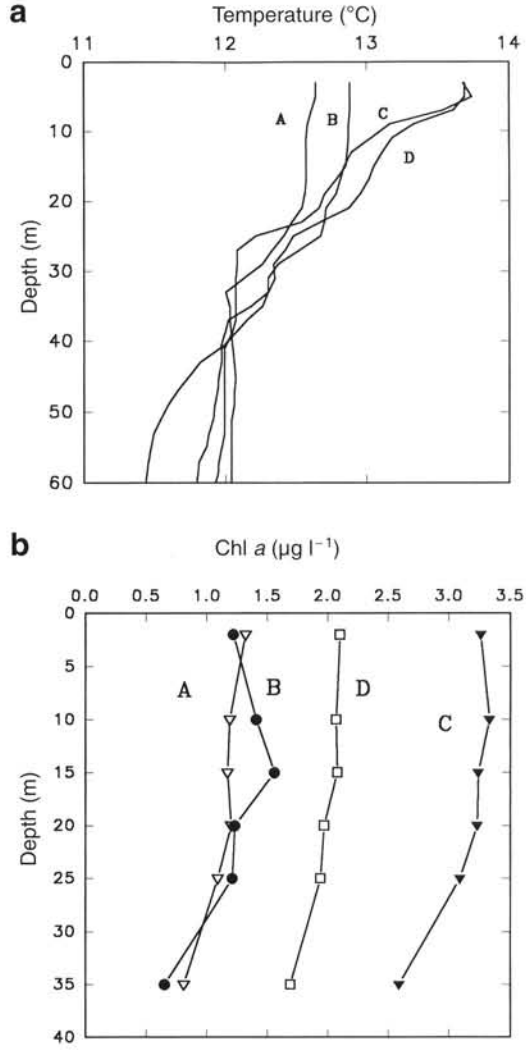

Fig. 1. Vertical distributions of (a) temperature (°C) and (b) chlorophyll (µg l^{-1}) over the upper water column for (A) May 9, (B) May 11, (C) May 17, and (D) May 19, 1990

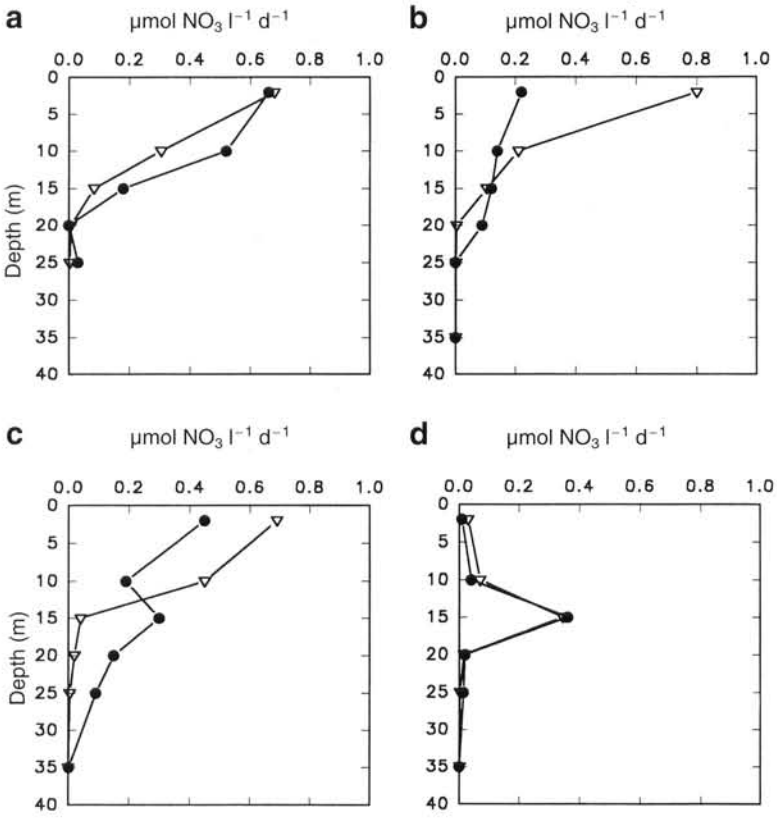

Fig. 2. Profiles of *in situ* nitrate uptake (µmol l^{-1} d^{-1}) vs depth (m) derived from incorporation of ^{15}N-labelled nitrate (▽) and the disappearance of NO_3 as measured by chemiluminescence (●) on (a) May 9, (b) May 11, (c) May 17, and (d) May 19, 1990. Error bars are all smaller than symbols

unpubl.). Nitrate uptake rates derived from the 2 methods generally showed good agreement on May 9 and 19 (Fig. 2a, d) with the above trends, such as the subsurface maximum in nitrate uptake, being observed in both the ^{15}N-uptake and NOx-uptake profiles. Reasonable agreement was also observed for the uptake rates from the 2 techniques on May 11 for samples from 10 to 35 m depth (Fig. 2b). However, the uptake rates derived from the 2 methods differed markedly for the 2 m sample on May 11 and for the profiles from May 17. On May 17, the uptake rates obtained from ^{15}N were higher than those noted for the NOx method in the upper 10 m.

In July 1991, nitrate uptake data from both techniques were available from samples from 2 m for 5 consecutive days from July 21 to 25 (Fig. 3). Despite surface chlorophyll concentrations of around 1 µg l^{-1} at this time, rates of uptake were variable over this period; however similar trends in uptake were obtained from both techniques (Fig. 3). The error bars calculated for uptake rates derived from both the NOx and ^{15}N techniques were larger in the July 1991 study than noted in May 1990.

DISCUSSION

Statistical analysis of the 4 nitrate uptake profiles (Table 1) reveal that significant near 1:1 relationships were noted for May 9 and 19 whilst on the other 2 dates non-significant relationships were recorded with regression slopes >1 being indicated. It was possible that the marked changes in ambient nitrate and chlorophyll concentrations which were noted over the study period may have influenced the processes measured by each technique on May 11 and 17.

Data presented in Table 2 showed that the % addition of tracer nitrate for the samples from 2 and 10 m on May 17 considerably exceeded the 10% level usually taken to allow measurement of *in situ* rates without correction (McCarthy 1980). In addition, ambient nitrate concentrations at these depths were less than 1 µmol l^{-1} (Table 2): ambient concentrations of this order have been shown to limit phytoplankton production, assuming there is no other nitrogen source for uptake (Eppley et al. 1969). It was therefore likely that perturbation of ^{15}N uptake rates was responsible for the observed disparity between the rates obtained by each technique for 2 m and 10 m on this

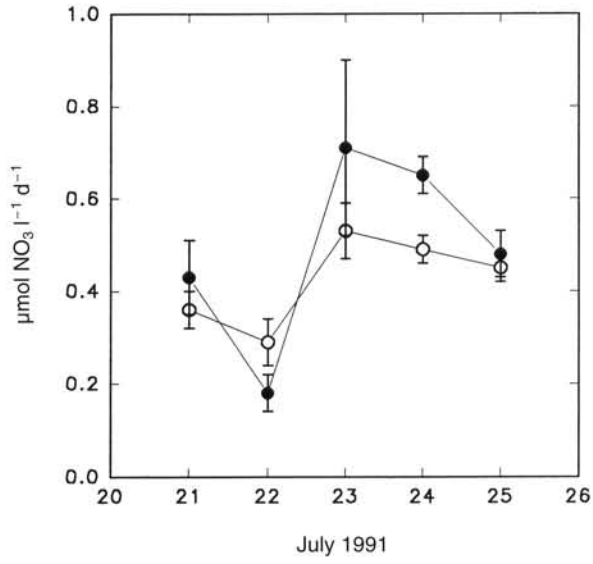

Fig. 3. Time series plot of nitrate uptake rates (µmol l^{-1} d^{-1}) from 2 m samples only, derived from incorporation of ^{15}N-labelled nitrate (●) and the disappearance of NO_3 as measured by chemiluminescence (O)

date. In contrast to the 2 m and 10 m samples on May 17, the uptake rates below 10 m were higher for the NOx method than for ^{15}N, even though the addition of tracer nitrate to the 15 m sample exceeded 10% (Table 2). The reasons for the reversal of trends from the upper to the lower portion of the surface mixed layer are not known. Due to the strong possibility of perturbation of nitrate uptake rates for the surface samples on the May 17 it is likely that these were not true tracer experiments.

Further examination of the nitrate uptake profiles from May 11 (Fig. 2b) indicate that the uptake rate estimated for the 2 m sample on May 11 using the ^{15}N technique was 3 to 4 times greater than the rate derived from NOx. In contrast, nitrate uptake data derived from both techniques for the other depths for May 11 showed reasonable agreement (Fig. 2b). Possible explanations for the 4-fold difference between the observed rates include overestimation of uptake rate by ^{15}N technique (perturbation) and/or underestimation of the uptake rate by the NOx technique (nitrification). The data in Table 2 suggested that perturbation of the uptake rate for the 2 m sample was unlikely since the addition of tracer nitrate was less than 10%. If nitrification was assumed to be responsible for the difference in uptake rate between the 2 techniques, then nitrification rate would have to have been 3 to 4 times greater than the nitrate assimilation rate in this surface sample. Since Ward et al. (1989) noted in a study in the Southern California Bight that the nitrite oxidation rate explained 2 to 20% of the variation in the change over time in ambient nitrate and nitrite concentrations respectively and that most nitrification occurred near the bottom of the euphotic zone, a nitrification rate of this magnitude would appear to be unlikely. In addition, the marked decrease in surface ambient nitrate concentrations and the concomitant increase in phytoplankton biomass over the 20 d study period suggested that assimilation, rather than remineralization, appeared to be the dominant nitrogen transformation/process. At present there is no clear explanation to account for this 3- to 4-fold difference in the relationship between the nitrate uptake rates from NOx and ^{15}N for the 2 m sample on 11 May.

A comparison of the nitrate uptake rates in July 1991 suggests that, with the exception of the rates obtained for July 24, there was no statistical difference between the uptake rates obtained for each technique (Fig. 3). A regression of all the nitrate uptake data obtained in both May 1990 and July 1991 (Fig. 4) yielded a significant near 1:1 relationship ($p < 0.005$; $r^2 > 0.67$, $n = 28$). This analysis suggested that the 2 techniques were measuring similar processes in these studies and gives confidence to the ability of the techniques to provide reliable estimates of 'new production' (Fig. 4). Eppley & Koeve (1990), stated that the use of the NOx technique may be preferred to estimate nitrate uptake rates at low ambient nitrate concentrations. The findings of the current study, using continuous flow IRMS as a tracer ^{15}N uptake method, show good agreement between techniques at low ambient nitrate concentrations and suggest that either method may be used to obtain reliable measurements of uptake rates at nanomolar concentrations.

In 2 recent comparisons of chemical and isotopic methods techniques, discrepancies were reported be-

Table 1. Regression analysis of a linear fit of nitrate uptake (NOx) against nitrate uptake (^{15}N). $^{*}p < 0.05$

Date (1990)	Slope	Intercept	r^2	n
May 9	0.885	−0.032	0.901*	5
May 11	2.799	−0.143	0.494	5
May 17	1.525	−0.085	0.562	6
May 19	0.993	0.002	0.997*	6

Table 2. Increase in ambient nitrate concentration (µmol l^{-1}) resulting from the addition of tracer ^{15}N-NO_3. na: no data available

Depth (m)	Ambient conc.	Tracer conc.	Increase (%)
May 9, 1990			
2	3.82	0.34	8.9
10	3.81	0.34	8.9
15	3.90	0.34	8.7
20	3.95	0.60	15.2
25	3.90	0.68	17.4
35	na	na	na
May 11, 1990			
2	3.42	0.34	9.9
10	3.52	0.34	9.7
15	3.90	0.34	8.7
20	5.27	0.59	11.2
25	7.01	0.68	9.7
35	na	na	na
May 17, 1990			
2	0.45	0.26	57.8
10	0.51	0.34	66.7
15	1.94	0.34	17.5
20	2.97	0.34	11.5
25	5.53	0.42	7.6
35	7.86	0.51	6.5
May 19, 1990			
2	0.02	0.02	100.0
10	0.04	0.04	100.0
15	0.37	0.09	24.3
20	1.82	0.17	9.3
25	2.66	0.25	9.4
35	5.73	0.51	8.9

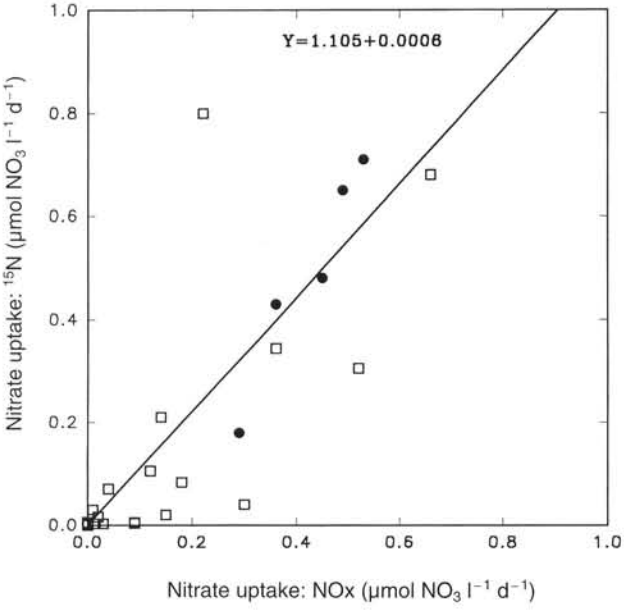

Fig. 4. Scatterplots of nitrate uptake rates (µmol l^{-1} d^{-1}) in May 1990 (□) and July 1991 (●) from the incorporation of ^{15}N-labelled nitrate and the disappearance of nitrate as measured by chemiluminescence. n = 28

tween contrasting methods for measuring nitrate uptake ranging from 1.4 (Slawyk et al. 1990) to 7.2 (Eppley & Renger 1992). Possible explanations for these findings have included bacterial utilization of nitrate and/or the release of labelled extracellular products. It should however be noted that the marked discrepancy between the 2 methods reported by Eppley & Renger (1992) may be due in part to the analysis of samples from different casts. Discrepancies of this order were not observed in the present study. Relationships of 1.0 and 1.3 have been demonstrated for oligotrophic and eutrophic regions by Eppley & Renger (1986) and Dugdale & Wilkerson (1986) respectively. As the seasonal cycle of the phytoplankton in the N Atlantic is limited by depth of mixing in spring and by nitrate limitation in late summer (Parsons & Lalli 1988) the region is probably intermediate between oligotrophic and eutrophic. The observed relationships in this instance for the mesotrophic NE Atlantic during the spring bloom in May 1990 and after the decline of a coccolithophore bloom in July 1991 is encouragingly close to the near 1:1 relationship observed between the 2 methods in oligotrophic and eutrophic waters.

CONCLUSIONS

(1) In this study the near 1:1 relationship between these 2 independent methods for estimating nitrate utilization permits some confidence to be adopted in our ability to estimate 'new production' over a wide range of ambient nitrate and chlorophyll concentrations in the NE Atlantic during studies in spring and summer.

(2) It appears unlikely that the synthesis and extracellular release of labelled DON or bacterial utilization of nitrate was of importance during the onset, duration and initial collapse of the spring bloom over the study period. Similarly, it appears unlikely that nitrification was an important process in the euphotic zone over the 2 study periods.

(3) The accuracy and precision obtainable by the use of continuous flow-IRMS gives confidence in the ability of the ^{15}N technique to be used successfully to measure nitrate uptake rates at low ambient concentrations as the technique has a lower detection rate to enable the accurate measurement of low nitrogen content and atom % ^{15}N values.

(4) The findings of the study confirm the need for real time ambient nitrate data from NOx/chemical techniques, particularly when ambient nitrate concentrations are changing rapidly on relatively short temporal and spatial scales, in order to prevent overspiking of a sample by ^{15}N technique.

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LITERATURE CITED

Bronk, D. A., Glibert, P. M. (1994). The fate of the missing ^{15}N differs among marine systems. Limnol. Oceanogr. 39: 189–195

Dugdale, R. C., Goering, J. J. (1967). Uptake of new and regenerated forms of nitrogen in primary productivity. Limnol. Oceanogr. 12: 196–206

Dugdale, R. C., Wilkerson, F. P. (1986). The use of ^{15}N to measure nitrogen uptake in eutrophic oceans; experimental considerations. Limnol. Oceanogr. 31: 673–689

Eppley, R. W., Garside, C., Renger, E. H., Orellana, E. (1990). Variability of nitrate concentration in nitrogen-depleted subtropical surface waters. Mar. Biol. 107: 53–60

Eppley, R. W., Koeve, W. (1990). Nitrate use by phytoplankton in the eastern subtropical North Atlantic, March–April 1989. Limnol. Oceanogr. 35: 1781–1788

Eppley, R. W., Renger, E. H. (1986). Nitrate-based primary production in nutrient-depleted surface waters off California. Oceanogr. Trop. 21: 229–238

Eppley, R. W., Renger, E. H. (1992). Nitrate utilization by plankton in the Equatorial Pacific March 1988 along 150° W. J. geophys. Res. 97 (C1): 663–668

Eppley, R. W., Rogers, J. N., McCarthy, J. J. (1969). Saturation constants for uptake of nitrate and ammonia by marine phytoplankton. Limnol. Oceanogr. 14: 912–920

Fitzwater, S. E., Knauer, G. A., Martin, J. H. (1982). Metal contamination and its effect on primary production methods. Limnol. Oceanogr. 27: 544–551

Garside, C. (1982). A chemiluminescent technique for the determination of nanomolar concentrations of nitrate and

nitrite in seawater. Mar. Chem. 11: 159–167
Goering, J. J., Dugdale, R. C., Menzel, D. W. (1966). Estimates of *in situ* rates of nitrogen uptake by *Trichodesmium* in the tropical Atlantic Ocean. Limnol. Oceanogr. 11: 614–620
Joint, I. R., Pomroy, A. J. (1983). Production of picoplankton and small nanoplankton in the Celtic Sea. Mar. Biol. 77: 19–27
Lewis, M. R., Harrison, W. G., Oakley, N. S., Hebert, D., Platt, T. (1986) Vertical nitrate fluxes in the oligotrophic ocean. Science 234: 870–873
McCarthy, J. J. (1980). Nitrogen and phytoplankton ecology. In: Morris, I. (ed.) The physiological ecology of phytoplankton. Blackwell, Oxford, p. 191–233
Owens, N. J. P., Rees, A. P. (1989). Determination of nitrogen-15 at sub-microgram levels of nitrogen using automated continuous flow isotope ratio mass spectrometry. Analyst 114: 1655–1657
Owens, N. J. P., Mantoura, R. F. C., Burkill, P. H., Howland, R. J. M., Pomroy, A. J., Woodward, E. M. S. (1986). Nutrient cycling studies in Carmarthen Bay: phytoplankton production, nitrogen assimilation and regeneration. Mar. Biol. 93: 329–342
Parsons, T. R., Lalli, C. M. (1988). Comparative oceanic ecology of the plankton communities of the subarctic Atlantic and Pacific oceans. Oceanogr. mar. Biol. A. Rev. 26: 317–359
Preston, T., Owens, N. J. P. (1983). Interfacing an automatic elemental analyser with an isotope ratio mass spectrometer: the potential for fully automated total nitrogen and ^{15}N analysis. Analyst 108: 971–977
Sarmiento, J., Frost, B., Wroblewski, J. (eds.) (1987). Workshop on Modelling in GOFS. U.S. GOFS Rep. No. 4. U.S. Global Ocean Flux Study Planning Office, Woods Hole Oceanographic Institution, Woods Hole, MA
Sathyendranath, S., Platt, T., Horne, E. P. W., Harrison, W. G., Ulloa, O., Outerbridge, R., Hoepffner, N. (1991). Estimation of new production in the ocean by compound remote sensing. Nature 353: 129–133
Savidge, G., Turner, D. R., Burkill, P. H., Watson, A. J., Pingree, R. D., Leach, H., Richards, K. J. (1992). The BOFS 1990 spring bloom experiment: temporal evolution and spatial variability of the hydrographic field. Prog. Oceanogr. 29: 235–281
Slawyk, G., Raimbault, P., Gentilhomme, V. (1990). On the discrepancies between a colorometric and isotopic method for measuring nitrate utilization in nutrient-depleted waters: implications for the design of experimental protocols in new production studies. Hydrobiologia 207: 333–339
Ward, B. B., Kilpatrick, K. A., Renger, E. H., Eppley, R. W. (1989). Biological nitrogen cycling in the nitracline. Limnol. Oceanogr. 34: 493–513

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