Nitrate-based primary production in nutrient-depleted surface waters off California

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ABSTRACT

Biological models of oceanic, subtropical and tropical surface waters conceive of a euphotic zone bisected by the nutricline forming two layers, a nutrient-depleted but light-rich upper layer and a nutrient-rich but light-poor lower layer. New production, driven by nitrate, and the generation of the sinking flux of biogenic particles take place primarily in the lower layer where nitrate is present. This study used a chemiluminescent analyzer (GARSIDE, *1982*) *to show that nitrate is present at nanomolar concentrations above the nitracline in southern California coastal waters. The nitrate concentrations often decreased over time on incubation of water samples implying its utilization by phytoplankton. This utilization appears to drive a low but significant rate of nitrate-based production in the upper layer. Depending upon the source of the nitrate this production may be new or regenerated production.*

KEY WORDS : Nitrate — Primary production — Surface waters.

RÉSUMÉ

PRODUCTION AU-DESSUS DE LA NITRACLINE : LE PLANCTON UTILISE LE NITRATE À DES CONCENTRATIONS NANOMOLAIRES DANS LES EAUX DE SURFACE ÉPUISÉES EN SELS NUTRITIFS

Les modèles biologiques des eaux océaniques subtropicales et tropicales de surface conçoivent la zone euphotique en deux parties séparées par la nutricline : une couche supérieure épuisée en sels nutritifs mais bien éclairée et une couche inférieure riche en sels nutritifs et faiblement éclairée. La production nouvelle entraînée par le nitrate, et la genèse des particules d'origine biologique qui vont sédimenter ont principalement lieu dans la couche inférieure où le nitrate est présent. La présente étude utilise un analyseur chemiluminescent (GARSIDE, *1982*) *pour montrer que le nitrate est présent à des concentrations nanomolaires au-dessus de la nitracline dans les eaux côtières de Southern California. Les concentrations en nitrate diminuent souvent avec le temps dans les échantillons mis en incubation, ce qui implique son utilisation par le phytoplancton. Cette utilisation semble entraîner un faible, mais significatif, taux de production basée sur le nitrate dans la couche supérieure. Selon la source de nitrate cette production peut être « nouvelle » ou régénérée.*

MOTS-CLÉS : Nitrate — Production primaire — Eaux superficielles.

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1. INTRODUCTION

The "new production" definition of DUGDALE and GOERING (1967) has provided a useful conceptual model of the relation between primary production and the sinking flux of biogenic particles out of the surface layer of the ocean (EPPLEY and PETERSON, 1979). It states that phytoplankton photosynthesis and growth can take place either by the utilization of nutrients recycled within the euphotic zone or nutrients coming into the euphotic zone from outside. Primary production based upon use of recycled nutrients, such as ammonium and urea nitrogen, is called regenerated production, while that based upon external inputs, such as nitrate from the deep reservoir of nitrate below the euphotic zone, is termed new production.

Recently, it has become useful to consider the vertical structure of the euphotic zone with respect to new production and the depth of origin of sinking particles (KNAUER *et al.*, 1984). For example, ALTABET and MCCARTHY (1985) found differences in the natural abundance of ^{15}N in particulate matter with depth in a warm core ring that imply an important contribution of nitrate at the base of the euphotic zone.

The chemiluminescent method of measuring nitrate (GARSIDE, 1982, 1985) indicates nitrate is present at nanomolar concentrations in the nutrient-depleted surface layer above the nitracline, even though it is scarcely detectable by ordinary methods. Presumeably this nitrate reaches the upper layer largely through physical mixing (GARSIDE, 1985) rather than via nitrification *in situ* (OLSON, 1981; WARD *et al.*, 1982; KAPLAN, 1983), but this is by no means clear. The absence of higher nitrate levels in the upper layer implies that mixing is either slow or intermittent such that nitrate concentrations are missed by ordinary sampling procedures. Alternatively it may be utilized as fast as it arrives. Phytoplankton at the base of the euphotic zone, for example in subsurface chlorophyll maximum layers, may serve as a nutrient trap, blocking nitrate transport across the layer (JAMART *et al.*, 1977; TAYLOR *et al.*, 1986).

BALCH *et al.* (1987) showed that the ability to take up nitrate is a constitutive property of phytoplankton. Phytoplankton, even in nutrient depleted surface waters are poised to take up nitrate. Thus any nitrate in the upper layer could be taken up by the plankton, even if it were not immediately assimilated into organic matter. Earlier studies of nitrate utilization, using additions of ^{15}N-nitrate to water samples from the upper layer containing undetectable nitrate, have shown that added ^{15}-N-nitrate can be utilized when the water is incubated several hours. One of us (RE) considered this artefactual when it was first noted in the oligotrophic waters of the N. Pacific central gyre (EPPLEY *et al.*, 1973) on the assumption that the phytoplankton in nitrate-free water would lack the enzymatic machinery to assimilate nitrate. Nitrate reductase in phytoplankton is induced by nitrate and is necessary for nitrate assimilation by phytoplankton (BLASCO *et al.*, 1984). Further, such additions of ^{15}N-nitrate violate an assumption of tracer theory, namely that the addition of tracer does not disturb the steady state of the system (DUGDALE and GOERING, 1967; HARRISON, 1983; GLIBERT *(in press)*. The new observations that nitrate concentrations are not zero but in the nanomoler range suggest that the plankton is continually exposed to nitrate. If so, then the organisms may contain nitrate reductase and other assimilatory enzymes required for nitrate utilization, perhaps at low levels consistent with low rates of nitrate supply and utilization.

Reduced forms of nitrogen, such as ammonium and urea-N will be the predominant forms of N utilized by phytoplankton in the N-depleted upper layer, as these are continuously produced *in situ* by the biota. And while micromolar levels of ammonium may block nitrate utilization, the barely-detectable or undetectable (i.e., <0.03 µM) concentrations encountered in oligotrophic ocean waters (see GLIBERT *(in press)*, for review) may not. Thus, the phytoplankton may simultaneously utilize nanomolar concentrations of nitrate and ammonium as in chemostat cultures provided with both nitrate and ammonium. Use of both N-sources is neither a practical nor a conceptual problem for this study (GLIBERT and MCCARTHY, 1984).

That nitrate utilization occurs above the nitracline is shown in this paper. To what extent it represents new production is an important question for further study.

2. METHODS

Cruises were made in October, 1985 and April 1986 in the Southern California Bight (Fig. 1). Several stations were made on each cruise. The vertical distributions of temperature, salinity, and visible light were recorded using a Plessey model CTD and quantum scalar irradiance detector (BOOTH, 1976), respectively. Both instruments were housed in a General Oceanics rosette equiped with 5 liter Niskin sampling bottles. These were closed on the up-cast at each of six depths in the euphotic zone corresponding to the light transmission of neutral density screens of deck incubators. The latter were used to incubate samples for physiological rate measurements Light transmission of the screens was 35, 21, 15, 3.5, and 1 % (one incubator had no screen). Samples were also collected with 30 liter Niskin bottles when

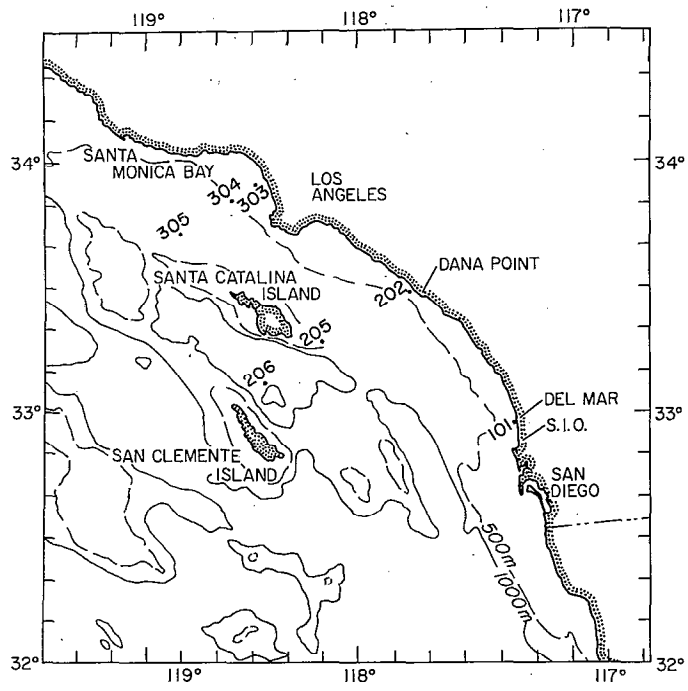

FIG. 1. — Map of the study area showing station positions off Southern California. Depth contours are shown for the 500 and 1 000 m isobaths. S.I.O. indicates the Scripps Institution of Oceanography. *Zone d'étude et position des stations au large des côtes de Californie du Sud. Les isobathes 500 et 1 000 m sont figurées. S.I.O. signale la position de la Scripps Institution of Oceanography*

larger sample volumes were needed as with time course experiments. Acid-cleaned polycarbonate bottles were used for incubations.

Temperature and salinity were averaged over one meter depth intervals using software developed here by E. F. STEWART. Water samples for photosynthesis measurement with Carbon-14 and for particulate carbon, nitrogen and pigment analysis were filtered using Whatman GF/F glass fiber filters (nominal pore size 0.8 μm). Samples for pigment analysis, chlorophyll *a* and phaeopigments, were extracted in 90 % acetone with grinding in a tissue homogenizer. After several hours extraction in the cold and dark, pigment fluorescence was determined using a Turner model 111 fluorometer and chlorophyll and phaeopigment calculated (STRICKLAND and PARSONS, 1972). An HP model 185B CHN analyzer was used to determine particulate carbon and nitrogen (SHARP, 1974). Radioactivity was determined with a scintillation counter for the photosynthesis measurements and carbon assimilation rates were calculated (STRICKLAND and PARSONS, 1972). Nitrate (micromolar concentrations), phosphate and silicic acid were determined in filtered, frozen water samples using methods described in STRICKLAND and PARSONS (1972).

Nanomolar concentrations of nitrate, in samples from above the nitracline, were determined using a chemiluminescence NO analyzer, Antek Instruments model 720 C, following the procedures of GARSIDE (1982). As used here, this method also includes nitrite. Unless specifically noted references to nitrate concentrations measured should be read as "nitrate plus nitrite". Containers for this work were acid-cleaned. Water for making up reagent solutions and for rinsing, and for reagent blanks was prepared with demineralized water repurified immediately prior to use with an ultrapure mixed-bed dimineralizer cartridge (Barnstead). Samples were measured on the ship as quickly as possible after collection. They were acidified to pH 1 with sulfuric acid to stop biological activity until the measurements could be performed. Standards and blanks were checked at least twice daily, with 2-7 measurements of each. Samples were analyzed routinely in duplicate and additional replicates were measured if differences exceeded 6 nM, the odd value being rejected. The mean difference between 73 sets of duplicate subsamples was 2.5 nM. The standard deviation of 19 sets of triplicate samples, where one of the three had been rejected, averaged 5.1 nM. The precision is similar to that reported by GARSIDE (1982). To date the minimum concentration observed in demineralized water is 1-2 nM.

Time course experiments were carried out on both cruises to study nitrate utilization rate and, in parallel incubations, the rate of daytime photosynthesis and nighttime loss of carbon-14 labelled particulate material. These experiments were started within two hours of local noon. Samples were removed for analysis at dusk, again the following dawn, and after 24h incubation. Samples were taken at two or more depths at each station for these experiments. In the October cruise, 100 nM ^{15}N-nitrate was added to most samples. Samples for ^{15}N analysis were filtered and stored in vacuum desiccator in a freezer for analysis ashore. They were analyzed using a Jasco model N-150 ^{15}N emission spectrometer following procedures of HARRISON (1983).

Nitrate-based primary production was calculated as carbon by multiplying the rate of nitrate use by the ratio POC/PON. This ratio is similar to the Redfield ratio in local surface waters (see Table I). Nitrate utilization rate data were lacking for 1-2 depths above the nitracline at each station and for all depths within the nitracline in the April cruise. Then we used the finding of HARRISON *et al* (1987) that new production averaged about 64 % of total (^{14}C) production in this region when nitrate was >1 micromolar concentration. This provided a means of calculating depth profiles of nitrate-based production that could be integrated over depth to give rate, beneath a square meter of sea surface. The rates based on ^{15}N-nitrate uptake above the nitraclines measured on the October cruise, were high and were considered artefacts. They were not used for production calculations. Instead, nitrate-based production above the nitracline was estimated for the fall cruise from ambient nitrate concentrations assuming that any nitrate present in excess of 20 nM would be consumed within 24 hours.

$$NO_3\text{-based Production} = (NO_3\text{-measured-20}) \times 14 \times (POC/PON) \times 10^{-3} \quad (1)$$

(mg C m^{-3} d^{-1}) (n moles l^{-1})

where the POC and PON are by weight.

Nitrate uptake was measured directly during the spring cruise. New production was calculated as follows:

$$NO^3\text{-based Production} = (NO^3\text{-uptake in 24 h}) \times 14 \times (POC/PON) \times 10^{-3} \quad (2)$$

(mg C m^{-3} d^{-1}) (n moles l^{-1} d^{-1})

The factor 14 converts nitrate uptake in n moles l^{-1} d^{-1} to ng l^{-1} d^{-1}. Multiplying by the POC/PON ratio gives the carbon equivalent (one could substitute the Redfield C/N ratio with equal justification). The factor 10^{-3} converts ng C l^{-1} d^{-1} to µg C l^{-1} d^{-1} or mg C m^{-3} d^{-1}.

3. RESULTS

3.1. Vertical structure of the euphotic zone

A summary of the properties of the surface waters is provided in Table I. The waters were stratified during both cruises, as is usually the case, with an upper mixed layer 8-26 m thick. Average nitrate concentrations in the mixed layer ranged from 18 to 270 nM, and were <60 nM at all but one station. The top of the nitracline was at 11-41 m depth. The chlorophyll maximum was near the top of the nitracline (Fig. 2), also as usual (CULLEN and EPPLEY, 1981). The depth of the euphotic zone averaged 46 m.

Surface waters differed in temperature and in the several measures of plankton standing stock between the two cruises. Temperature was lower in the spring. Depth integrals of primary production and chlorophyll *a* were higher in the spring cruise (Table II).

TABLE I

Surface Water properties during two cruises in the Southern California Bight. Mixed layer salinity was 33.5-33.6 in October 1985 and 33.3-33.4 in April 1986. *Caractéristiques des eaux superficielles pendant les deux croisières dans la Baie de Californie du Sud. La salinité de la couche de mélange est de 33,5-33,6 en octobre 1985 et de 33,3-33,4 en avril 1986*

CRUISE	SCBS-24			8-15 October, 1985				SCBS-25			2-8 April, 1986			
STATIONS	101	202	205	206	303	304	305	101	202	205	206	303	304	305
Euphotic Depth (m)	>13	30	59	49	34	49	47	17	37	46	37	40	39	41
Nitracline Depth	>13	25	41	35	33	35	35	ND	13	38	33	26	17	22
Chlorophyll Max Depth	12	11	36	35	34	39	37	10-17	14	36	29	29	27	30
Mixed Layer Depth	8	9	16	17	22	18	14	ND	9	18	26	19	16	17
Mixed Layer Properties														
Temperature °C	19.7	18.9	20.3	20.3	18.8	19.7	19.8	ND	15.2	16.0	15.9	15.4	15.4	15.6
Nitrate conc. nM	ND	270	32	36	59	42	25	54	40	18	34	58	38	27
Chlorophyll *a* µg l^{-1}	0.40	0.27	0.21	0.18	1.28	0.15	0.22	0.50	0.33	0.26	0.30	0.41	0.42	0.35
Particulate Carbon µg l^{-1}	135	128	89	59	ND	55	64	207	152	112	140	110	152	112
Particulate Nitrogen µg l^{-1}	22	20	13	8.8	ND	8,6	10	33	22	16	20	20	23	17

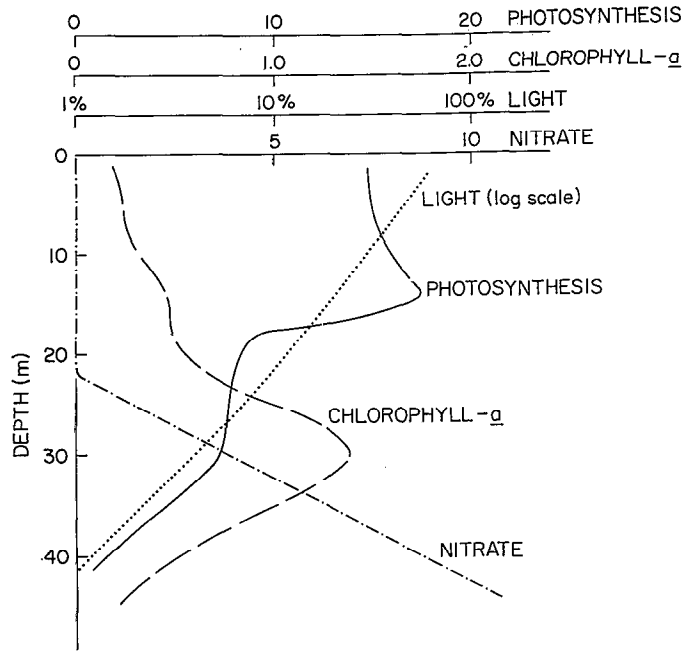

FIG. 2. — Depth profile of chlorophyll *a* (mg m^{-3}) and nitrate (millimoles m^{-3}) concentrations, light (quantum scalar irradiance, log scale, expressed as % surface irradiance), and photosynthetic rate (mg C m^{-3} d^{-1}). April, 1986, Station 305. *Profil de la teneur en chlorophylle* a *(mg m^{-3}) et en nitrate (millimoles m^{-3}), de la quantité de lumière (rayonnement photonique scalaire, échelle logarithmique, pourcentage du rayonnement de surface) et du taux de photosynthèse (mg C m^{-3} d^{-1}). Avril 1986, station 305*

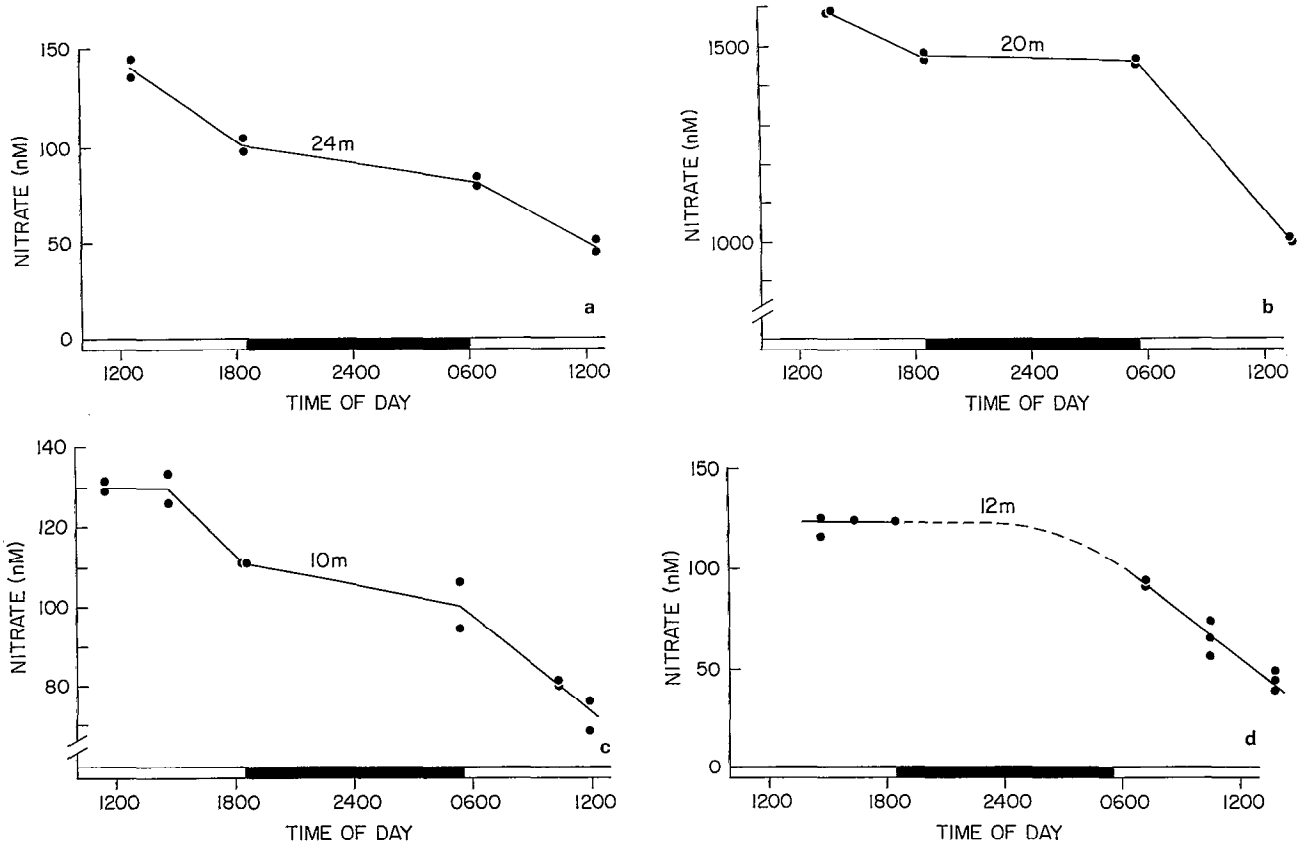

FIG. 3. — Time courses of nitrate depletion during incubation of seawater samples. a: October, 1985, Station 304, 24 m; b: April, 1986, Station 305, 20 m; c: October, 1985, Station 206, 10 m; d: October, 1985, Station 205, 12 m. Samples from the October cruise contained +100 nM ^{15}N-nitrate. *Décroissance de la teneur en nitrate au cours de l'incubation des échantillons d'eau de mer. a: Octobre 1985, station 304, 24 m; b: Avril 1986, station 305, 20 m; c: Octobre 1985, station 206, 10 m; d: Octobre 1985, station 205, 12 m. Les échantillons de la croisière d'octobre contenaient + 100 nM de ^{15}N-nitrate*

3.2. Changes in nitrate during incubation

Seawater samples were incubated at each station in order to follow nitrate changes over time. Samples spiked with 100 nM ^{15}N-nitrate during the October cruise provided rather spectacular results. Near-surface samples showed uptake in both light and dark, the dark rate being about one-half of the light rate (Fig. 3a). A few samples taken near the top of the nitracline, not spiked with ^{15}N-nitrate, showed nitrate depletion primarily during the daylight (Fig. 3b).

In October the shallow samples at two of the offshore stations showed a lag period of several hours before there was any change in nitrate concentration. In one case uptake began later in the afternoon (Fig. 3c) while in the other experiment no nitrate uptake was evident until the following morning (Fig. 3d). Both samples had added ^{15}N-nitrate.

The incubation experiment in October at station 206 was continued for about 55 hours to see how low nitrate concentrations might be after extensive depletion by plankton growth. The minimum value was 18 nM. Even lower values were seen in the April experiments.

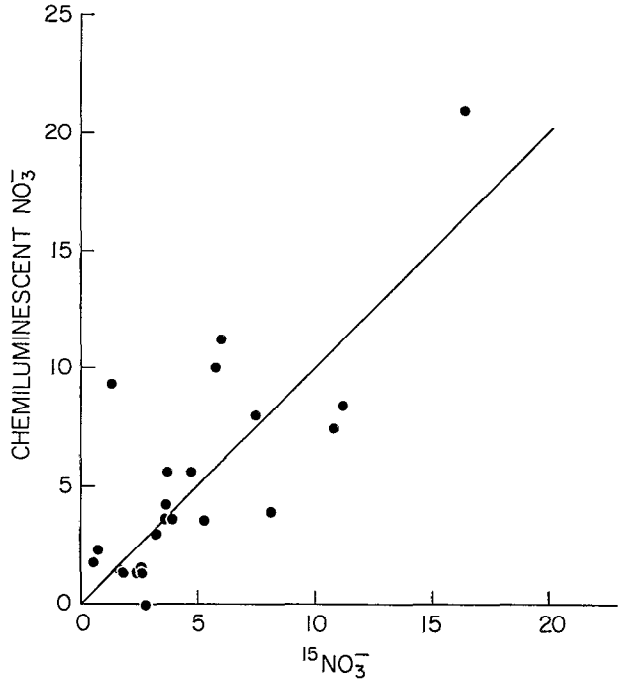

FIG. 4. — Comparison of nitrate uptake measured during time course experiments by the chemiluminescent method vs. the ^{15}N method. 100 nM ^{15}N-nitrate was added to all samples. The line is a 1:1 relationship. Regression line slope was 0.97, y-intercept 0.54, r^2 0.64. *Comparaison de la fixation de nitrate mesurée pendant la durée des expériences par la méthode de chimioluminescence et par la méthode de l'^{15}N. 100 nM de ^{15}N-nitrate ont été ajoutés à tous les échantillons. Il est figuré la droite de pente 1. La pente de la droite de régression était de 0,97, l'ordonnée à l'origine de 0,54 et r^2 de 0,64*

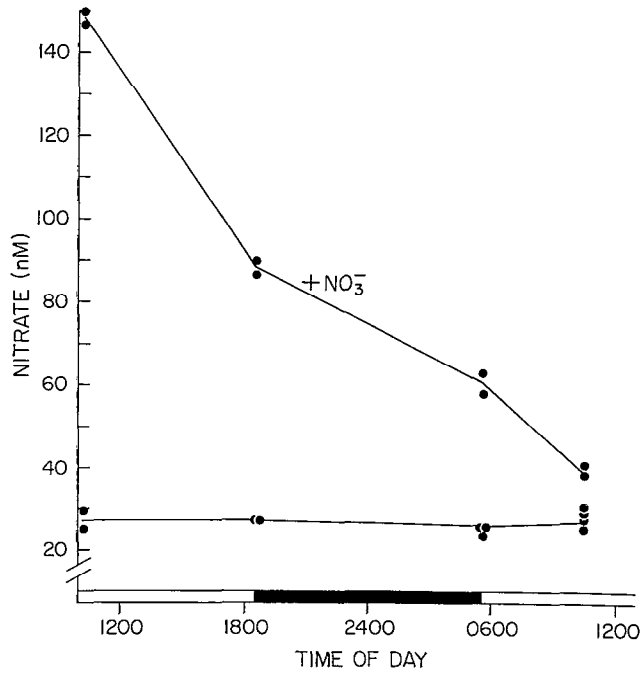

FIG. 5. — Comparison of nitrate (plus nitrite) concentration changes with and without addition of approximately 100 nM nitrate. April, 1986, Station 305, 8 m. There was no measurable nitrate uptake in the sample without nitrate addition. Nitrite was 5-7 nM in the sample with no nitrate addition, with no temporal change. Nitrate concentrations, corrected for nitrite, were 18-27 nM. *Comparaison de l'évolution de la teneur en nitrate (et nitrate ajouté) avec et sans ajout de, approximativement, 100 nM de nitrate. Avril 1986, station 305, 8 m. Il n'y avait pas de fixation de nitrate mesurable dans l'échantillon non additionné de nitrate. La teneur en nitrite était de 5-7 nM dans l'échantillon non additionné de nitrate, sans variation dans le temps. Les teneurs en nitrate corrigé du nitrite étaient de 18-27 nM*

Nitrate utilization in the October cruise was measured by both the ^{15}N and chemiluminescence methods using samples with added ^{15}N-nitrate. The scatter plot and regression line (Fig. 4) suggest 1) the two methods were measuring the same rate process and 2) the nitrate utilized appeared in the particulate phase. The slope and intercept of the regression line were not significantly different from one and zero, respectively. DUGDALE and WILKERSON (1986, their Fig. 3) show a similar graph based upon studies of nitrate utilization in the Peru upwelling where there were micromolar rather than nonomolar changes in nitrate.

Nitrate utilization rates without added nitrate were much lower than when nitrate was added at

100 nM (Fig. 5). It is clear that adding ^{15}N to samples taken from above the nitracline, even when added 1t 50-100 nM levels, can sometimes result in erroneously high nitrate assimilation rates. In Fig. 5 there was no nitrate uptake in the sample without added nitrate. Most samples, however, showed nitrate depletion during the first afternoon of incubation (Fig. 6). Both samples of Fig. 6 showed nitrate uptake in the afternoon. At night the concentration either decreased at a slower rate or even increased (Fig. 6). It remained unchanged in still other samples (not shown).

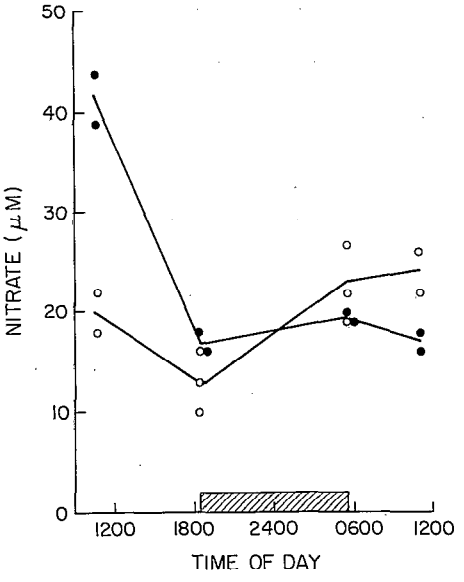

FIG. 6. — Time course of nitrate (corrected for nitrite) concentration changes in April, 1986. Open circles: Station 305, 18 m; filled circles: Station 303, 9 m. Station 303 was made after a wind event, Station 305 before the wind event. Note the difference in initial nitrate concentration. *Évolution de la teneur en nitrate (corrigé du nitrite) avec le temps en avril 1986. Symboles blancs : station 305, 18 m ; symboles noirs : station 303, 9 m. La station 303 a été tenue après un coup de vent, la station 305 avant celui-ci. Noter la différence des teneurs initiales en nitrate*

3.3. **Carbon assimilation**

Rates of ^{14}C-bicarbonate incorporation were measured in the time course experiments along with nitrate changes. Carbon uptake was not observed in the dark while nitrate uptake often was. Nighttime loss of carbon was observed in each experiment (Fig. 7) and averaged 20 % of the 24 hour rate. Depth integrated daily primary production ranged from about 0.4 to 1.5 g Cm^2 d^{-1} (Table II).

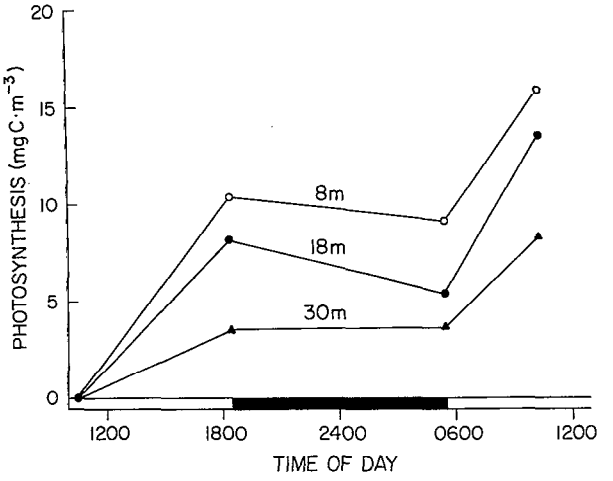

FIG. 7. — Time course of photosynthetic carbon assimilation measured with ^{14}C. April, 1986, Station 305. Samples from 8, 18, and 30 m depth were incubated at 35, 12, and 3.5 % light incubators, respectively. *Assimilation photosynthétique du carbone en fonction du temps, mesurée au ^{14}C. Avril 1986, station 305. Les échantillons provenant des profondeurs 8, 18 et 30 m ont été incubés, respectivement, à des taux de lumière de 35, 12 et 3,5 %*

TABLE II

Total primary production, nitrate-based production (NBP), their ratio (NBP/Total) and chlorophyll *a* concentration integrated over the depth of the euphotic zone. Units of production are mgC m^{-2} d^{-1} and of chlorophyll *a* mg m^{-2}. *Production primaire totale, production dérivée du nitrate (NBP), rapport de ces deux paramètres et teneur en chlorophylle* a *intégrée sur l'ensemble de la couche euphotique. Unités : mgC m^{-2} d^{-1} en production et mg m^{-2} en chlorophylle* a

Station	101	202	205	206	303	304	305
		Cruise SCBS-24		8-15 October, 1985			
Total production	860	1050	660	425	1150	470	530
NBP	ND	445	88	66	74	110	67
Ratio (NBP/Total)	ND	0.42	0.13	0.15	0.06	0.23	0.13
Chlorophyll a	9.3	18.2	8.8	16.7	27.3	18.2	19.9
		Cruise SCBS-25		2-8 April, 1986			
Total production	1490	1170	349	716	666	453	411
NBP	ND	468	58	153	180	120	112
Ratio (NBP/Total)	ND	0.40	0.17	0.21	0.25	0.26	0.27
Chlorophyll a	34.0	26.3	26.2	24.1	20.2	16.3	26.9

TABLE III

Examples of nitrate-based production (NBP) estimates above the nitracline based on nitrate concentration changes. NBP rates are compared with total (^{14}C) production rates and (NBP/Total), both with units mg C m^{-3} d^{-1}. Nitrate concentrations are nM. Nitrate uptake rate units are nmoles l^{-1} d^{-1}. The POC/PON ratios are by weight. Cruise SCBS-25, 2-8 April, 1986. *Exemples d'estimations de production dérivée du nitrate (NBP) au-dessus de la nitracline, à partir des variations des teneurs en nitrate. Les taux de NBP sont comparés aux taux de production totale (^{14}C) et aux rapports NBP/production totale, l'unité dans les deux cas étant le mg C m^{-3} d^{-1}. Les teneurs en nitrate sont exprimées en nM, les taux de fixation de nitrate en nmoles l^{-1} d^{-1}. Les rapports POC/PON sont des rapports de poids. Croisière SCBS-25, 2-8 avril 1986*

Station	Depth	Incubation Time	Nitrate Uptake Rate*	NO_3 Concentration		$\left(\frac{POC}{PON}\right)$	Nitrate-based Production†	^{14}C Production	NBP/Total
				Initial	Final				
205	20	12	0.67	23	15	6.67	1.1	9.36	0.12
305	8	8	NS	29	27	5.66	NS‡	15.2	NS
	18	8	1.0	27	19	6.13	1.5	8.89	0.13
304	7	5.1	0.98	38	33	5.8	1.4	20.6	0.07
303	9	8.1	2.7	45	23	5.72	3.9	33.6	0.12
	17	24	11.8	331	49	5.85	23 (7.6)	12.7	>1 (0.6)
206	1	12	2.2	44	18	7.31	4.0	16.6	0.24
	9	12	1.4	29	12	7.10	2.5	22.7	0.11
	17	12	1.1	25	12	7.03	1.9	33.3	0.06
	18	12	1.3	38	22	7.0	2.4	22.5	0.10

* Nitrate uptake rates per hour incubation time. These are extrapolated to 24 h in the nitrate-based production calculation by assuming nighttime rate was one-half the day rate. *Taux de fixation de nitrate par heure d'incubation. Dans le calcul de la production dérivée du nitrate, ces taux sont extrapolés à 24 h en supposant que le taux nocturne est égal à la moitié du taux diurne.*

† Nitrate-based production mg C m^{-3} d^{-1} = (nitrate uptake in 24 h, μmole m^{-3}) $\times$ 14 $\times$ $\frac{\text{POC mg m}^{-3}}{\text{PON mg m}^{-3}} \times \frac{1}{1000}$. *Production dérivée du nitrate mg C m^{-3} d^{-1} = (fixation de nitrate en 24 h, μmole m^{-3}) $\times$ 14 $\times$ $\frac{POC\ mg\ m^{-3}}{PON\ mg\ m^{-3}} \times \frac{1}{1000}$.*

‡ NS = not significant. *NS: non significatif.*

3.4. **Primary Production based on nitrate**

The nitrate consumption measurements were used, along with measurements of particulate organic C and N (POC and PON), to estimate daily production of carbon above the nitracline due to nitrate utilization (see 2.). This production, based upon the chemiluminescent measures of nitrate depletion, ranged from not measurable to 24 % of the total (^{14}C) production above the nitracline (Table III).

The sample from station 303, 17 m (Table III) gave an interesting result. It was from the top of the nitracline where the nitrate concentration was 331 nM. It was incubated at 12 % of surface light. Nitrate-based production calculated as the product of the nitrate uptake rate and the POC/PON ratio exceeded the carbon assimilation measured with ^{14}C. This was noted also at two other samples from the top of the nitracline with nitrate concentrations <2 micromolar. These samples were incubated at 12 or 3.5 % surface light. In these cases we assumed the imbalance between C and N uptake was transient and related to the differences in the light responses of carbon and nitrate assimilation (MACISAAC and DUGDALE, 1972; MCCARTHY and NEVINS, 1986). We calculated nitrate-based production assuming a new/total ratio of 0.6 (HARRISON *et al.*, 1986), as shown in parenthesis in Table III.

Nitrate-based production integrated over the depth of the euphotic zone ranged from 6 to 42 % of total production (Table II).

4. DISCUSSION

Nitrate is clearly present above the nitracline in southern California coastal waters. The depth profiles indicated average concentrations from 18 to 270 nM (Table I). There seem to be onshore-offshore differences in these concentrations, with highest levels at stations nearest the coast. Concentrations decreased at stations 101, 202, 303, 304 in the same order as their distance offshore in October, 1985. In April, the highest mean concentration was found at station 303. That station was occupied at the end of a wind event. The winds apparently eroded the thermocline about 5 m, bringing nitrate from the upper nitracline into the surface layer.

The nitrate above the nitracline is biologically

available even although it is present only at nanomolar concentrations (Fig. 6, closed circles).

Nitrate uptake over the first hours of incubation was calculated per hour (Table III) and normalized to chlorophyll in order to compare these results with expected phytoplankton growth. Maximum rates were about 25 nmoles nitrate (μg chlorophyll a)$^{-1}$ (hour)$^{-1}$ in April when only ambient concentrations were studied (no ^{15}N nitrate additions). If a microgram of chlorophyll were equivalent to approximately one micromole of phytoplankton nitrogen (a rule of thumb from R. C. DUGDALE, *pers. com.*, 1969) then this rate would correspond to a specific growth rate about 0.3 day^{-1}. One expects actual growth rates exceeded this value, a supposition consistent with an additional utilization of reduced forms of nitrogen, such as ammonium. These rates of nitrate use are consistent with expected rates of nitrate consumption by phytoplankton.

The nitrate removed from solution was incorporated into particulate matter, based upon the ^{15}N-nitrate experiments (Fig. 4). The nitrate-based production above the nitracline is small but not trivial. In local waters high production is not confined to the vicinity of the nitracline. Half of the time it is a maximum at or above the 30 % light depth, commonly well above the nitracline (CULLEN and EPPLEY, 1981). Roughly one-half of the primary production takes place above the nitracline. A nitrate-based production that is about 5 % of total production above the nitracline, and about 60 % of the total production within the nitracline, results in a depth integrated nitrate-based production about 33 % of the total production, with about 8 % of the depth integrated nitrate-based production taking place above the nitracline. These approximations are consistent with earlier results off southern California (EPPLEY *et al.*, 1979). They further point to the importance of nitrate-based production within the nitracline. The rough calculations suggest about 90 % percent of the nitrate-based production takes place in the nitracline.

The depth of the nitracline is quite variable relative to the depth of the euphotic zone and this variability explained about half of the variation in phytoplankton standing stock and production in local waters (EPPLEY *et al.*, 1979) and even more in the eastern tropical Atlantic (HERBLAND and VOITURIEZ, 1979). Because of the variable nitracline depth the contribution of nitrate-based production above the nitracline to depth integrated new production will not be constant.

The source of the nitrate above the nitracline is a fundamental question. If the source is external to the euphotic zone, i.e. from vertical mixing or atmospheric input (DUCE, 1986), then the production based upon utilization of the nitrate is new production. If it is from biological processes taking place within the euphotic zone, then the resulting production is regenerated production. The wind event during the April cruise appeared to deepen the mixed layer and bring nitrate into the surface layer. Use of this nitrate (Fig. 6, filled circles) would represent new production. It is interesting to compare nitrate concentrations above the nitracline over time. Stations visited before the wind event were 101, 202, 205, 305 and 304 (Table I). Station 303 was done the first day after the winds and station 206 the following day. The average nitrate concentrations above the nitracline were higher in morning than evening bottle casts at those two stations, but not at station 205 where morning and evening casts were made before the winds. On the other hand, we also noted nitrate production within the incubation bottles (Fig. 6, open circles). This must represent biological processes, although we have not completely ruled out the possibility of contamination. Further examples of nitrate production in the incubation bottles have been noted on two subsequent cruises. The source of this nitrogen needs to be defined. One assumes it is due to nitrification. If so, the chemiluminescent method may be of some value in future nitrification studies, as well as in studies of wind mixing and nitracline erosion.

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