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Interactions of light and inorganic nitrogen in controlling nitrogen uptake in the sea*

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Abstract—The uptake of ammonium and nitrate in natural populations of marine phytoplankton is light dependent and often can be described adequately by the Michaelis–Menten equation. The half-saturation constant for light intensity in nitrate and ammonium uptake is found to be from 1 to 14% of surface light intensity, an intensity range occurring near the bottom of the euphotic zone. Since the uptake of these compounds as a function of substrate concentration is also described by the same equation, many vertical profiles of nitrate and ammonium uptake obtained with the ^{15}N technique can be interpreted from the interaction of light and nutrient concentration at different depths.

In oligotrophic waters, nutrient uptake is severely limited by nutrient concentrations; but in eutrophic areas, light intensity very often is the limiting factor. In the former, maximal uptake may occur deep in the euphotic zone, while in the latter, the maximum occurs near the surface. Ammonium is taken up more readily than nitrate by populations in all areas, and in oligotrophic regions may account for 80% of the inorganic nitrogen uptake. In eutrophic areas, most of the inorganic nitrogen uptake is based on nitrate. Ratios of carbon to nitrogen taken up by phytoplankton vary over a wide range (12–76), with some indication that the lower values are associated with regions having a certain degree of environmental stability—either very rich or very poor waters.

INTRODUCTION

The considerable geographic and vertical variability in the rates and relative importance of nitrate and ammonium uptake by natural populations of marine phytoplankton have been described by Dugdale and Goering (1967). Certain variability in natural uptake can be attributed to nutrient concentration variations (MacIsaac and Dugdale, 1969), but light intensity also is important in controlling uptake, either through photosynthesis or directly. A light requirement for nitrogen uptake is suggested by the similarities in shape between vertical profiles of nitrogen and carbon uptake by marine phytoplankton (Dugdale and Goering, 1970), and in certain freshwater algae the relation of nitrate assimilation to light intensity is known to be described by a saturation curve (Bongers, 1956; Hattori, 1962).

A computation model for the uptake of nitrate described by Dugdale and MacIsaac (1971) had variables of light intensity, and nitrate and ammonium concentration. The model was based upon the kinetics of nitrogen uptake as a function of ambient concentration (MacIsaac and Dugdale, 1969) and upon unpublished experiments measuring inorganic nitrogen uptake as a function of light intensity. These experiments with light are described in this paper and nutrient uptake profiles are discussed and classified in accordance with currently available theory.

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METHODS

Experiments

The results presented here are from cruise 13 of Stanford University's R.V. *Te Vega* and cruises 26, 36, 37 and 47 on the University of Washington's R.V. *Thomas G. Thompson* (Fig. 1). *Thompson* stations often will be identified by a hyphenated number indicating cruise and station number, respectively. The *Te Vega* cruise and cruises 26 and 37 of the *Thompson* were made in the eastern tropical Pacific Ocean during March 1967, January and February 1968, and May 1969, respectively. Cruise 36 of the *Thompson*, in April 1969, was an intensive study of a small region of upwelling off the coast of Peru; and cruise 47 took place in the Mediterranean, in March 1970, for the most part in waters bounding the Attic Peninsula of Greece.

The nitrogen-15 method used on these cruises to measure the uptake of nitrate and ammonium by natural populations of phytoplankton has been described previously (Neess, Dugdale, Dugdale and Goering, 1962; Dugdale and Goering, 1967). Briefly, the procedure involves incubating a phytoplankton population with the nitrogen-15-labeled compound for a period of time, collecting the population on a

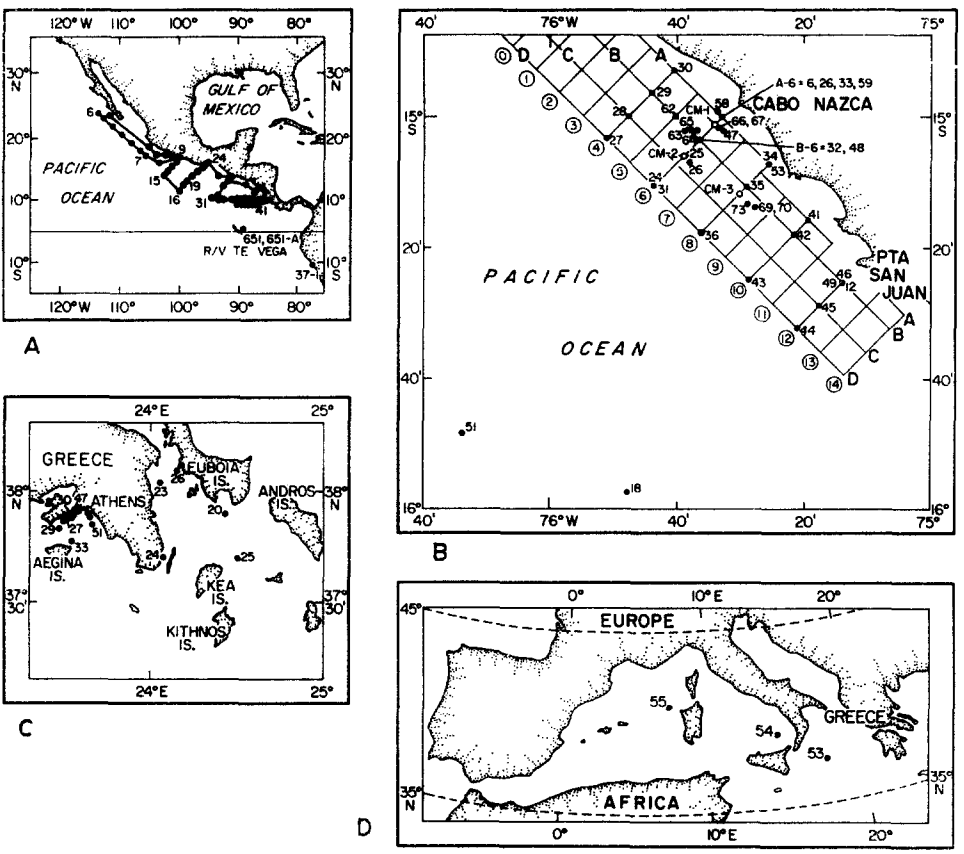

Fig. 1. Station locations from (A) *Te Vega* cruise 13, and *Thompson* cruises 26 and 37, (B) *Thompson* cruise 36 to Peru, (C) *Thompson* cruise 47 to the eastern Mediterranean, and (D) *Thompson* cruise 47 to the western Mediterranean.

glass-fiber filter, and analyzing by mass spectrometry for enrichment in the particulate nitrogen (PN) fraction. Sea water was collected with large-volume nontoxic samplers and, depending on the phytoplankton population density was transferred into 1, 4, or 9-liter Pyrex serum bottles. After enrichment with nitrogen-15, the bottles were placed for varying periods of time into sea-water cooled plexiglass incubators exposed to natural sunlight. After incubation and filtration (on to Hurlbut 984H ultrafilters) the samples were dried and held for mass spectrometry. The *Te Vega* experiments were analyzed at the Institute of Marine Science, University of Alaska, with a Bendix 17-210 time-of-flight mass spectrometer; an Associated Electrical Industries MS-10 instrument (180° analyzer, 5-cm radius) was used to process the *Thompson* experiments, for the most part at sea. All the samples were converted to N_2 by the automated Dumas procedure described by BARSDATE and DUGDALE (1965).

The largest number of nitrate and ammonium uptake measurements on these cruises were ' nitrogen productivity ' experiments in which uptake rates were determined under simulated *in situ* conditions for populations from several depths in the euphotic zone and were accompanied by a suite of other experiments and measurements normally including at least carbon-fixation measurements, plankton counts, chlorophyll-*a* and particulate nitrogen determinations, and analysis of the nitrate, nitrite, ammonium, phosphate and silicate content of the water. These productivity stations were begun around 0800 local time when ship scheduling permitted. Samples were taken on most occasions from the depths to which 100, 50, 25, 10 and 1 % of the surface light penetrated as determined by submersible photometer or Secchi disk. During the 24-hr incubation period used for these experiments, *in situ* light intensities were simulated by covering the bottles with appropriate neutral-density filters made from nickel screens (Perforated Products, Inc., No.15G, 50%; No.40/10P, 25%; No.125P, 10% ; No.125W, 1 %). In the past, rough calibration of the screens with a photocell have agreed with the specifications given by the manufacturer. But recently, measurements made by Dr. André Morel on board the N.O. *Jean Charcot* with both a photometer and a quantum meter suggest changes in transmittance by some of the screens with age and orientation. But treating earlier data in terms of these new light values increases the scatter of the points, and, for the present, the data will be considered according to the original screen calibrations. Identical incubating procedures were applied to the measurements of carbon-fixation rates done with carbon-14. Incident surface radiation was measured with an Eppley pyranometer.

The remaining nitrate and ammonium uptake data are the results of two other types of experiments. On *Thompson* 26 a study was made of the kinetics of uptake as related to the concentration of the nitrogen compound being taken up. This work has been described in detail (MACISAAC and DUGDALE, 1969). Kinetic constants have been measured on subsequent cruises as well. Beginning with *Thompson* 36, attention was devoted to the relation between natural light intensities and inorganic nitrogen uptake. In these experiments phytoplankton populations from selected depths were first enriched with an excess of labeled nitrate or ammonium (a ' saturating ' concentration of nitrogen nutrient) and were exposed to a series of light intensities including those corresponding to the standard sampling depths and occasionally 7 and 3 % of surface light (screen No.40/10W, 7%; No.80T, 3%) and total darkness as well. These experiments ordinarily were incubated for 4–6 daylight hours before filtration. Carbon fixation often was measured under the same incubation conditions in samples

of unmodified and nitrogen-enriched sea water.

The nitrogen chemistry for the experiments was done at sea in duplicate or triplicate, almost always on fresh samples. Manual methods were used until the introduction of automated chemistry on *Thompson* 36. Manually, nitrite was measured by the method of BENDSCHNEIDER and ROBINSON (1952), nitrate by that of WOOD, ARMSTRONG and RICHARDS (1967), and ammonium by the ammonium-specific extraction procedure of PROCHÁZKOVÁ (1964). Silicate and phosphate were determined with methods of MULLIN and RILEY (1955) and MURPHY and RILEY (1962), respectively. The automated methods used were adaptations of the manual methods for nitrite, ammonium (MACISAAC and OLUND, 1971) and nitrate; that of STRICKLAND and PARSONS (1968) for silicate; and that of HAGER, GORDON and PARK (1968) for phosphorus. Particulate nitrogen was measured with a Coleman nitrogen analyzer.

Computation of in situ *rates of uptake*

The *in situ* rates of nitrogen productivity sought under simulated conditions in the productivity measurements can only be approximated by the nitrogen-15 tracer method, as the technique involves nitrogen additions. However, with very low enrichments (10% or less over the ambient nutrient concentrations) good approximations often result, designated ' measured *in situ* uptake rates '. But it is also possible and sometimes advantageous to compute *in situ* uptake rates from the higher rates (' enhanced measured rates ') determined with relatively larger enrichments. For example, in populations that occur where the ambient nitrate and ammonium concentrations are low, even the required minimum enrichment is apt to result in a significant stimulation of uptake over *in situ* rates (DUGDALE and GOERING, 1967; MACISAAC and DUGDALE, 1969). These same populations often demonstrate *in situ* uptake rates that are barely measurable. At most stations on *Thompson* 26 and 47, in unproductive, nutrient-poor waters, samples were enriched substantially above the 10% level to increase the nitrogen-15 content in the sample particulate nitrogen to enhance the precision of the mass spectrometry. The Michaelis–Menten kinetic expression then is used to calculate *in situ* uptake rates from the enhanced measured rates. This equation,

$$V = \frac{V_{\max} S}{k_t + S} , \tag{1}$$

has been found to describe, in many cases, the nitrate and ammonium uptake of natural populations of marine phytoplankton (MACISAAC and DUGDALE, 1969). The terms of the equation, which describes a rectangular hyperbola, are defined as follows:

V = velocity of uptake of substrate (in this study units of nitrogen taken up per unit time per unit PN-nitrogen, or time^{-1});

$V_{\max}$ = maximal velocity of uptake;

S = concentration of substrate or nutrient;

k_t = that substrate concentration at which $V = V_{\max}/2$.

The constant is designated k_t or ' transport constant ' to emphasize that a mathematical and not necessarily biochemical equivalence to Michaelis–Menten kinetics is involved here. Throughout this paper the term ' uptake ' refers to V, velocity of uptake, unless specifically designated otherwise.

The calculation of *in situ* uptake rates uses the enhanced measured rate and the nutrient concentration at which it was made as V and S, respectively. The values for k_t

were determined at several stations on the cruises, and for *Thompson* 26 are given in MACISAAC and DUGDALE (1969). The k_t measurements from *Thompson* 47 are discussed later in this paper, where the question is raised of interpreting the results of nutrient kinetic experiments in oligotrophic waters. A k_t of 0·1 μg-atoms/l. was used as a best approximation to calculate *in situ* uptake at stations from the latter cruise. This value of k_t may be an underestimate, the possible consequences of which are discussed later.

In waters with naturally saturating nutrient concentrations, it is not possible to measure k_t, but measurements in eutrophic waters with lower nutrient concentrations indicate a k_t of about 1·0 μg-atoms/l. can be assumed for both nitrate and ammonium (MACISAAC and DUGDALE, 1969). For example, four measurements of k_t for ammonium in coastal Peruvian waters gave values of 0·66 – 2·01, with a mean of 1·11 μg-atoms NH_4^+–N/l. For convenience, a k_t of 1·0 μg-atoms/l. was accepted for nitrate and ammonium uptake at enriched stations of *Thompson* 47 and for ammonium uptake on *Thompson* 36. No k_t for nitrate was needed to evaluate the *Thompson* 36 data, as the measured uptake rates were accepted as good approximations of *in situ* productivity rates and V_{max}. Surface nitrate concentrations at most stations there were 10–20 μg-atoms/l. and additional enrichment would not be expected to influence uptake rates (MACISAAC and DUGDALE, 1969).

From the measurements of V, S and k_t, V_{max} is calculated for the depth in question by rearranging equation (1):

$$V_{max} = \frac{V(k_t + S)}{S} \tag{2}$$

Once V_{max}, k_t and the ambient nitrate or ammonium concentration at depth are available, a V appropriate to the *in situ* nutrient concentration can be calculated with equation (1). Finally, the transport rate, ρ, (DUGDALE and GOERING, 1967), is calculated from:

$$\rho = V \cdot \mathrm{PN};\ \text{units for } \rho \text{ are } \mu\text{g-atoms N/l./da when PN is expressed as } \mu\text{g-atoms N/l. and } V \text{ as } \mathrm{da}^{-1}. \tag{3}$$

In a later section it will be shown that a single k_t appears to be applicable to all depths down to about the 10% light penetration depth, and this assumption was made in all calculations. In a strongly stratified system, this assumption might be questioned. Although a single k_t was applied to all calculations at any one station, V_{max} was calculated at each depth considered, as it would be influenced by variations in concentration of nitrogen-containing detritus in the different populations. DUGDALE and GOERING (1967) have described the manner in which detritus influences nitrogen-15 rate measurements by diluting the active phytoplankton nitrogen and hence the nitrogen-15/nitrogen-14 ratio and V. Detritus does not affect the k_t measurement, however, since k_t depends on a ratio of V and V_{max} which is unchanged by detrital dilution. The detrital effect likewise is cancelled in calculating ρ.

RESULTS AND DISCUSSION

Kinetics of light-limited nitrate and ammonium uptake

The results of some of the experiments investigating the response of nitrate and ammonium uptake to light intensity are shown in Fig. 2. This group of experiments

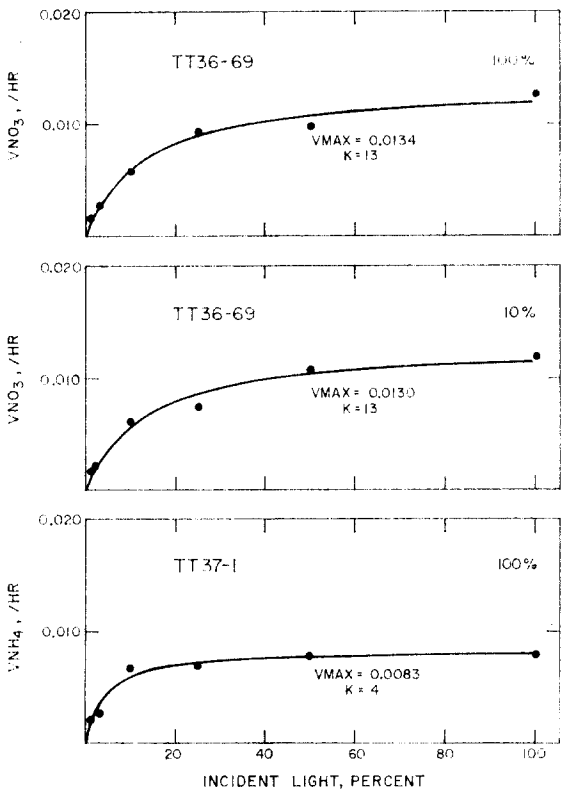

Fig. 2. Representative response curves for nitrate and ammonium uptake as a function of light intensity. The hyperbolae fitted to the data points are described by the Michaelis–Menten equation. The values of V_{max} are in terms of the nutrient used, and those designated K are light intensities in percent incident light (k_{LT}). The sample depths are indicated by the light intensity (% surface light) at the depths.

shows a hyperbola-shaped response to light intensity, as Bongers (1956) and Hattori (1962) have observed, similar to the response of photosynthetic rate to uninhibiting light that can be described by the Michaelis–Menten equation (Caperon, 1967). The hyperbolae fitted by a least squares analysis to the points in Fig. 2 also are described by the Michaelis expression. In these hyperbolae, the parameters V_{max} and k_t (designated k_{LT} for this purpose) describe quantitatively the relationship between light intensity and inorganic nitrogen uptake. The V_{max} values are measured and expressed in terms of nitrate or ammonium and are identical to nutrient V_{max} values. The values of k_{LT} however, designate a light intensity—that intensity permitting uptake of one-half V_{max} for the nitrogen compound used. Table 1 summarizes all the measurements made where the response of nitrate and ammonium uptake to light could be described by the Michaelis equation.

The data in Table 1 have been divided according to station location in oligotrophic or eutrophic waters. Eutrophic waters may be characterized as having shallow mixed layers, low transparencies, and easily detectable concentrations of nitrate, phosphate, and silicate. Oligotrophic waters conversely may be identified by deep mixed layers,

Table 1. Kinetic constants for light dependent nitrate and ammonium uptake when the dependency is described by the Michaelis–Menten equation. k_{LT} is the average light level during the experiment at which the uptake rate for nitrate or ammonium was $V_{max}/2$.

Cruise	*Sta.*	*Light intensity at sample depth* (% surface light)	*Nitrogen compound*	V_{max} (hr^{-1})	k_{LT} % Surface light	k_{LT} Langleys/min*	
TT26	13	25	NO_3–N	0·0060†	14·0	—	oligotrophic
TT36	19	100	NO_3–N	0·0020	4·4	0·013	
		10	NO_3–N	0·0015	1·0	0·004	
TT36	20	100	NO_3–N	0·0316	0·9	0·006	
	27	100	NO_3–N	0·0420	3·9	0·024	
		10	NO_3–N	0·0316	9·1	0·057	
	59	10	NO_3–N	0·0306	8·5	0·038	
	66	100	NO_3–N	0·0152	8·2	0·031	eutrophic
		10	NO_3–N	0·0177	13·3	0·051	
	69	100	NO_3–N	0·0134	12·7	0·025	
		10	NO_3–N	0·0130	12·9	0·026	
	70	100	NO_3–N	0·0109	1·3	0·004	
		10	NO_3–N	0·0107	0·9	0·002	
TT37	1	100	NH_4–N	0·0083	4·0	—	

*Apparent inconsistencies in the transformation of % light values to langleys/min between experiments at one station reflect differences in incubation periods.

†Experiment was incubated for 23 hr giving hourly value for V of 0·0030; value used in table approximates that expected in a shorter, daylight-only experiment.

high transparencies, and low or undetectable levels of the primary nutrients. In addition, inorganic nitrogen uptake at oligotrophic and eutrophic stations has been found to have, respectively, lower and higher values of V_{max} (MACISAAC and DUGDALE, 1969).

The data in Table 1 confirm the observation of MACISAAC and DUGDALE (1969) both in the ready distinction between the value of V_{max} characteristic of each water type and in the range of values occurring for each type. The values of k_{LT} in relative light intensities ranged from about 1–14% of the surface values encountered in both eutrophic and oligotrophic areas. When the values of k_{LT} are expressed in absolute terms (langleys min^{-1}) to take into account the differences between surface intensities at the stations, the spread is even greater. In most cases the differences between the kinetic characteristics of populations taken from 10 and 100% light-penetration depths in the Peru work (*Thompson* 36) are insignificant, probably a reflection of the basic similarity in species composition observed between the population pairs (BLASCO, 1971, and personal communication). The correlation between the values of V_{max} and k_{LT} is low, i.e., high values of V_{max} are found with both high and low values of k_{LT}.

Both nitrate and ammonium are known to be taken up at low rates in the dark,

with ammonium being taken up more readily (Dugdale and Goering, 1967), but dark uptake was measured in only a few of the experiments described here. Because dark uptake was measured so infrequently, it was ignored in fitting the hyperbolae in Fig. 2 and the calculations are based on zero uptake occurring at zero light. The consequences of not subtracting dark from light uptake are significant when uptake in the dark is greater than about 15% of uptake in full light (Fig. 3). Under such conditions, linear plots of the kinetic data (e.g. $1/S$ versus $1/V$) are distorted beyond usefulness unless dark uptake is subtracted.

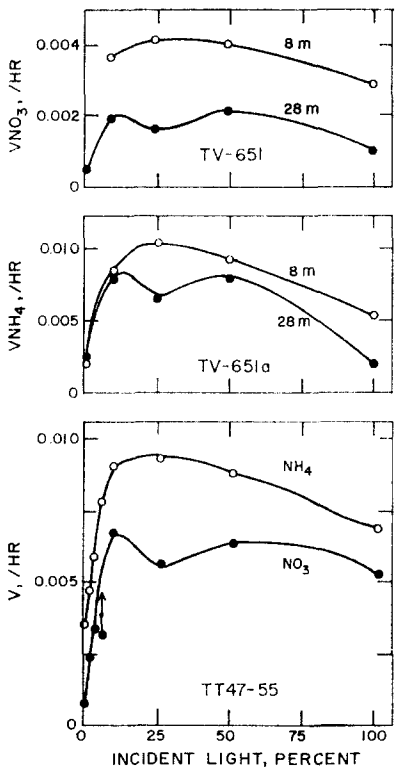

Fig. 3. Representative response curves for nitrate and ammonium uptake where a reduction in uptake rate occurred with the higher light intensities. The experiment from *Te Vega* (TV) utilized water from two depths indicated in the figures, the depths to which 50 and 10% of the surface light penetrated. The *Thompson* (TT) experiments were done with water from the 50% light-penetration depth; dark uptakes were measured in these two experiments and are plotted. The reduced uptake frequently observed at the 25% light intensity is thought to be the result of orientation of the screened bottles such that a lower light intensity actually was reaching the population (see Methods in text).

On several occasions the observed response of inorganic nitrogen uptake to light intensity could not be described by equation (1), the light intensities above 10 or 25% of surface light being associated with a reduction in uptake (Fig. 3). This type of response has been found only in oligotrophic regions. (However, the saturation response described above also occurs there). For purposes of comparison Table 2 is presented to show the highest uptake rate that was measured at each of these stations and the light intensity associated with half that rate.

Table 2. Interaction between light intensity and inorganic nitrogen uptake, not described by the Michaelis–Menten equation. The values for light levels at one-half the highest V achieved are averages during the experiment.

Cruise	Sta.	Light intensity at sample depth (% surface light)	Nitrogen compound	Highest V achieved (hr^{-1})	Light at one-half highest V achieved: % Surface light	Light at one-half highest V achieved: Langleys/min*
TV13	651	50	NO_3–N	0·0042	2·0	0·009
		10	NO_3–N	0·0022	5·0	0·024
	651A	50	NH_4–N	0·0150	5·0	0·025
		10	NH_4–N	0·0085	2·0	0·010
TT47	46A	100	NH_4–N	0·0075	3·5	0·023
		1	NH_4–N	0·0055	1·5	0·010
	53	50	NO_3–N	0·0015	2·5	0·008
		50	NH_4–N	0·0090	1·5	0·005
	55	50	NO_3–N	0·0070	4·0	0·020
		50	NH_4–N	0·0095	2·0	0·007

*Apparent inconsistencies in the transformation of % light values to langleys/min between experiments at one station reflect differences in incubation periods.

Where dark uptake and sufficient data points up to the 10 or 25% light intensity were measured in these experiments, values for k_{LT} and V_{max} can be calculated from a linear plot of this portion of the curve. However, subtracting the dark uptake results in a calculated V_{max} lower than the highest measured V, and the calculated value of k_{LT} is higher than the light value that relates to the measured V. For example, at Stas. 47-53 and 47-55, the calculated values for k_{LT} for ammonium were 3% and 4%, respectively. The light intensities associated with one-half the highest V measured were 2% in both cases. The calculated values of V_{max} were, respectively, 0·0051 and 0·0061 hr^{-1}; in both cases lower than the highest V's measured in the experiments (Table 2) by almost exactly the values of dark uptake, which were, respectively, 0·0042 and 0·0035 hr^{-1}.

The following equation,

$$V = V_D + V_{max}\left(\frac{S}{k_{LT} + S}\right) ,$$

where V_D is dark uptake and S is light intensity, describes uptake in these experiments over the hyperbolic part of the curve. The assumption is made that dark uptake is a constant at all light intensities, but it is interesting to consider that if the absolute value of dark uptake gradually decreased as light intensity increased beyond 10 or 25%, uptake would appear to be inhibited at the higher light intensities. For example, as the data for ammonium uptake at Sta. 47-55 are now plotted (Fig. 3), dark uptake is considered as included in the measurement at full light. If in fact, dark uptake was stopped under these conditions, the measured value of dark uptake should be added to the rate measured in full light to adjust the plot of the data correctly. In this example, the effect would be to cancel the apparent inhibition of uptake at full light. Obviously, there are many questions in the interpretation of these data and it appears

justified to present them in the simplest form possible, as in Table 2.

From Table 2, differences can be seen between the populations from two depths at a single station, with lower uptake rates being associated with the deeper populations; however these differences may reflect different concentrations of detritus. In single populations the uptake of ammonium occurred at a faster rate than for nitrate, on both an absolute basis and relative to light intensity (Stas. 47-53, 47-55).

Profiles of nitrogen uptake—eutrophic regions

Since the uptake of inorganic nitrogen reflects both light and nutrient conditions, the profiles of uptake measured in the marine euphotic zone may be analyzed in terms of the interacting influences of these variables. The emphasis in the following discussion is upon the identification and interpretation of basic patterns of uptake profiles, rather than upon their exact prediction. In general, such predictions require more data than are available for many of the stations.

Nitrate uptake. In the nitrate productivity measurements at Sta. 26-38 (Fig. 4) and many other eutrophic stations, a condition of *in situ* nitrate limitation in the upper euphotic zone and light limitation near the bottom of the zone is illustrated clearly. At Sta. 26-38, nitrate increased with depth, being found in concentrations of about 0·10 μg-atom/l. at the upper four sample depths and 0·39 μg-atom/l. in the remaining

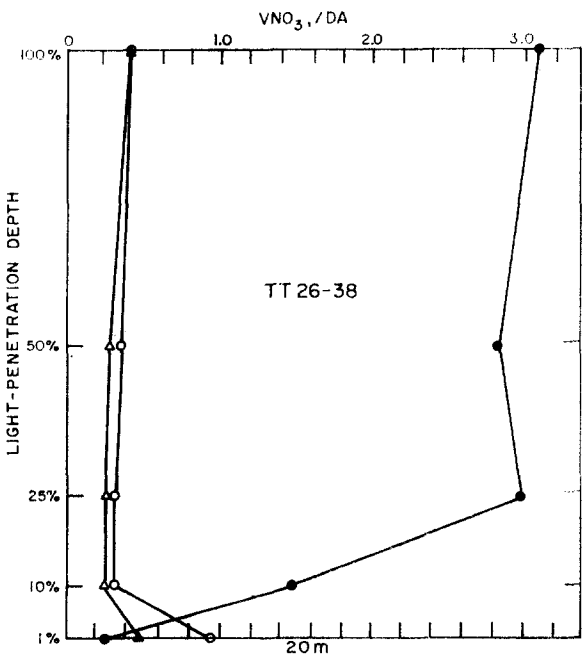

Fig. 4. Example of the agreement between calculated and measured values of approximate *in situ* rates of nitrate uptake in a euphotic zone profile. The ambient nitrate concentration at this station was 0·10 μg-atom/l. at the upper four depths and 0·39 μg-atoms/l. at the bottom depth. The solid circles show values of enhanced uptake rates measured with an enrichment of 5·31 μg-atoms NO_3^-–N/l. The open circles show values of *in situ* uptake rates calculated from the measured-enhanced rates; the open triangles are measured *in situ* rates, with an enrichment of only 0·05 μg-atom NO_3^-–N/l. 20 m was the 1% light-penetration depth.

and deepest sample. The particulate nitrogen concentrations were nearly constant at all depths (4·2–4·7 μg-atom PN-N/l.) implying the presence of a single well-mixed population.

The uptake of nitrate by the samples from the upper four depths at Sta. 26-38 was enhanced considerably by the addition of nitrate, a situation indicative of *in situ* nutrient limitation according to the theory advanced by DUGDALE (1967). *In situ* uptake rates computed from the enhanced rates by application of equations (1) and (2), using a $k_t = 1{\cdot}0$ measured at that station on surface water, compare closely with measured *in situ* rates. However, in the population from the 1% light-penetration depth, the calculated *in situ* rate was higher than that measured with either low or high nitrate enrichment and was obviously unrealistic. The uptake at this depth was limited by light, a variable not considered in the calculation.

The saturated uptake curve and the measured *in situ* uptake curve at Sta. 26-38 can be considered as examples of the approximate extremes of profiles of V for nitrate expected in eutrophic regions. The exact point of crossover between nutrient and light limitation will depend upon the nitrate concentration profile, the extinction coefficient of the water, and the surface radiation value. In the real ocean this crossover depth varies with the time of day.

Stas. 26-16, 36-66, 36-69 and 47-29 (Fig. 5, Table 3) are other straightforward examples of the occurrence of nitrate or light limitation in eutrophic waters. The profiles shown in Fig. 5 include *in situ* uptake rates, and where the experimental

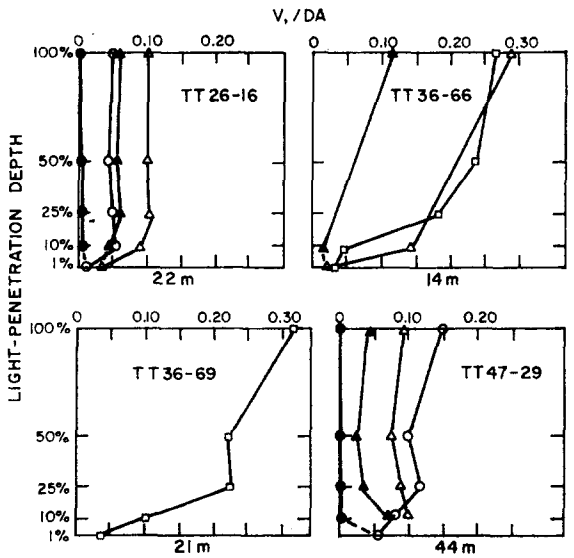

Fig. 5. Some representative euphotic-zone profiles of nitrate and ammonium uptake in eutrophic areas, showing measured enhanced, calculated *in situ*, and measured *in situ* uptake rates. The depths to which 1% of the surface light penetrated are given in meters. Table 3 gives data related to these figures. Key, for nitrate and ammonium uptake respectively: measured enhanced uptake, open circles and open triangles; calculated *in situ* uptake, solid circles and solid triangles; measured *in situ* uptake, nitrate only, open squares.

Table 3. Inorganic and particulate nitrogen concentrations at the sampling depths at which nitrogen productivity was measured for the stations considered in Fig. 5.

Sta.	TT26-16			TT36-66			TT36-69			TT47-29		
μg-atoms/l.	NO_3	NH_4	PN	NO_3	NH_4	PN	NO_3	NH_4	PN	NO_3	NH_4	PN
Light intensity at sample depth (% surface light)												
100	0·02*	0·31	5·19	11·93	0·68	12·34	17·93	0·53	3·92	0·00	0·06	1·38
50	0·02	0·28	5·70	12·28	0·45	11·76	18·80	0·40	4·89	0·00	0·04	1·48
25	0·02	0·32	4·73	13·00	0·10	9·54	19·03	0·45	5·10	0·00	0·04	1·32
10	0·04	0·22	5·13	13·11	0·10	13·24	18·97	0·33	4·95	0·00	0·14	1·19
1	4·94	0·77	2·30	20·20	0·16	6·63	22·10	0·43	3·35	0·02	—	0·88

*Estimate.

technique necessitated the calculation of these rates, the values of the measured enhanced uptake from which the *in situ* rates are derived are shown as well. Because the enhanced rates usually were measured with nutrient enrichments near saturation concentrations, they approximate the values for V_{max} of the populations and contribute information useful in describing nitrogen uptake. Uptake at the 1% light-penetration depth is assumed in all cases to be light-limited as at Sta. 26-38 (Fig. 4), and not affected by the experimental nutrient concentration. Therefore no calculated values of uptake are made or required for the deepest populations.

The nitrate uptake profile of Sta. 47-29 can be described exactly as that of Sta. 26-38; ambient nitrate was undetectable at the upper four sample depths and, by equation (1), the resultant calculated *in situ* uptake must be zero as well. The type of uptake profile measured at Stas. 36-66 and 36-69 was observed frequently at stations having saturating concentrations of nitrate throughout the euphotic zone. There are obvious similarities between these two profiles measured at low ^{15}N enrichments and those enhanced uptake profiles at Stas. 26-38 and 47-29, and the shapes of all four apparently were determined by light intensity. The possibility of some other kind of limitation being in effect at these stations was unlikely, as the water was highly fertile in all measured parameters and in other experiments in such waters the addition of other nutrients did not stimulate nitrate uptake (MACISAAC and DUGDALE, 1969).

The shapes of nitrate uptake profiles measured under either experimental or natural conditions of saturating nitrate concentration often are roughly similar in shape to the light–nitrate response hyperbolae. For example, at Sta. 26-38 (Fig. 4), a k_{LT} for nitrate of 10% full light intensity can be estimated from the profile of enhanced nitrate uptake, agreeing closely with many of the values in Table 1. At Sta. 36-69 (Fig. 5), a V_{max} of about 0·013 hr^{-1} (0·312 da^{-1}) and a k_{LT} for nitrate of approximately 15% full light intensity can be estimated from the uptake profile, and the directly measured nitrate–light responses of the surface and 10% light-penetration depth populations at the same station (Fig. 2, Table 1) gave essentially the same results with both having a V_{max} of 0·013 hr^{-1} and a k_{LT} for nitrate of about 13% full light. The agreement between the two types of measurements further emphasizes the role of light in determining nitrate uptake at these eutrophic stations. But such agreement reflects the special condition of an unstratified euphotic zone with a common

population that takes up nitrate with a response determined primarily by light intensity and nitrate concentration.

Ammonium uptake. The data for ammonium uptake are considerably fewer, but generally light and nutrient limitation may be distinguished in the eutrophic uptake profiles for ammonium, much as for nitrate. Ammonium often occurs in the sea at concentrations below k_t [0·1–1·0 μg-atom/l. (MACISAAC and DUGDALE, 1969)] and the data in Fig. 5 and Table 3 suggest by comparison of the calculated *in situ* and measured enhanced uptake rates, the frequent occurrence of *in situ* ammonium limitation through the 10% light-penetration depths (Stas. 26-16, 36-66). Station 26-16 shows light limitation setting in below the 10% light-penetration depth. Light limitation of ammonium uptake appears to occur deeper in the euphotic zone than does limitation of nitrate uptake, an observation in agreement with the few pairs of nitrate and ammonium light-response curves measured, where the k_{LT} for nitrate was usually on the order of twice that of k_{LT} for ammonium (Table 2).

Effect of ammonium on nitrate uptake. Ammonium concentration also influences nitrate uptake in eutrophic regions. When ammonium is found in concentrations of about 0·5 μg-atoms NH_4^+–N/l. or more, nitrate uptake in inhibited. Two series of stations (Fig. 1) were made on *Thompson* 47 during a survey in a highly productive region of the Saronikos Gulf near Athens (DUGDALE, KELLEY and BECACOS-KONTOS, 1970). The stations progressed away from a sewage outfall and ammonium concentrations went from almost 2 to near 0 μg-atoms NH_4^+–N/l. in each series. Nitrate and ammonium uptake rates were measured with saturating nitrogen-15 enrichments at each station. The ratios of nitrate to ammonium uptake were related similarly to *in situ* ammonium concentrations in both series and reflected the inhibitory effect of ammonium on nitrate uptake (Fig. 6). Inhibition of nitrate uptake by ammonium has been observed in cultures (SYRETT and MORRIS, 1963; EPPLEY, COATSWORTH and SOLORZANO, 1969), in a natural marine phytoplankton population grown in a shipboard incubator (H. L. Conway, personal communication) and in natural freshwater

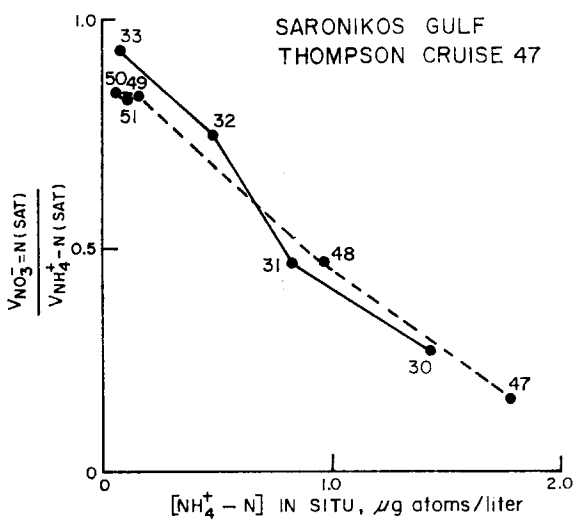

Fig. 6. The inhibitory effect of ammonium on nitrate uptake. Station numbers are indicated. Samples were taken from the 50% light-penetration depth.

populations (Procházková, Blažka and Králová, 1970). The computer model predicting the uptake of nitrate in the eutrophic waters of coastal Peru (Dugdale and MacIsaac, 1971) includes a term describing this inhibitory effect.

Profiles of nitrogen uptake—oligotrophic regions

Nitrate uptake. The low mixing rates characteristic of the oligotrophic open ocean effectively isolate much of the euphotic zone and its phytoplankton from the deeper, nutrient-rich water. As a result of these conditions, many of the oligotrophic stations sampled on the several cruises showed a vertical stratification of response to nitrate, apparently imposed by the variable capability of the populations to respond to nitrate. In most cases, with the exception of some of the deeper samples, the phytoplankton at stations with very low or undetectable concentrations of ambient nitrate in the upper depths barely responded to added nitrate. The measured enhanced and *in situ* nitrate uptake profiles for Stas. 26-5 and 26-18 (Fig. 7) show such sluggish nitrate uptake. Station 26-5 had almost no ambient nitrate in the euphotic zone (Table 4) and thus no *in situ* uptake, but also the populations showed only slight response to the nitrate

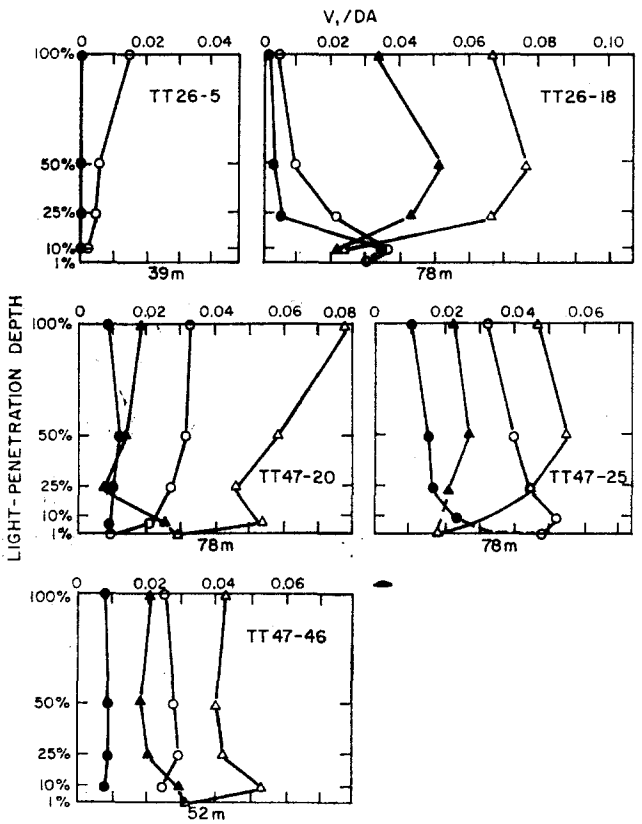

Fig. 7. Some representative euphotic-zone profiles of nitrate and ammonium uptake in oligotrophic areas, showing measured enhanced and calculated *in situ* uptake rates. The depths of the deepest samples are given in meters. Table 4 gives data related to these figures. Key, for nitrate and ammonium uptake, respectively: measured enhanced uptake, open circles and open triangles; calculated *in situ* uptake, solid circles and solid triangles.

Table 4. Inorganic and particulate nitrogen concentrations at the sampling depths at which nitrogen productivity was measured for the stations considered in Fig. 7.

Sta.	TT26-5			TT26-18			TT47-20			TT47-25			TT47-46		
μg-atoms/l.	NO_3	NH_4	PN	NO_3	NH_4	PN	NO_3	NH_4	PN	NO_3	NH_4	PN	NO_3	NH_4	PN
Light intensity at sample depth (% surface light)															
100	0·00	—	0·56	0·04	0·08	0·29	0·04	0·03	0·29	0·05	0·06	0·75	0·05	0·06	0·27
50	0·01	—	0·43	0·04	0·08	0·39	0·07	0·03	0·39	0·06	0·06	0·45	0·05	0·06	0·34
25	0·00	—	0·35	0·04	0·14	0·80	0·06	0·02	0·66	0·06	0·06	0·50	0·05	0·06	0·13
10	0·02	—	0·63	3·45	0·25	0·96	0·08	0·09	0·83	0·09	—	0·23	0·05	0·08	0·57
1	0·50*	—	—	32·17	—	0·37	0·11	0·28	0·80	0·07	0·02	0·13	0·05	0·04	0·49

* At 70 m.

added in the experiment; Sta. 26-18 had traces of nitrate in the upper euphotic zone (Table 4) and significant increases beginning with the 10% light-penetration depth, where nitrate uptake rate reached a maximum for the station. Thus, shallower phytoplankton populations which cannot be expected normally to encounter more than traces of nitrate seem unable to respond within 24 hr to nitrate enrichment. On the other hand, proximity to or occurrence in nitrate-rich water appears to condition the deeper populations such that the maximum uptake rate often is attributable to the population at the 10% light-penetration depth. Below this depth, light limitation apparently restricts further increases in uptake rate. Goering, Wallen and Nauman (1970) in their study of nitrogen uptake in the discontinuity layer of the eastern subtropical Pacific Ocean, also found that maximal uptake occurs deep in the euphotic zone. The inability of populations not usually exposed to nitrate to take up the compound immediately (within 24 hr) upon exposure to it probably reflects the absence of the enzyme nitrate reductase. Recent studies of the enzyme in natural and cultured marine phytoplankton show that its occurrence is positively related to ambient nitrate concentrations, and its induction in a population upon the introduction of nitrate may be related to several environmental parameters (nitrate and ammonium concentrations, light, time of day) such that in a 24-hr experiment nitrate uptake may not be significantly stimulated (Eppley, Coatsworth and Solórzano, 1969; Eppley, Packard and MacIsaac, 1970; Packard, Blasco, MacIsaac and Dugdale, 1971).

The Mediterranean oligotrophic stations observed in the Petalion Gulf (Fig. 1) on *Thompson* cruise 47 were not underlain with nutrient-rich water, as a consequence of the extremely low nutrient concentration in the eastern Mediterranean and the near complete mixing of the water column that occurs in that region in late winter. About one-half of the profiles of *in situ* and enhanced uptake for nitrate determined under these conditions, nonetheless, showed significantly increased uptake with depth as at Sta. 47-25 (Fig. 7), and the other half did not, as at Sta. 47-20, and 47-46 (Fig. 7). It appears, however, that in addition to the complication of variable detritus levels, the shapes of these curves cannot be explained easily in terms of nutrient and light kinetics as in the data discussed above. For example, the light-response curves measured in the Mediterranean and at some oligotrophic Pacific Ocean stations attain a maximal V for nitrate uptake at 10–25% of full light intensity, with more intense light failing to further stimulate uptake and usually being associated with decreases in uptake rate (Fig. 3). The occurrence of light inhibition of photosynthesis is well-known and such inhibition quite naturally suggests itself as an explanation of the failure of nitrate uptake in the sea to respond to increasing natural light intensities under some conditions.

Other experiments with unresponsive oligotrophic populations suggest that their nitrate uptake may at times be ' other-limited '. When the uptake of a particular nutrient is held below V_{max} for that nutrient by a limiting concentration of a second nutrient, Dugdale (1967) has described the condition as other-limited. At Sta. 47-23, in an experiment testing the response of a population to five concentrations of nitrate, a set of duplicate samples was prepared and additionally enriched with 0·56 μg-atoms PO_4^{3-}–P/l. over the ambient concentration of 0·04 μg-atoms/l. The phosphate-enriched samples all took up nitrate at faster rates (0·034–0·059 da^{-1}) than the controls without added phosphate (0·028–0·036 da^{-1}). The enhancement of nitrate uptake by enrichment with other nutrients has not been observed before this (MacIsaac and

DUGDALE, 1969) but previous experiments had not been attempted in such infertile water. It must be emphasized here that this condition is one of potential other-limitation, since it applies to the nitrate uptake of these populations only at rates somewhat above *in situ* uptake. The *in situ* rates of nitrate uptake appear to be limited by the ambient nitrate concentrations, a conclusion based on the initial positive response of uptake rate to nitrate enrichment seen in Fig. 8a (DUGDALE, 1967; MACISAAC and DUGDALE, 1969).

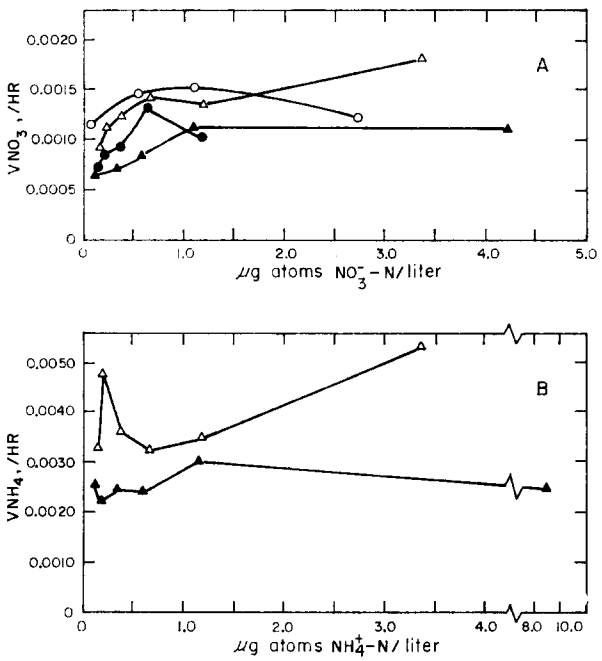

Fig. 8. The response of some Mediterranean phytoplankton populations to experimental additions of nitrate (A) and ammonium (B) concentrations. The symbols designate stations on *Thompson* cruise 47: 13, solid circle; 23, open circle; 46A, open triangle; 53, solid triangle. All samples were taken from the 50% light-penetration depth.

With the exception of the light-limited populations at the 1% light-penetration depth, the variations in nitrate uptake for phytoplankton in the eastern Mediterranean are not described simply by relationships between light and nitrate. The nitrate uptake of the populations actually is limited by the low nitrate concentrations but not equally or systematically so, and it may be assumed that the generally inadequate supply of most nutrients in the region imposes considerable physiological variability in the phytoplankton in both time and space. The uneven distribution of the populations reflected in the distribution of PN (Table 4), perhaps a result of growth rate and grazing variations, adds to the unpredictable nature of nitrate productivity in the area.

Ammonium uptake. Ammonium productivity is often more than double nitrate productivity in oligotrophic regions, if only because ammonium often occurs there in higher concentrations than does nitrate. Light intensity and ammonium concentration appear to determine the rates of both *in situ* and enhanced uptake in most cases

(Fig. 7, Table 4, Stas. 26-18 and 47-25). In the Mediterranean, several stations did show some deep stimulation of ammonium uptake, as at Sta. 47-46 (Fig. 7), and these occasions may reflect differences in physiological conditions of the populations. Ammonium uptake in the Mediterranean, except for the deep light-limited populations, is limited by the low ambient concentrations of the nutrient, but as in the case of nitrate, potential other-limitation is suggested by the weak response of populations to enrichments in ammonium (Fig. 8b). Silicate was found to stimulate the rate of ammonium uptake at two otherwise fertile stations in the Saronikos Gulf (Stas. 47-30, and 47-31). The ambient silicate concentrations in the samples from the two stations were 1·64 and 1·52 μg-atoms Si/l., and the rates of ammonium uptake were 0·089 and 0·087 da^{-1}. The ammonium uptake rates measured after silicate enrichments of 0·1–4·4 μg-atoms Si/l. were 0·166–0·190 and 0·159–0·168 da^{-1}, respectively. Because *in situ* ammonium concentrations were high at these two stations (1·44 and 0·84 μg-atoms NH_4^+–N/l.), it is possible that natural silicate concentration limits the *in situ* nitrogen productivity at these stations.

As in the case of nitrate uptake in certain oligotrophic regions, ammonium uptake shows irregularities that are not explained at present. In addition to light intensity and ammonium concentration other characteristics of these impoverished waters appear to influence uptake.

Relative rates of nitrogen productivity in the sea

The differences between inorganic nitrogen uptake in temperate productive seas and tropical unproductive waters described by Dugdale and Goering (1967) are confirmed further by the data (Table 5) collected on the cruises discussed in this paper. Dugdale and Goering (1967) reported that both the values of V (hr^{-1}) for nitrate and ammonium uptake and of the ratio of nitrate uptake to nitrate plus ammonium uptake were higher in productive seas. The data reported in Table 5 (da^{-1}) have been grouped by cruise and regional productivity (eutrophic or oligotrophic). Comparing the extremes of productivity encountered, it is apparent that the integrated values of ρ in the euphotic zone, the maximal values of ρ, and V_{max} all decrease in the oligotrophic regions. The decreases are more significant for nitrate uptake than for ammonium, which in part reflects the much greater range and higher concentrations of available nitrate, but also reflects the readiness of phytoplankton to take up ammonium rather than nitrate. The relative importance of ammonium in total nitrogen productivity doubles in the poorest waters, agreeing with the suggestion of Thomas (1966) and Dugdale and Goering (1967) that ammonium is an important nitrogen source in tropical unproductive waters. The table also shows that the regional differences in integrated ρ are greater than population sizes (PN) alone would generate, and differences in the physiological characteristics of the populations as exemplified in the regional variation in V_{max} are very important.

The true values of V_{max} and k_t admittedly are questionable, especially in oligotrophic waters. Figure 8 shows all the results of measurements of nutrient k_t and V_{max} made on *Thompson* 47. Little can be done with the ammonium results, and linear plots of the nitrate data are difficult to interpret, but suggest that k_t for nitrate lies between much less than 0·10 and 0·30 μg-atoms/l., and V_{max} is 0·0014–0·0020 hr^{-1}. Other-limitation has been mentioned in this paper, and should it occur (i.e. should the uptake of nitrogen be held below V_{max} by the limiting concentration of a second nutrient), it would be difficult to recognize it where uptake rates are as low as these

Table 5. A summary of means of inorganic nitrogen productivity measurements made in the euphotic zone on Thompson *cruises* 26, 36, *and* 47; *including data of related parameters and carbon uptake. Numbers in parentheses indicate number of samples.*

Cruise	Classification	NO_3–N *productivity*			*Nitrogen/unit area* (mg-atoms/m^2)			NH_4–N *productivity*							
		$\Sigma\rho$ (mg-atoms m^2/da)	Max ρ* (μg-atoms/ liter-da)	V_{max}† (da^{-1})	NO_3–N	PN–N	NH_4–N	$\Sigma\rho$ (mg-atoms m^2/da)	*Max* ρ* (μg-atoms/ liter-da)	V_{max}† (da^{-1})	$\Sigma\rho NO_3/(\Sigma\rho NO_3+\Sigma\rho NH_4)$	$\Sigma^{14}C$‡ (mg-at/ m^2/da)	$\Sigma^{14}C/\Sigma\rho N$§	$\Sigma^{14}C/\Sigma\rho N$ *range*	*Mean 1% light penetration depth*, (m)
TT36	Eutrophic	20·85 (27)	1·844 (27)	0·2878 (27)	359·8 (27)	114·91 (27)	11·87 (6)	6·49 (5)	0·662 (6)	0·2066 (6)	0·68 (5)	438·89 (27)	11·7 (6)	6·4 – 22·4	22
TT26	Eutrophic	5·947 (6)	0·395 (6)	0·2612 (6)	193·84 (6)	81·95 (9)	22·74 (8)	5·315 (8)	0·229 (8)	0·14	0·47 (5)	377·04 (5)	75·7 (4)	14·0 – 178·0	35
TT26	Oligotrophic	1·136 (4)	0·031 (4)	0·09	388·75 (4)	48·82 (4)	14·48 (2)	0·969 (2)	0·030 (2)	0·12	0·57 (2)	57·67 (1)	27·7 (1)	—	79
TT47	Oligotrophic enriched by sewage	0·721 (3)	0·055 (3)	0·1366 (3)	4·60 (3)	51·56 (3)	16·30 (3)	2·777 (3)	0·170 (3)	0·2021 (3)	0·20 (3)	67·24 (3)	20·8 (1)	—	39
TT47	Oligotrophic	0·338 (7)	0·007 (8)	0·0350 (8)	5·03 (7)	37·04 (7)	5·67 (7)	0·988 (7)	0·026 (8)	0·0874 (8)	0·30 (7)	16·42 (6)	15·7 (8)	7·8 – 46·3	76
TT47 Oligotrophic/ TT36 Eutrophic × 100		1·2%	0·4%	1·2%	1·4%	32·3%	47·8%	15·4%	3·9%	42·2%	44·1%	3·7%			

*Max ρ designates the highest value of *in situ* ρ at each station.
†V_{max} designates the highest value of calculated or measured V_{max} at each station. Values with only two significant figures are estimated.
‡Total carbon uptake as measured with ^{14}C.
§Calculated only from those stations having carbon, nitrate, and ammonium uptake measurements.

(MacIsaac and Dugdale, 1969). Until better measurements of V_{max} for nitrogen can be determined in oligotrophic regions, it seems most straightforward to accept the apparent values and their associated values of k_t. In calculating V_{max} it can be seen from equation (2) that small errors in k_t are relatively unimportant when k_t is much smaller than S. For that reason, approximations of k_t have been used in this paper. If a resulting underestimated V_{max} were used where *in situ* uptake is calculated (as for the Mediterranean data) the uptake would be overestimated, but from Table 5 it is seen that even then the uptake rates are extremely low.

The importance of nutrient distribution within the euphotic zone to productivity is suggested by the data in Table 5. The total nitrate available in the euphotic zone was greater in the oligotrophic region of *Thompson* 26 than in the eutrophic region off Peru studied on *Thompson* 36. In Peru, however, the waters were recently upwelled, bringing high nitrate concentrations to the illuminated surface, while the nutrient was concentrated towards the bottom of the euphotic zone on *Thompson* 26.

Carbon and nitrogen uptake in the sea

Both total carbon and total inorganic nitrogen productivity differ by about the same percentage between eutrophic Peruvian waters (*Thompson* 36) and the oligotrophic eastern Mediterranean (*Thompson* 47), and the ratios of carbon to nitrogen uptake are similar for the two regions. But in Table 5 it is seen that the relation between the uptake of these two elements is not constant in all waters and often does not agree with the ratios of oxidizable carbon to nitrogen that have been measured on species in pure culture. Parsons, Stephens and Strickland (1961) reported composition ratios of 4–9, and Thomas (1964) observed an increase in the ratio from 5·4 to 16·8 in pure cultures of *Dunaliella primolecta* as the medium became increasingly nitrogen deficient; and Hobson and Pariser (1971) found cultures of *Thalassiosira fluviatilis* and *Cyclotella nana* grown without nitrate to have higher C/N composition ratios (means of 23 and 9, respectively) than cells grown with nitrate (means of 5 and 4, respectively). The higher uptake ratios suggest excess photosynthesis and/or high rate of turnover for carbon. The highest ratios were found at certain of the eutrophic stations sampled on *Thompson* 26. The populations at these stations were healthy and able to grow on nitrate, but the ambient nitrate concentrations were far too low to sustain V_{max} and the total nitrogen taken up was quite low. For example, at Sta. 26-16, a dense bloom (5 μg-atoms PN–N/l.) of phytoplankton was found in water with less than 0·1 μg-atoms NO_3^-–N/l. through the 10% light-penetration depth (Table 3). The calculated *in situ* uptake of nitrate naturally was quite low (Fig. 9), but enriching the sample with 0·5 μg-atoms NO_3^-–N/l. stimulated uptake significantly (Fig. 9), suggesting that the population recently had been exposed to nitrate. Station 26-16 was located in an area found to be extremely patchy in physical and biological parameters, and it is likely that the bloom had developed in an isolated patch of nutrient-rich water and consumed the nitrate itself. Total nitrate uptake based on calculated maximal uptake rates assuming an unlimited supply of nitrate, are very much higher than the rates possible at the measured ambient nutrient concentrations. When the maximal rates of ammonium uptake also are calculated (Fig. 9), it is possible to compute a new ratio of total carbon to total nitrogen uptake. Using the *in situ* uptakes the ratio is about 86:1, but the ratio based on the apparent maximal rates of uptake is close to

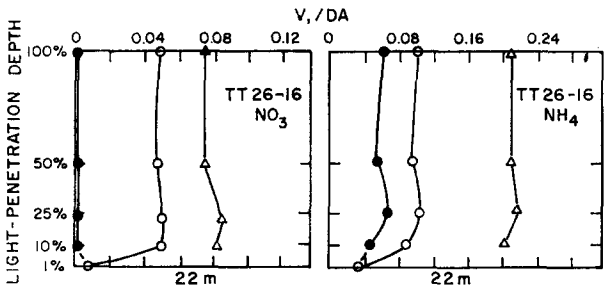

Fig. 9. Measured enhanced uptake rates for nitrate and ammonium uptake and the *in situ* and V_{max} rates calculated from them. The 1% light-penetration depth is given in meters. Open circles, measured enhanced uptake; solid circles, calculated *in situ* uptake; open triangles, calculated V_{max} uptake.

17:1. The lower ratios appear in nature to be associated with conditions approximating steady-state, either very rich (*Thompson* 36) or very poor (*Thompson* 47).

In short-term experiments (6–24 hr), there is no detectable effect of inorganic nitrogen enrichment on photosynthetic rate, with the possible exception of some of the eastern Mediterranean phytoplankton populations (Table 6). The independence of

Table 6. Effect on photosynthetic rate (as measured by 14C-uptake) of inorganic nitrogen enrichment in nitrogen-poor water, expressed in percent of maximum count.

Sample	*Maximum* (cpm)	N *enrichment* (μg-atoms N liter^{-1}) 0·00	0·05	0·10	0·20	0·25	0·50	5·00	
N-free chemostat water	1195	72	—	80	98	—	100	76	Nitrate
TT47-53	122	—	100	75	—	66	—	—	
TT47-46A	280	100	65	79	—	84	—	—	Ammonium
TT47-53	112	—	65	75	—	100	—	—	
TT47-55	158	48	65	100	—	52	—	56	
Mean (Sample size)		73 (3)	74 (4)	82 (5)	98 (1)	76 (4)	100 (1)	66 (2)	

carbon uptake response from nitrogen concentration as shown both by the wide range of carbon to nitrogen uptake ratios and the absence of carbon uptake response to nitrate and ammonium enrichment, presents a problem in the use of carbon-14 measurements to analyze primary production qualitatively, For example, DUGDALE and GOERING (1970) and RYTHER, MENZEL, HULBURT, LORENZEN and CORWIN (1970) worked on the same bloom of phytoplankton on Peru but reached different conclusions as to the existence of nutrient limitation as the bloom aged. The former found evidence of limitation in the pattern of inorganic nitrogen uptake, but monitoring carbon uptake, the latter determined there was no nutrient limitation.

Because the ratio of carbon to nitrogen uptake is lowest when V_{max} rates of

nitrogen uptake are considered, it may be suggested that instantaneous maximal inorganic nitrogen uptake is limited ultimately by photosynthetic rate, or perhaps more generally, by the physiological state of the cell as shown by photosynthetic rate. The information relating photosynthesis and nitrogen uptake is far from complete, but as a starting point the energetics of both processes appear related intimately and independently to light intensity, and secondarily, the maximum rate of uptake under conditions of saturating nitrogen nutrient is set by photosynthetic rate.

SUMMARY

Profiles of nitrate and ammonium uptake with depth, obtained by the nitrogen-15 technique on a number of cruises to different regions, can be understood as the primary result of the interaction between light intensity and concentration of nitrogen. The relationship between light or limiting nutrient is often described adequately by the Michaelis–Menten equation.

In eutrophic regions at high ambient nutrient concentration the profile of nitrate uptake may be controlled by light. As the nitrate concentration falls, nitrate uptake in the upper part of the euphotic zone becomes nitrate limited, providing other nutrients are in excess, while in the lower part, nitrate uptake is limited by light. Although the crossover point is determined primarily by the nitrate concentration profile, it often occurs where light intensity is about 10% of the surface value. The uptake of ammonium can be predicted in the same manner. However, the concentration of ammonium seldom approaches near-saturation levels and as a consequence, the ammonium uptake in the upper euphotic zone is nearly always ammonium limited. Ammonium also affects the uptake of nitrate, apparently acting to reduce the maximum uptake rate for nitrate. The inverse relationship has been quantified for several regions at specific times. The effect is noted in vertical profiles of nitrate uptake in the upper euphotic zone as distinct irregularities correlated with abrupt changes in the concentration of ammonium.

The uptake of nitrate and ammonium in oligotrophic regions appear to be controlled by the same processes with some additional complications. For example, nitrate uptake is usually sluggish in the upper euphotic zone, reflecting lack of exposure to significant concentrations of that species of nitrogen but there is increased response near the bottom of the euphotic zone where small quantities of nitrate enter from below. Ammonium uptake is more similar to that observed in eutrophic regions. However, both nitrate and ammonium uptake often show evidence of control by some other factor, apparent in the small responses to increased nutrient concentration and by reduced uptake rates at the higher light concentrations.

A comparison between oligotrophic and eutrophic regions of the rates of uptake of ammonium and nitrate integrated through the euphotic water column shows that ammonium is by far the more important of the two sources in oligotrophic waters, while in eutrophic waters less than half the nitrogen taken up is ammonium.

The ratios of carbon to nitrogen taken up throughout the euphotic zone are shown to vary widely, apparently as the result of loose coupling between photosynthesis and nutrient uptake. While the maximum level of nutrient uptake appears to be set by the current rate of photosynthesis, the instantaneous rate of nutrient uptake may be reduced independently by limiting concentrations of nutrient. Variations in nutrient concentration do not appear to affect photosynthesis in less than 24 hours.

The measurements and discussion included here should be recognized as only a beginning in understanding nitrogen productivity in the sea. At this point, the ability both to do the experiments and to interpret the results is marginal. Possible refinements of the experimental approach include temperature and light control. On a few occasions, however, G. Slawyk (personal communication) has compared the uptake measured in true *in situ* experiments with the results of simulated *in situ* uptake and has not been able to see any differences. But using natural populations and the nitrogen-15 method, small differences in uptake rates may be obscured. Some of the subtleties of nitrogen uptake by phytoplankton no doubt will be seen first or only in the laboratory.

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