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R. C. Dugdale

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NUTRIENT LIMITATION IN THE SEA: DYNAMICS, IDENTIFICATION, AND SIGNIFICANCE¹

R. C. Dugdale²

Institute of Marine Science, University of Alaska, College

ABSTRACT

A mathematical model has been constructed to provide a theoretical framework for the investigation and discussion of nutrient limitation in the sea. The euphotic zone is divided into nutrient-limited and light-limited regions. For simplicity, the regeneration term is ignored, and a steady state is assumed. The uptake of major nutrients is assumed to follow the Michaelis-Menton expression, and some data indicate that the assumption is probably correct. Also assuming a dominant phytoplankton population, with characteristic Michaelis-Menton kinetic parameters, it is demonstrated that the size of the population, fractional growth rate, the rate of production, and the concentration of limiting nutrient are determined by the sum of the fractional loss rates for the phytoplankton. The role of micronutrient components of enzymes is developed theoretically using the effect of molybdenum on a nitrate-limited system as an example.

For the sea, the significance of nutrient limitation theory is primarily in the study of phytoplankton competition and succession. Applications to lakes are discussed, and it appears that the effects of micronutrient deficiencies are more likely to be observed there than in the sea.

INTRODUCTION

The role of nutrients in limiting primary production in the sea is widely acknowledged. A nutrient term was incorporated into the productivity models of Riley (1963a) and Steele (1962), while Harvey (1963) wrote of threshold levels of a limiting nutrient. However, there has been no serious attempt to develop a model for the dynamics of nutrient-limited productivity in the sea. As a result, there is confusion regarding the design of adequate experiments and the interpretation of the results. The purpose of this paper is to present theoretical considerations based on one possible model for nutrient limitation. Virtually no data are included, partly because very little relevant data exist, but also for another more important reason: my conviction that biological oceanography suffers from a lack of theoretical work conducted

on a "best guess" basis in advance of at-sea or laboratory experiments.

Thus, this paper is an attempt to elaborate a framework for understanding the processes of growth and production under nutrient limitation sufficiently well to allow the intelligent design of experiments. Therefore, no attempt is made to predict standing crops or productivity in particular regions of the sea as Riley, Steele, and others have done with much success.

In an attempt to reach a larger audience, no mathematics more complicated than elementary algebra have been employed. This procedure lacks rigor in the derivations, but does not affect steady-state solutions for the equations. Another major simplification has been made by lumping all losses from the phytoplankton population into a single loss rate. By doing so, the nature of stability and restoring reactions becomes easier to understand.

THEORY

Primary nutrients

In subtropical and tropical regions, a thermocline at approximately the same depth as the bottom of the euphotic zone restricts the movement of nutrients from

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²Present address: Department of Oceanography, University of Washington, Seattle 98105.

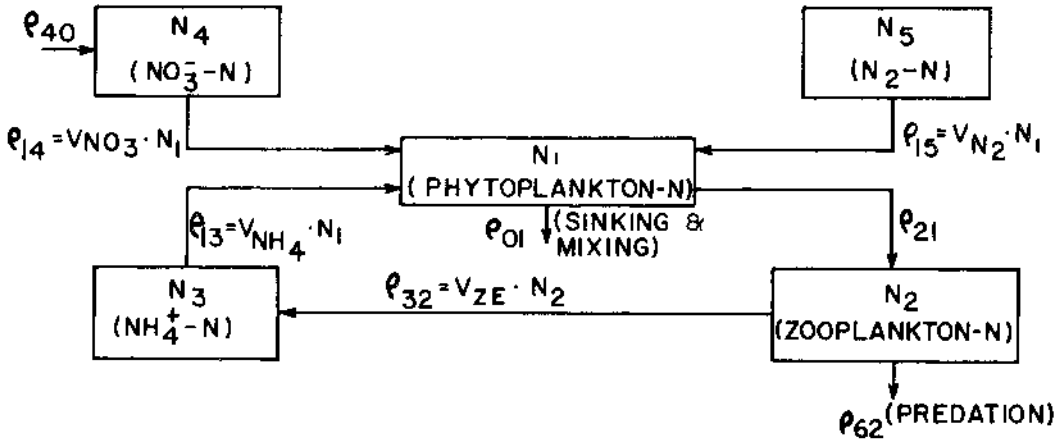


FIG. 1. Flow of nitrogen in the euphotic zone.

the rich layers below the thermocline upward to replace those used by the phytoplankton. A gradient in nutrient concentration is thus developed with sign opposite to that of light. Making the initial assumption that, at low concentrations, some positive correlation exists between phytoplankton productivity and the concentration of a limiting nutrient, two regions can be defined: 1) a lower euphotic region where light is less available than nutrients and is, therefore, the limiting factor, and 2) an upper euphotic region where adequate light is available but where nutrient concentration has been sufficiently reduced to become the factor limiting growth. These will be referred to as the light-limited and the nutrient-limited regions. Later, some important differences will be pointed out.

The productivity models of Riley (1963a, 1965) and Steele (1962) include terms for the effect of nutrients, and both have been remarkably successful in predicting populations and productivity for particular regions of the sea. These models have been constructed using carbon as a base, and much of the information regarding nutrient limitation has been obscured. There are significant advantages in constructing a model for nutrient limitation based on the flow of the limiting nutrient and this is the approach used here.

Dugdale and Goering (1967) proposed the measurement of primary production in the sea by measuring the flow of nitrogen using the stable isotope ¹⁵N as a tracer. Their diagram for the flow of nitrogen in the euphotic zone (Fig. 1) designates transport rates by ρ 's with subscripts indicating the direction of flow from one compartment to another, after the terminology of Sheppard (1962). For example, ρ_{14} is the rate of nitrogen transport [weight or atoms of N (unit time)⁻¹ (unit volume)⁻¹] into compartment 1 from compartment 4, in this case the rate of nitrate uptake by the phytoplankton population. Velocities, designated as V 's, are transport rates reduced to unit nitrogen concentrations. For example, $V_{NO_3} = \rho_{14}/N_1$ and has units of NO₃⁻-N taken up (unit time)⁻¹ (unit N in the phytoplankton)⁻¹. The units reduce to time⁻¹. V_{NO_3} can therefore be considered to be a growth rate in terms of nitrogen. The nitrogen available to the phytoplankton is designated as new (for example, nitrate from below the thermocline or formed by nitrogen fixation, or regenerated, such as decomposition of organic nitrogen into ammonia).

The model (Fig. 1), while representing quite accurately the processes occurring in nature, is more complicated than necessary for an initial approach to nutrient limitation theory. Steele and Menzel (1962) in

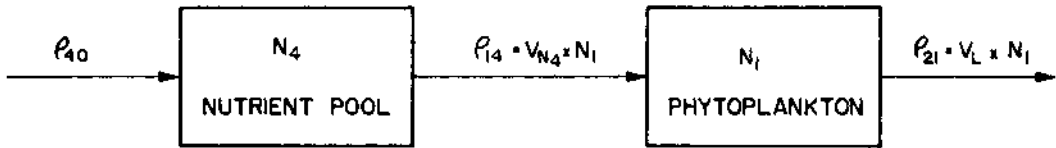


FIG. 2. Simplified flow-diagram of a major nutrient in the euphotic zone with regeneration pathways omitted.

their model for the Sargasso Sea near Bermuda neglected nutrient regeneration, using only nitrate concentrations for the nutrient term. This simplifying procedure will be followed and, in addition, the discussion will be restricted to those processes occurring in the nutrient-limited region of the euphotic zone. Thus, in its simplest form the primary production system is diagrammed as in Fig. 2, the notation remaining unchanged. N now stands for a limiting nutrient rather than specifically for nitrogen, and ρ_{40} is the new productivity, the absolute rate of supply of limiting nutrient, assumed here to be supplied by mixing from below the nutrient-limited region; N_1 is the phytoplankton concentration; V_{N_4} is the growth rate of the phytoplankton in terms of the limiting nutrient, units t^{-1} ; and V_L is the loss rate of the phytoplankton per unit phytoplankton, principally from grazing, sinking, and mixing, units of t^{-1} .

Then

$$\rho_{14} = V_{N_4} \times N_1, \quad (1)$$

the absolute transport rate of limiting nutrient into the phytoplankton, and

$$\rho_{21} = V_L \times N_1, \quad (2)$$

the absolute transport rate of limiting nutrient out of the phytoplankton, that is, the sum of all losses. At steady state, all ρ values must be equal. Thus,

$$\rho_{14} = \rho_{21},$$

and from equations (1) and (2)

$$V_{N_4} \times N_1 = V_L \times N_1,$$

and

$$V_{N_4} = V_L. \quad (3)$$

The growth rate of the phytoplankton is therefore determined by the sum of the loss

rates due to sinking, grazing, and mixing. The nature of the term, V_L , is crucial to an understanding of the implications of the model. The sinking rate of the phytoplankton appears to be a function of species, age, and physiological state. The inclusion of a separate term for zooplankton has been avoided deliberately for simplicity, and it should be emphasized that a solution for the size of the zooplankton population is not necessary for the purpose of this model. Different phytoplankton-zooplankton communities will probably stabilize in different relative proportions to give varying values for the grazing component of V_L . The effect of mixing in removing the phytoplankton is less in this model than in those of Steele (1958) and Riley (1965). This results from consideration here of a nutrient-limited layer underlain by a light-limited layer containing a finite population, whereas Steele (1958) and Riley (1965) treat the euphotic zone as a whole with a phytoplankton population exchanging with an underlying zone containing no phytoplankton. In mathematical terms:

$$\rho_{21}(\text{mixing}) = m[N_1 - N_{1(0)}],$$

where $N_{1(0)}$ is the concentration of phytoplankton in the light-limited layer.

A mechanism for achieving a steady state can be demonstrated if a positive relationship exists between the concentration of limiting nutrient and the velocity of uptake of the nutrient by the phytoplankton. Work with chemostats has depended on the extension of Michaelis-Menton enzyme kinetics to whole organisms, usually bacteria. In that case the following expression holds (Monod 1942):

$$V_{N_4} = N_4 \frac{V_{\max}}{K_s + N_4}, \quad (4)$$

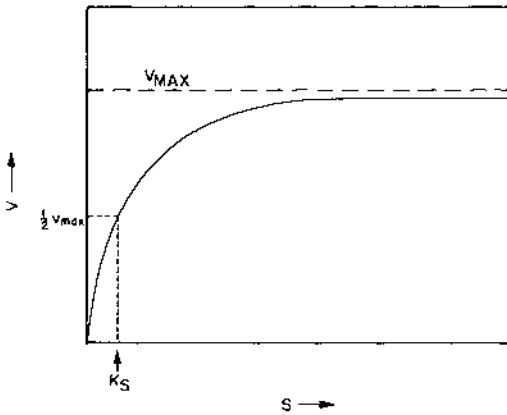


FIG. 3. Nutrient uptake as a function of nutrient concentration, according to the Michaelis-Menton expression.

where V_{max} is the maximum uptake velocity for the organisms under the experimental conditions, and K_s is the substrate concentration at which $V_{N_4} = V_{max}/2$ (Fig. 3).

Evidence for the validity of Michaelis-Menton kinetics for algae is beginning to accumulate. Caperon (1965), using the chemostat, showed Michaelis-Menton kinetics to apply to nitrate-limited growth of *Isochrysis galbana*. MacIsaac (unpublished), using batch methods and ^{15}N for a tracer, has evidence that the same is true for ammonia uptake by *Chlorella* sp. The data of Harvey (1963) for the uptake of phosphate by *Phaeodactylum tricorutum*, when replotted (Fig. 4), also show Michaelis-Menton kinetics. Although the data are scanty at present, the preliminary assumption that the nutrient uptake behavior of algae is described by equation (4) appears to be upheld.

To apply this function in the model, it must be assumed either that all species of algae have an identical K_s value or that one species or a group of species with similar K_s values are in sufficient majority to produce the effect of a unialgal population. Wright and Hobbie (1966) have studied the kinetics of glucose uptake by natural populations of microorganisms in lakes. They designate the K value so obtained as K_t , a coefficient for transport, to distinguish it clearly from K_s , which has in the

past always referred to a single species. The distinction is important and will be observed here.

The steady-state value for N_4 corresponding to the required V_{N_4} , which has the same value as V_L , can be found from a curve similar to Fig. 3 plotted with the appropriate values of K_t and V_{max} . From equations (3) and (4), an expression can be obtained for the concentration of limiting nutrient:

$$N_4 = K_t \left/ \frac{V_{max}}{V_L} - 1 \right. \quad (5)$$

The important point is that the concentration of limiting nutrient is set by the magnitude of the loss rate and by the characteristic uptake kinetic parameters of the population, V_{max} and K_t . This simple system is passively regulated according to control theory (Milsom 1966). In qualitative terms, the system can be seen to regulate through the interaction between phytoplankton and the nutrient concentration. For example, an increase in the loss rate would result in a decrease in the size of the population, N_1 , thereby reducing ρ_{14} . N_4 increases as a result and forces an increase in uptake rate until V_{N_4} again equals V_L .

The size of the standing crop of phytoplankton can be obtained from equation (2):

$$N_1 = \rho_{21}/V_L.$$

At steady state $\rho_{21} = \rho_{40}$, and then

$$N_1 = \rho_{40}/V_L. \quad (6)$$

The size of the phytoplankton population therefore varies directly according to the rate of nutrient supply and indirectly as the loss rate. In the two-layered system, the rate of nutrient supply is, according to Riley (1965),

$$\rho_{40} = m(N_0 - N_4), \quad (7)$$

where m is the mixing coefficient between the nutrient-limited region and that lying just below, and N_0 is the concentration of limiting nutrient just below the nutrient-limited region.

N_4 is a function of the kinetic character-

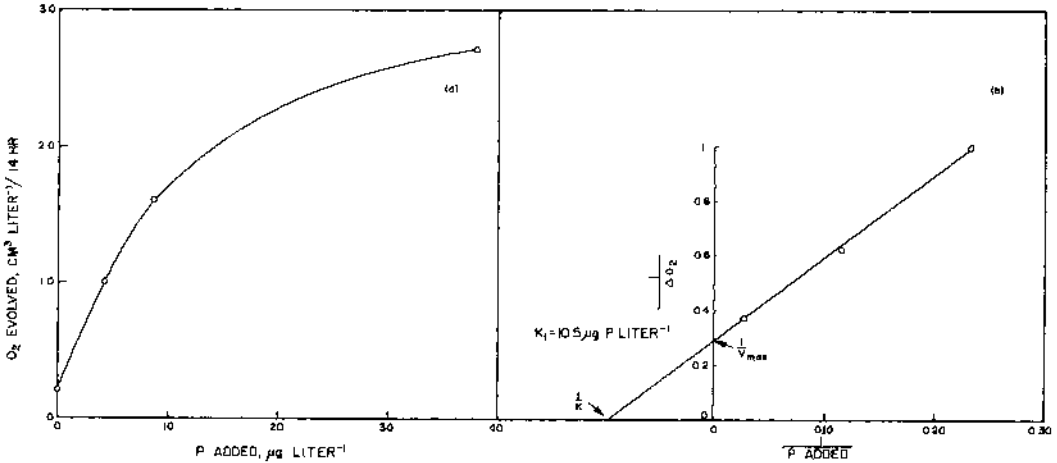


FIG. 4. The data of Harvey (1963) replotted to show the response of *Phaeodactylum tricoratum* according to Michaelis-Menten kinetics. (a) Oxygen evolved as a function of added phosphorous. (b) Reciprocal plot of the same data according to the Lineweaver-Burke modification to obtain values for V_{max} and K_t .

istics of the dominant phytoplankton species as given in equation (5) and

$$\rho_{40} = m \left[N_0 - \left(K_t / \frac{V_{max}}{V_L} - 1 \right) \right]. \quad (8)$$

Combining equations (6) and (7),

$$N_1 = \frac{m}{V_L} \left[N_0 - \left(K_t / \frac{V_{max}}{V_L} - 1 \right) \right]. \quad (9)$$

The size of the phytoplankton population and the productivity of the system, therefore, depend upon the size of the term $K_t / [(V_{max}/V_L) - 1]$ occurring in equations (8) and (9). That is, $N_1 \rightarrow 0$ and $\rho_{40} \rightarrow 0$ as

$$K_t / \left(\frac{V_{max}}{V_L} - 1 \right) \rightarrow N_0, \quad (10)$$

while for maximum productivity

$$\rho_{40} \rightarrow m N_0 \quad \text{and} \quad N_1 \rightarrow m N_0 / V_L \quad \text{as}$$

$$K_t / \left(\frac{V_{max}}{V_L} - 1 \right) \rightarrow 0. \quad (11)$$

Thus, low loss rates or the presence of a dominant species with high V_{max} or low K_t values are conditions under which a large fraction of the maximum production will be realized. It is also apparent that the maximum allowable loss rate is set at

some value below V_{max} by the same mechanism. This can be seen from equations (3) and (4):

$$V_L = V_{max} N_4 / (K_t + N_4),$$

and since $N_4 \rightarrow N_0$ as a maximum value,

$$V_{Lmax} = V_{max} N_0 / (K_t + N_0). \quad (12)$$

Equation (12) sets the maximum loss rate beyond which the population cannot respond with an increased growth rate.

The reactions of a nitrate-limited system to changes in loss rates can be seen in Fig. 5 for the following conditions: $V_{max} = 0.05/\text{hr}$, $K_t = 2.5 \mu\text{g-at./liter}$, $m = 0.001/\text{hr}$, and $N_4 = 10.0 \mu\text{g-at. NO}_3^-/\text{liter}$. A common feature of the curves is the rapid change that occurs as the limits are approached, for example, the high rate of change in ambient nitrate concentration, N_4 , and in productivity, ρ_{40} , in the region where V_L increases from 0.03 to 0.04. The standing crop increases rapidly as $V_L \rightarrow m$. In the case $V_L = m$, from equation (9),

$$N_1 = \left[N_0 - \left(K_t / \frac{V_{max}}{V_L} - 1 \right) \right].$$

At low V_L values, $N_1 \approx N_0$. Fig. 5 also illustrates the principle that high phytoplankton growth rates result in low pro-

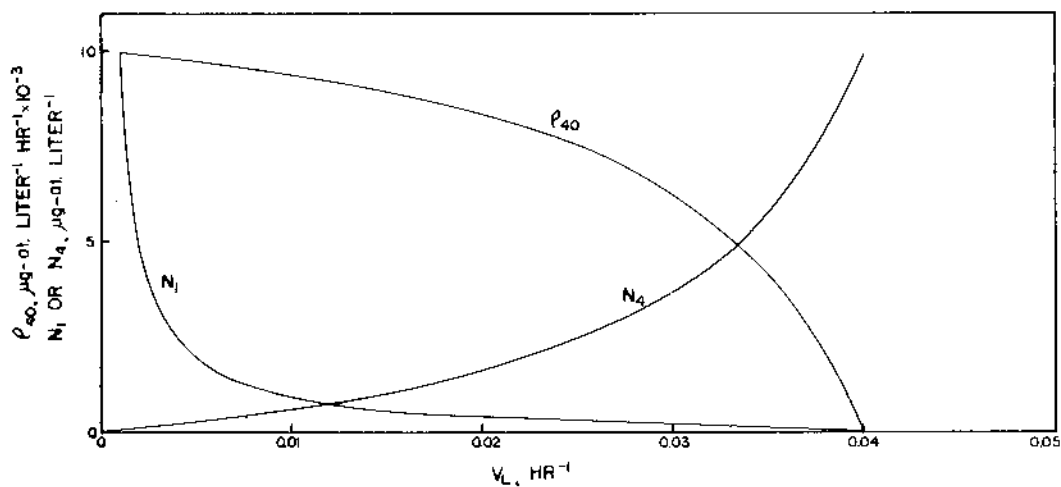


FIG. 5. Size of phytoplankton population, N_1 , rate of production, ρ_{40} , and concentration of limiting nutrient, N_4 , as functions of fractional loss rate, V_L , in the model for a nutrient-limited system without regeneration, for assumed values of K_t , V_{max} , N_0 , and m .

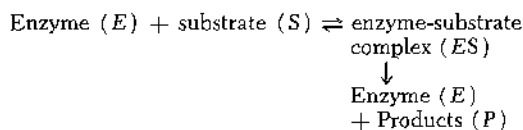
ductivity; that is, the nutrient available is wasted as a result of high ambient nutrient concentration. In the case illustrated, 90% or more of the potential productivity can be realized only when $V_L < 0.3 V_{max}$.

Micronutrients

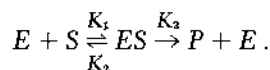
Metal constituents of enzymes such as iron and molybdenum have been named as limiting nutrients. For example, Goldman (1960) believed molybdenum to be limiting primary productivity in Castle Lake, California, and Menzel and Ryther (1961) added iron to Sargasso Sea water and obtained enhanced photosynthetic activity for 24 hr. In view of these findings, it is appropriate to examine theoretically the role of this class of micronutrients.

Molybdenum is a constituent of nitrate reductase and might reasonably be expected to affect the uptake of nitrate if it were to be in short supply. The question then revolves about the manner in which the concentration of the enzyme affects the conversion of nitrate to ammonia within the algal cell. Some insight is provided if the reactions forming the basis for the Michaelis-Menton theory of enzyme kinetics are examined. The derivations can be found in White et al. (1959) and else-

where. In their notation, the basic reaction is written:



and



K_1 , K_2 , and K_3 are first order rate constants. The final expression is as equation (4):

$$V = V_{max}S/(K_m + S),$$

where V is the velocity of conversion of substrate to product; $K_m = (K_2 + K_3)/K_1$ is the Michaelis constant; and

$$V_{max} = K_3E. \quad (13)$$

A short supply of molybdenum might be expected to decrease the concentration of the enzyme nitrate reductase, thereby reducing linearly the magnitude of V_{max} .

Assuming that V_{max} for the cellular uptake of nitrate is set in this manner, the effect of a reduced V_{max} can be seen from equation (5) to result in an increased value of ambient nitrate concentration, N_4 . Increased N_4 results in turn, from equations

(6) and (7), in a decrease in the supply rate ρ_{40} and in the size of the phytoplankton population, N_1 . The productivity of the system has thereby been reduced. The maximum allowable loss rate, $V_{L_{max}}$, set by equation (12) is also reduced. Although the system is molybdenum limited, regulation or accommodation to changes in V_L is still dependent upon nitrate at the new value of the kinetic parameter, V_{max} . This is the case when the molybdenum requirement of the population is small compared to the amount available, a condition met in the sea where Barsdate (1963) has shown that the concentration of molybdenum varies only slightly.

The effects of reduced molybdenum concentration in the model are shown in Fig. 6a and 6b for the following conditions:

$V_{max} = 0.05/\text{hr}$, $K_t = 2.5 \mu\text{g-at./liter}$, $m = 0.001/\text{hr}$, and $N_4 = 10 \mu\text{g-at. NO}_3^-/\text{liter}$.

Fig. 6a was obtained from equation (13) and the additional assumption that the concentration of nitrate reductase will be directly proportional to the molybdenum concentration in the surrounding water according to the expressions:

$$V_{max} = 0.5 \times \text{Mo concentration,} \\ \text{Mo} < 0.1 \mu\text{g-at./liter;}$$

$$V_{max} = 0.05/\text{hr, Mo} \geq 0.1 \mu\text{g-at. Mo/liter.}$$

The curves for ambient nitrate, N_4 , productivity, ρ_{40} , and phytoplankton, N_1 , show high rates of change when the molybdenum concentration falls to about one-half the saturating concentration, assumed here to be $0.1 \mu\text{g-at./liter}$. At one-quarter of the saturating molybdenum concentration, $V_{max} = V_{L_{max}}$, and the population collapses. The existence of a critical range may be of particular interest in lakes where relatively large changes in concentration of molybdenum are likely to be observed (Barsdate 1963).

IDENTIFICATION

From the foregoing discussion it should be clear that the investigation of nutrient limitation should be made by considering the production system as a whole and with

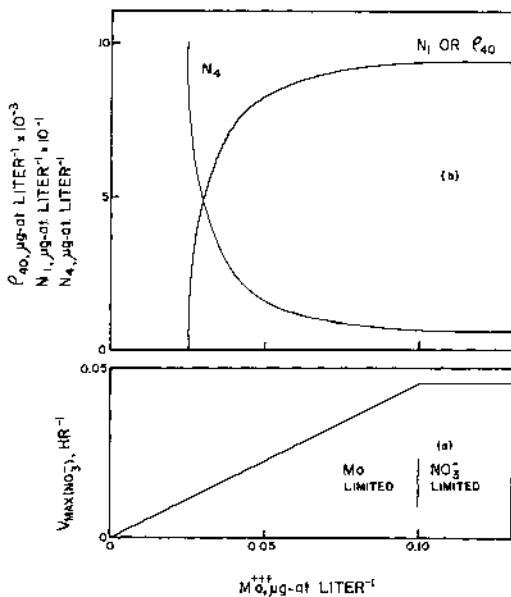


FIG. 6. Effects in the model of a diminished supply of molybdenum on an initially nitrate-limited system for assumed values of K_t , V_{max} , N_0 , and m . (a) Assumed relationship between molybdenum concentration and V_{max} . (b) Size of phytoplankton population, N_1 , rate of production, ρ_{40} , and concentration of initially-limiting nitrate, N_4 , as functions of molybdenum concentration.

some model in mind. If the model proposed here were to be used to design experiments, some technique or combination of techniques for the measurement of uptake rates must be chosen. The necessity for obtaining results quickly calls for the use of tracer methods. Radioisotopes or stable isotopes are available for measuring the uptake of common nutrients or micronutrients (for example, ^{15}N , ^{32}P , ^{99}Mo , and ^{30}Si). It should be obvious that the kinetics of a particular nutrient should be measured directly, if possible, with a labeled form of the nutrient, for example, $^{15}\text{NO}_3^-$ and $^{32}\text{PO}_4^{3-}$.

Indirect methods, in which a nutrient that may be limiting is added and the response measured by the reaction of some other system in the cell, have also been used. The ^{14}C method of Steemann Nielsen (1952), providing a highly sensitive assay of the photosynthetic uptake of carbon

by phytoplankton, was used by Goldman (1960, 1961) for his investigations of the effects of trace metals on primary production in Brooks Lake, Alaska, and Castle Lake, California; by Menzel and Ryther (1961) in studies of nutrient limitation in the Sargasso Sea; and by Becacos (1962) on Lago Maggiore, Italy.

Results obtained with the ^{14}C technique are subject to uncertainties of interpretation since additions of suspected limiting nutrients may influence the photosynthetic system specifically. This is especially likely to occur with micronutrients; Fogg (1965) has pointed out that the rate of photosynthesis can be changed simply by altering the divalent: monovalent ion ratio. In a nutrient-limited system, such a disturbance would be followed by an eventual return to the preexisting photosynthetic rate. An observation of enhanced photosynthesis under these conditions has no validity.

The possibility of confusing transient and steady-state response to experimental additions of limiting nutrient also exists when using the direct method, that is, observing the uptake of limiting nutrient. It has been shown in equation (5) that the concentration of the limiting nutrient depends upon the growth rate V_N , and upon the parameters V_{\max} or K_t . Thus, any experimental manipulation, accidental or deliberate, that affects either V_{\max} or K_t will result in a temporary change in V_N and ρ_{21} , followed by eventual restoration of the previously existing rates at a new ambient concentration of nutrient. No data for algae appear to be available for the effect of environmental conditions on K_t . Vaccaro and Jannasch (1966) have shown that, for a species of marine bacteria resembling *Achromobacter aquamarinus*, the value of K_t is temperature dependent. A large number of factors may be important in setting the value of V_{\max} and changing the concentration of any one of them may be expected to throw the system into transient oscillation through its effect on V_{\max} . No information appears to be available regarding the time-scale for these perturbations. The magnitude and period of oscillation

probably depend on the size of the population and the rate of flow of limiting nutrient.

Uptake velocities for nitrate and ammonia in seawater have been obtained by Dugdale and Goering (1967) using ^{15}N . The method has the advantage that growth rates in terms of nitrogen, $V_{\text{NO}_3^-}$ and $V_{\text{NH}_4^+}$, can be obtained. Although the accuracy of a single measurement is influenced by the amount of detritus present, relative velocities can be obtained from a variety of experiments made upon a single sample of seawater. For example, the search for a limiting nutrient at an oceanic station might proceed by a series of experiments in which serial additions of phosphate and nitrate were made to seawater samples with $^{15}\text{NO}_3^-$ added as a tracer. After incubation for a few hours in saturating light, the samples would be filtered and the filters processed to obtain $V_{\text{NO}_3^-}$. If a kinetic response is observed for nitrate but not for phosphate, the system apparently would be nitrogen limited. In another series of experiments, the influence of molybdenum could be demonstrated if its addition resulted in altered nitrate kinetics, possibly as an increase in V_{\max} for nitrate uptake.

SIGNIFICANCE OF NUTRIENT LIMITATION

Redfield, Ketchum, and Richards (1963) pointed out that inorganic nitrate and phosphorus occur in deep oceanic water in approximately the same ratio that these elements occur in the phytoplankton. In general, both become exhausted through uptake by phytoplankton at about the same time. Since both nutrients are supplied from below the thermocline by upwelling or mixing processes, it is nearly as correct to say that primary production is limited by the rate of supply of both nutrients as it is to name the nutrient that actually limits the growth rate of the phytoplankton cells at any given moment. The importance of nutrient limitation theory lies, rather, in the dynamic behavior of the system.

One of the most interesting aspects of nutrient limitation theory is concerned with phytoplankton succession and competition.

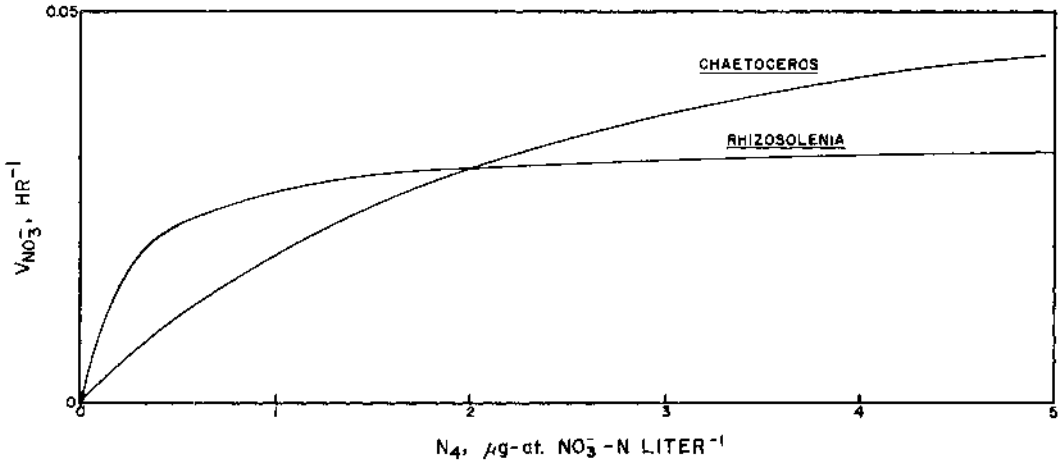


FIG. 7. Hypothetical curves for nitrate uptake vs. nitrate concentration for two species of algae. Values for V_{\max} were taken from Riley (1963b); hypothetical values of K_t for nitrate uptake were assigned. For *Chaetoceros socialis*, $V_{\max} = 0.068/\text{hr}$, $K_t = 2.50 \mu\text{g-at. NO}_3\text{-N/liter}$; for *Rhizosolenia alata*, $V_{\max} = 0.034/\text{hr}$, $K_t = 0.25 \mu\text{g-at. NO}_3\text{-N/liter}$.

The model proposed in this paper requires the assumption that a single species of phytoplankton or a group of species with similar kinetic characteristics dominates the population.

The effect of a dominant population, N_1 , will be to fix the level of dissolved nutrient concentration, N_4 , since the sum of $\rho_{14}' + \rho_{14}'' + \dots + \rho_{14}^n$ is assumed to be small compared to ρ_{14} . The minor populations N_1' , N_1'' , \dots , N_1^n will have cellular growth rates set by the existing level of N_4 and their uptake characteristics K_t' , K_t'' , \dots , K_t^n , and V_{\max}' , V_{\max}'' , \dots , V_{\max}^n . The fate of these minor populations will be determined by the relative size of the loss rates V_L' , V_L'' , \dots , V_L^n , in comparison to the uptake rates V_{N_4}' , V_{N_4}'' , \dots , $V_{N_4}^n$. Since these populations have no feedback response system while they remain small, they are likely to be growing or diminishing in size.

Values for V_{\max} are available for some species under culture conditions. Data of Lanskaya are given in Riley (1963b) for generation times of diatoms obtained from the Black Sea and from these a value of V_{\max} for growth can be computed. These values range from 0.226/hr for *Skeletonema costatum* (Grev) Cl. to 0.034/hr for *Rhizosolenia alata* Bright and 0.068/hr for *Chaetoceros socialis* f. *autumnalis* Pr.-Lavr. The

important question is whether the species having lower V_{\max} values have lower K_t values, enabling them to compete with species having higher V_{\max} values. For example, in Fig. 7 the instantaneous growth rate is plotted against nitrate concentration for *R. alata* and *C. socialis* with the values given above for V_{\max} . The effect of a low value of K_t in compensating for low maximum growth rates is shown. *R. alata* with a maximum growth rate half that of *C. socialis* would show higher instantaneous growth rates at any nitrate concentration below 2.0 $\mu\text{g-at./liter}$ than would *C. socialis*. The situation represented in Fig. 7 may be extreme, but it does serve to illustrate the potential importance of the kinetic characteristics for nutrient uptake.

Competition for available nutrients at low concentrations, such as those prevailing in the Sargasso Sea, appears likely to result in an evolution of species with low K_t values, and it is possible that this cannot be achieved and still maintain a high value of V_{\max} . In that case, species characteristic of low productivity tropical regions can be expected to show low values for both V_{\max} and K_t . Other consequences follow, especially the necessity to reduce loss rates correspondingly in a variety of ways, for example, by reduction of sinking rates and

the acquisition of armor to reduce vulnerability to predation. If diatoms are eventually shown to be organisms that have evolved with a high maximum growth rate at the cost of a correspondingly high K_z value, then the puzzle of diatom dominance in nutrient-rich areas may be explained.

Although a steady state was assumed in developing the model, that condition probably never occurs in nature. The existence of a control mechanism, however, tends to restore equilibrium when the system is perturbed. The feeding activities of zooplankton may produce perturbations with interesting consequences. Grazing is not carried on at a steady rate over the 24-hr period but rather is concentrated during the dark hours when at least parts of the population migrate toward the surface and feed. A daily cycle in ammonia concentration may be expected to occur because the phytoplankton population will be reduced allowing ammonia to accumulate temporarily. An increase in supply rate for ammonia will probably also occur as a result of its excretion by the zooplankton. The increased concentration of ammonia during the night hours will, however, result in an increase in $V_{NH_4^+}$, offset in part by a decreased uptake rate in the dark. Cycles of this nature have been described at Bermuda by Goering, Dugdale, and Menzel (1964) and by Beers and Kelly (1965). In the first case, the results were interpreted to mean an inherent daily rhythm of nitrogen uptake by the plant cells; however, it appears to be more likely that the phytoplankton were responding to the increased ammonia concentration.

With sufficient experience, it may be possible to apply nutrient limitation theory to situations where natural populations are perturbed deliberately through the addition of nutrients, for example, by the addition of sewage effluent to lakes or to coastal regions of the sea. The usefulness of an adequate theory may prove especially valuable in lakes where the ratio between nutrients in the water may vary widely from the ratio required by the phytoplankton. A detailed knowledge of the uptake

kinetics for common algae might make it possible to control fishponds to obtain desired algae if a continuous addition of nutrients were to be made in place of the usual batch additions.

SUMMARY

The model proposed provides only a beginning towards understanding the dynamic behavior of nutrient-limited production. Regeneration terms for zooplankton grazing and bacteria should be added, but when this is done, the model becomes considerably more complex. The existence of additional forms of nitrogen, especially ammonia, must be taken into account. The possibility of interaction between nutrient concentrations and K_z values must be taken into account, particularly in the case of nitrate uptake, which is likely to be influenced by the ambient concentration of ammonia. The study of nitrate and phosphate uptake by Ketchum (1939) shows evidence for phosphate-nitrate interaction also. For simplicity, silicate has been ignored here but must also be considered in any generalized model.

The model provides a framework for the investigation of nutrient limitation in the sea and should be helpful in experimental design and interpretation. There is an urgent need to discover the important kinetic parameters for the uptake of nutrients (if other than Michaelis-Menton kinetics as postulated in this paper) and to measure them for phytoplankton algae characteristic of different productivity regimes. If this can be done, valuable new information about the adaptations of these organisms to their environment will become available, and a new tool will be provided to help in the prediction of their occurrence and behavior under nutrient-limited conditions.

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