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Munk and Riley revisited: nutrient diffusion transport and rates of phytoplankton growth

by Jerome Gavis¹

ABSTRACT

Although phytoplankton nutrient uptake rates are controlled primarily by biological properties of the organism and nutrient concentration, diffusion transport of nutrient to the organism through the medium in which the organism is immersed can influence uptake rates. The original ideas of Munk and Riley on control of nutrient uptake by diffusion transport are recast in terms of present knowledge of the interaction of diffusion transport and biological control of uptake rates. The effect of relative motion between the organism and the medium in decreasing diffusion transport limitation of uptake rate is described for spherical organisms. Motion can reduce diffusion transport limitation, but not eliminate it completely. Expressions relating growth rate to uptake rate are utilized to evaluate the influence of diffusion transport limitation on growth rate. Its influence on competition among species and on organism size is also considered. Diffusion transport has less influence on growth rate than on uptake rate. It may alter competitive relationships. It may explain, in part, why small size phytoplankton predominate in impoverished regions of the oceans.

1. Introduction

More than two decades ago Munk and Riley (1952) published a paper that has now become a classic on the role of diffusion and convective mass transport in the nutrition of aquatic plants. Titled "Absorption of Nutrients by Aquatic Plants," it presents expressions from which nutrient uptake rates are to be calculated in terms of organism mass, size, and shape, and nutrient diffusivity and concentration. Munk and Riley assumed that uptake rates are controlled solely by physical parameters relating to diffusion transport of nutrient to the organism. They discussed how such physically controlled uptake rates influence growth and adaptation, especially with respect to phytoplankton size.

Since Munk and Riley's paper, a better understanding of the kinetics of phytoplankton nutrition has emerged with the realization that the nutrient uptake rate is limited by nutrient concentration, C (μM), through the biological parameters of the organism V_m ($\mu\text{mol}/\text{cell}/\text{hr}$), the maximum uptake rate, and K (μM), the half

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saturation constant, contained in the Michaelis-Menten or Monod type of expression that describes observed uptake rates

$$V = V_m C / (K + C). \quad (1)$$

Diffusion transport can influence uptake rates at low nutrient concentrations, however, as has recently been shown by Pasciak and Gavis (1974, 1975). Because low enough concentrations do exist in nature, the physical parameters of diffusion transport may remain important determinants of growth and adaptation in the sense considered by Munk and Riley. *How* they act as determinants must differ from the means described by them, however.

The purpose of this paper is to recast the arguments of Munk and Riley in terms of present knowledge about the kinetics of nutrient uptake by phytoplankton, especially focusing on the influence of diffusion transport on uptake rates.

2. Nutrient uptake kinetics

Phytoplankton respond to concentrations of nutrients at their external surfaces. If a phytoplankter can consume nutrient at a given ambient concentration, C , at a rate that is greater than the rate at which the nutrient can diffuse to its surface, the concentration at the surface, C_0 , must be less than C . A nutrient depleted region is thus set up around the organism. The uptake rate is determined by the rate at which diffusion can supply nutrient in the concentration gradient established.

The uptake rate should be written

$$V = V_m C_0 / (K + C_0), \quad C_0 < C \quad (2)$$

with the value of C_0 determined from the differential equations describing diffusional processes. Pasciak and Gavis (1974, 1975) showed that C_0 is given as a function of C by the solution of the quadratic equation

$$(C_0/K)^2 + (1/P + 1 - C/K) (C_0/K) - (C/K) = 0 \quad (3)$$

where

$$P \equiv 14.4 \pi R \alpha D K / V_m, \quad (4)$$

in which R (cm) is a linear dimension characteristic of the organism, α is a shape factor depending upon the geometry of the organism, D (cm²/sec) is the diffusivity of the nutrient, and the constant factor 14.4 contains conversion factors to make P a dimensionless quantity for the units used for the other parameters.

If the organism is spherical, R is the spherical radius and α is unity. Values of α are always less than unity for non-spherical organisms, and are smaller the farther the organism is from spherical. Shape factors are readily calculable only for simple, regular geometric shapes. Pasciak and Gavis (1975) have been able to calculate

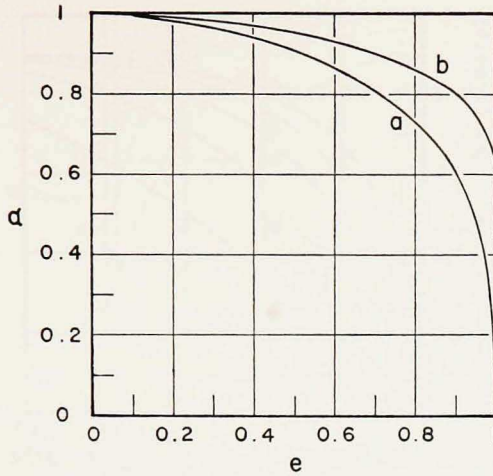


Figure 1. Shape factor, α , for prolate and oblate spheroids as a function of eccentricity, e . Curve (a) prolate; curve (b) oblate.

them for prolate and for oblate spheroids, using the "uniformly accessible surface" approximation.² For the former

$$\alpha \equiv 2e / \ln [(1 + e)/(1 - e)], \quad (5)$$

and for the latter

$$\alpha \equiv e / \tan^{-1} (e / \sqrt{1 - e^2}) = e / \sin^{-1} e \quad (6)$$

where

$$e = \sqrt{1 - a^2/R^2}, \quad (7)$$

a is the semi-minor axis of the spheroid, and R is the semi-major axis. Because slender prolate spheroids (e close to unity) resemble cylinders and flat oblate spheroids (e close to unity) resemble discs, equations (3)-(7) may be used to obtain approximate values of P and thus C_0 for organisms that resemble cylinders and discs. In order to facilitate its use, α is plotted as a function of e for prolate and oblate spheroids in Fig. 1.

Although simply obtained, the solution of equation (3) for C_0 is algebraically complicated. When it is inserted into equation (2) in order to ascertain the nutrient uptake rate as a function of ambient concentration, C , the result is best illustrated graphically. Fig. 2 shows the plot of V/V_m against C/K with P as a parameter, for several values of P . The quantity P is a criterion of the influence diffusion transport can have on the nutrient uptake rate of an organism. It determines which curve of Fig. 2 describes the uptake rate as a function of ambient nutrient concentration.

2. This is described in §3, below.

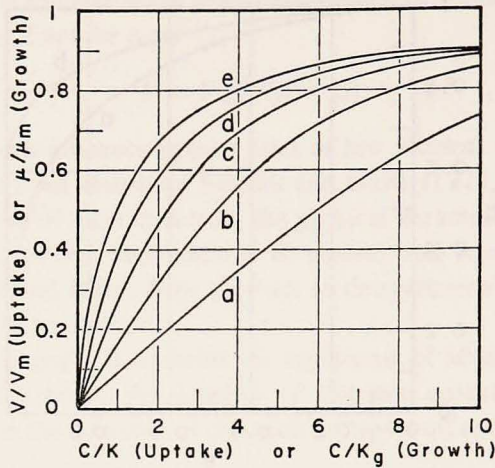


Figure 2. Ratio of uptake rate, V , to maximum uptake rate, V_m , or ratio of growth rate, μ , to maximum growth rate, μ_m , as functions of the ratio of ambient nutrient concentration, C , to the half-saturation constant for uptake, K , or the half-saturation constant for growth, K_g . Curve (a) $P = 0.1$; (b) $P = 0.2$; (c) $P = 0.4$; (d) $P = 1.0$; (e) $P \rightarrow \infty$.

When P is large (uppermost curve of Fig. 2), $C_0 = C$ and the uptake rate, given by equation (1), is independent of diffusion processes. The rate is also independent of diffusion processes when C/K is large, since then V is equal to V_m , independent of C . The lower curves, for small P , which depict diffusion transport limited uptake rates, all converge to the uppermost curve when C/K is large. Diffusion transport influences uptake rates most when C/K and P are small. Fig. 3, a plot of the ratio of the diffusion transport limited uptake rate to the corresponding rate in the absence of limitation against C/K for several values of P , illustrates this more clearly. The ratio is unity when $P \rightarrow \infty$, but is much smaller than unity when P and K/C are small.

3. The influence of motion

When diffusion transport limitation occurs, relative motion between the organism and the medium in which it is immersed increases the uptake rate relative to that in a motionless system. In relative motion the nutrient depleted region around an organism is distorted and decreased in extent so that diffusion transport is facilitated. For phytoplankton relative motion can occur because of organism motility, sinking and rising resulting from buoyancy changes, and the creation of shear fields around the organism as a result of wave action, convection, and turbulence.

Diffusion transport rates are not increased uniformly around an organism, however, because the depleted region is reduced in size by the motion to an extent vary-

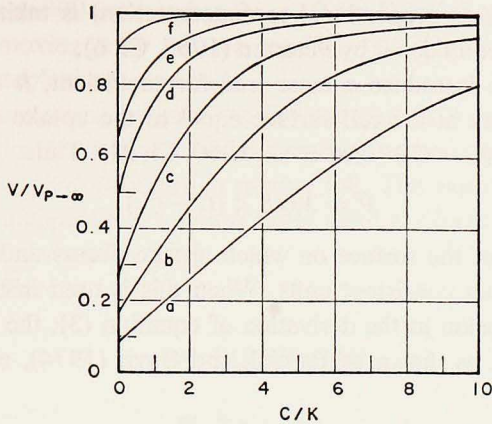


Figure 3. Ratio of diffusion transport limited uptake rate to non-limited uptake rate, $V/V_{P \rightarrow \infty}$, as a function of C/K . Curve (a) $P = 0.1$; (b) $P = 0.2$; (c) $P = 0.4$; (d) $P = 1.0$; (e) $P = 2.0$; (f) $P = 10$.

ing with position. This causes the uptake rate to vary with position around the organism. Mathematical complexity prevents solution of the diffusion equation for such conditions. The problem is identical to that of mass transfer of a reactant to an immersed catalyst particle, long of interest to chemical engineers who have been forced to use the "uniformly accessible surface" hypothesis to deal with it. This is an approximation in which the mass transfer (diffusion transport) rate is calculated as a function of position for an infinitely rapid reaction rate, and zero reactant concentration, everywhere on the surface of the particle. The mass transfer rate is then averaged over the entire surface. The averaged rate, now considered uniform over the surface, in turn is used to determine the mass transfer rate when the surface reaction rate is finite. In this way the reactant concentration and reaction rate are constrained to be uniform everywhere on the surface. The reaction rate is now an overall one for the particle. When the method is applied in the corresponding nutrient uptake problem, the resulting uptake rate is the overall uptake rate for the organism. This approximation has been invoked in the derivations that follow.

A similar problem occurs in the derivation of the equations for diffusion transport limited uptake rates of non-spherical organisms in quiescent media. Diffusion transport rates, nutrient concentrations, and uptake rates are higher at surfaces of greater curvature in non-spherical geometries. Pasciak and Gavis (1975) invoked the "uniformly accessible surface" approximation in the derivation of the shape factors for prolate and oblate spheroid shaped organisms when they constrained the concentration, C_0 , at the organism surface to be uniform around it.

The errors introduced by this approximation are difficult to ascertain. They have been shown to be small for mass transfer to a semi-infinite plane surface where a

first order reaction (rate proportional to concentration) is taking place. The problem has been discussed in detail by Petersen (1965, Ch 6).

It is convenient to introduce a mass transfer coefficient, h (cm/sec), which relates the transport rate at the cell surface equal to the uptake rate, V , to the concentration difference ($C - C_0$) (Bird et al., 1960, Ch 21). Thus

$$V = 3.6 h A (C - C_0) \quad (8)$$

where A is the area of the surface on which uptake occurs and the constant factor 3.6 is used to maintain consistent units. When this is used instead of the differential equations of diffusion in the derivation of equation (3), the results are identical to those given above, as shown by Pasciak and Gavis (1974), except that P is now expressed as

$$P' = 3.6 h A K/V_m. \quad (9)$$

In the absence of motion equation (9) is equivalent to equation (4). For motionless spherical organisms, therefore, for which $A = 4 \pi R^2$, $h = D/R$.

Generally, when relative motion occurs, h cannot be obtained from the solution of the diffusion equations, but must be obtained from experiment. However, for small spheres in slow rectilinear motion, approximate expressions for h in terms of diffusivity and the parameters of the motion can be obtained from the equations. Reviews of methods and results are given by Brenner (1966, §4) and by Levich (1962, §14).

Pasciak and Gavis (1974) used

$$h = (D/R) (1 + Ru/2D + \dots) \quad (10)$$

from which they obtained

$$P' = P (1 + Ru/2D) \quad (11)$$

where u (cm/sec) is the relative velocity between the organism and the medium. The neglected terms in equation (10) contribute less than 2% to h . Equation (10) is valid only when (Brenner, 1966, §4)

$$2 Ru/v \ll 1 \quad (12)$$

and

$$2 Ru/D \ll 1 \quad (13)$$

where ν is the kinematic viscosity of the medium (~ 0.01 cm²/sec for water). The dimensionless group of parameters ($2 Ru/\nu$) is the Reynolds number, Re , of the flow system, and ($2 Ru/D$) is the Peclet number, Pe .

The Reynolds number is always very small for phytoplankton motion. For example, a 100 μm organism swimming at 300 $\mu\text{m}/\text{sec}$ has $Re \sim 0.06$. The Peclet number, however, is large in many cases of phytoplankton motion. The 100 μm

organism swimming at 300 $\mu\text{m}/\text{sec}$ has $\text{Pe} \sim 40$ for $D = 1.5 \times 10^{-5} \text{ cm}^2/\text{sec}$. Even a 10 μm organism moving at 50 $\mu\text{m}/\text{sec}$ has $\text{Pe} \sim 0.7$. Equation (10) is, therefore, not valid for all phytoplankton motion.³

Unfortunately there are no expressions like equation (10) available for very small Reynolds numbers in the range of Peclet numbers between about 0.1 and 40, the range in which many phytoplankton in motion fall. The expressions used by Munk and Riley are also inapplicable, because those valid for larger values of the Peclet number are valid only when $\text{Re} \gg 1$.

In general, when $\text{Re} \ll 1$

$$h = \frac{1}{2} (D/R) f(\text{Pe}) \quad (14)$$

so that

$$P'/P = \frac{1}{2} f(\text{Pe}). \quad (15)$$

Friedlander (1957, Fig. 1) has given $f(\text{Pe})$ as a function of Pe graphically for mass transfer to immersed spheres when $\text{Re} \ll 1$ over a wide range of values of Pe , including the range between 0.1 and 40. This can be used to determine P'/P as a function of u for different values of R . The result is illustrated in Fig. 4. The maximum phytoplankton swimming velocity observed (Lewin, 1962, p. 597) is about 300 $\mu\text{m}/\text{sec}$. Therefore, even for a 100 μm organism P' is, at most, about twice as large as P .

How uptake rate changes with u at any ambient nutrient concentration can be ascertained for spherical organisms if the values of P'/P obtained from Fig. 4 are used in conjunction with equations (2) and (3), for $\alpha = 1$, or, alternatively, with Fig. 3. For example, let $C = K$, $P = 0.1$, and $P'/P = 2$ from Fig. 4 for a motile organism. Then $V/V_{P \rightarrow \infty} = 0.18$ from Fig. 3 for $P = 0.1$, while $V/V_{P \rightarrow \infty} = 0.32$ from that figure for $P' = 2P = 0.2$. Motion, therefore, increases the uptake rate by the factor $0.32/0.18 = 1.8$.

In particular, the effect of sinking and buoyant rise in reducing diffusion transport limitation can be estimated in this way. As an example, Eppley et al. (1967, Fig. 3) were able to correlate sinking rate and cell size approximately for single-celled marine diatoms, and Smayda (1970, Fig. 1) showed that several flagellates had the same sinking rate-cell size correlation as the diatoms. Sinking rates, determined for different cell sizes from the plot given by Eppley et al., can be used in conjunction with Fig. 4 to obtain P'/P for sinking as a function of cell size. The result is shown in Fig. 5.

The increase in uptake rate depends upon P and upon the ratio C/K . It can be determined as a function of R through the dependence of P'/P on R for sinking, as

3. Pasciak and Gavis (1974) incorrectly used the equation to determine P' in their Table II for *G. splendens* and *D. tertiolecta*. Because the organisms are non-spherical, correct values for P' cannot be given. If the organisms are considered spherical, the values for P' , taken from Fig. 4, would be about 0.9 for *G. splendens* and about 44 for *D. tertiolecta*.

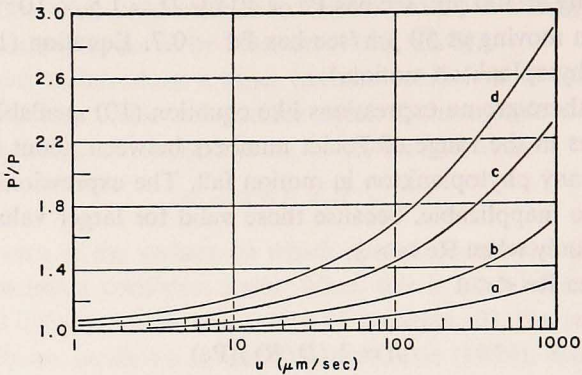


Figure 4. The ratio P'/P as a function of velocity, u , for spherical organisms. The maximum phytoplankton swimming velocity is about $300 \mu\text{m}/\text{sec}$. Curve (a) $R = 2 \mu\text{m}$; (b) $R = 10 \mu\text{m}$; (c) $R = 40 \mu\text{m}$; (d) $R = 100 \mu\text{m}$.

given by Fig. 5, by means of equations (2) and (3) or Fig. 3. The ratio of the uptake rate of a sinking marine diatom cell to that of a non-diffusion transport limited cell is plotted against R , in Fig. 6, for several values of P at $C/K = 1$, where diffusion transport limitation is significant.

Increase in uptake rates caused by sinking is appreciable only for large organisms with small values of P . The rate is less than doubled for $R = 100 \mu\text{m}$ and $P = 0.1$. Even for such an organism sinking is able to increase the uptake rate only to 0.3 of the uptake rate that the organism would have in the absence of diffusion transport limitation. Sinking is not a very effective means of eliminating diffusion transport limitation.

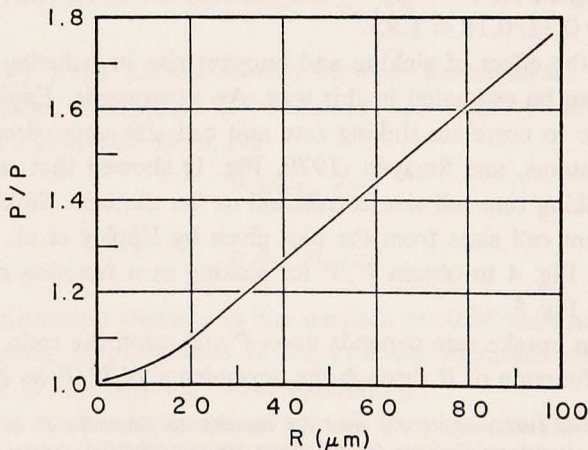


Figure 5. The ratio P'/P as a function of radius, R , for sinking spherical organisms.

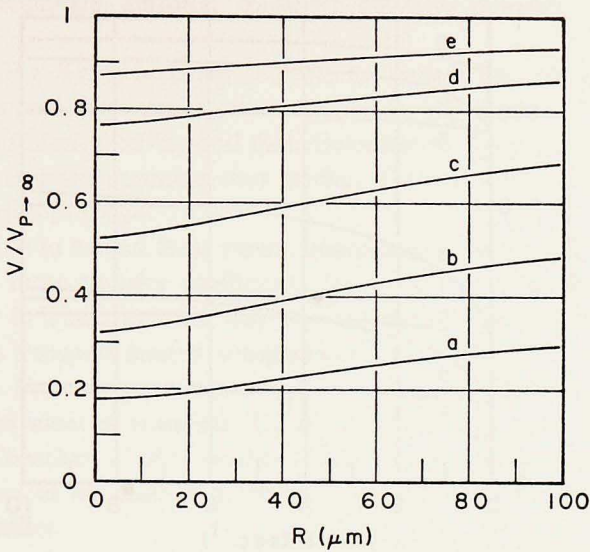


Figure 6. Ratio of diffusion transport limited uptake rate to non-limited uptake rate, $V/V_{P \rightarrow \infty}$, as a function of radius, R , for sinking spherical organisms. Curve (a) $P = 0.1$; (b) $P = 0.2$; (c) $P = 0.4$; (d) $P = 1.0$; (e) $P = 2.0$. $C/K = 1$.

The ratio of the uptake rate of a diffusion transport limited spherical swimming organism to that of a non-diffusion transport limited cell is plotted against swimming velocity in Fig. 7 for several values of R and P at $C/K = 1$. Although organ-

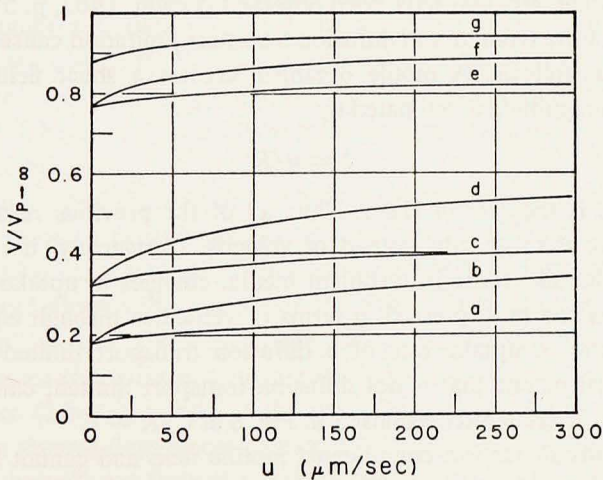


Figure 7. Ratio of diffusion transport limited uptake rate to non-limited uptake rate, $V/V_{P \rightarrow \infty}$, as a function of velocity, u . Curve (a) $P = 0.1$; $R = 10 \mu\text{m}$; (b) $P = 0.1$, $R = 100 \mu\text{m}$; (c) $P = 0.2$, $R = 10 \mu\text{m}$; (d) $P = 0.2$, $R = 100 \mu\text{m}$; (e) $P = 1.0$, $R = 10 \mu\text{m}$; (f) $P = 1.0$, $R = 100 \mu\text{m}$; (g) $P = 2$, $R = 100 \mu\text{m}$. $C/K = 1$.

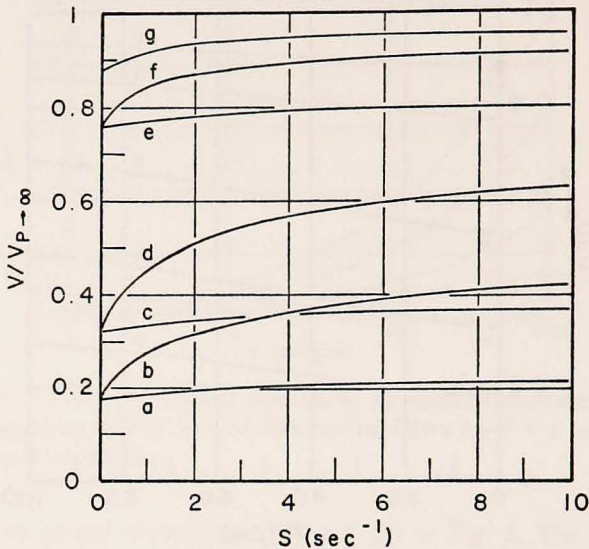


Figure 8. Ratio of diffusion transport limited uptake rate to non-limited uptake rate, $V/V_{P \rightarrow \infty}$, as a function of shear rate, S . Curve (a) $P = 0.1$, $R = 10 \mu\text{m}$; (b) $P = 0.1$, $R = 100 \mu\text{m}$; (c) $P = 0.2$, $R = 10 \mu\text{m}$; (d) $P = 0.2$, $R = 100 \mu\text{m}$; (e) $P = 1$, $R = 10 \mu\text{m}$; (f) $P = 1$, $R = 100 \mu\text{m}$; (g) $P = 2$, $R = 100 \mu\text{m}$. $C/K = 1$.

ism motility is more effective than sinking in reducing diffusion transport limitation, swimming does not completely eliminate it at phytoplankton swimming velocities, between $50\text{-}300 \mu\text{m}/\text{sec}$, that have been observed (Lewin, 1962, p. 597).

An estimate of the reduction in diffusion transport limitation caused by turbulence may be made as follows. A motile organism creates a shear field in its vicinity whose order of magnitude is estimated by

$$S = u/R \quad (16)$$

where S (sec^{-1}) is the rate of shear. Thus all of the previous results may be expressed in terms of shear rate instead of velocity. Conversely, it can be assumed that in shear fields like those in turbulent media, changes in uptake rate caused by shearing motions can be expressed in terms of velocities through equation (16). In this way the ratio of uptake rate of a diffusion transport limited organism in a shear field to that of one that is not diffusion transport limited, calculated as were the ratios in Fig. 7, are plotted against S in Fig. 8 at $C/K = 1$.

Open water turbulence is a complicated motion field and cannot be described by any single shear rate. Pasciak and Gavis (1974) have estimated that shear rates up to about 6 sec^{-1} are to be expected in open ocean water with finite probability. Fig. 8 shows that most of the change in uptake rate occurs below 6 sec^{-1} for all the plotted values of P and R . Like sinking and organism motility, shearing motions

are unable to eliminate diffusion transport entirely, however, even for large organisms.

The curves of Fig. 8 may be compared with the data of Pasciak and Gavis (1975, Fig. 5), who observed that uptake rate increased rapidly as shear rate increased to about 5 sec^{-1} but leveled off beyond that. Quantitative comparison, however, cannot be made because the organism they studied, *Ditylum brightwellii*, is cylindrical rather than spherical in shape.

It is not possible to extend these results quantitatively to nonspherical organisms. Expressions for mass transfer coefficients for nonspherical shapes are available only for $Pe \ll 1$. These indicate that motion causes smaller increases in uptake rates of diffusion transport limited nonspherical organisms than of spherical cells of the same size, R . For example, Brenner (1963) showed that the terms in the parentheses of the equivalent of equation (10) for a thin disc ($\alpha = 2/\pi$) have the form $(1 + Ru/\pi D)$. Therefore P'/P is smaller for the disc shaped organism than for the spherical organism of the same R at the same u , and the corresponding increase in uptake rate is smaller.

If the mass transfer coefficients of nonspherical shapes increase less than those of spheres of equivalent size R at higher values of Pe as a result of relative motion, it can be concluded that, in general, motion is less able to overcome diffusion transport limitation of uptake of nonspherical organisms than of spherical ones. At least, the results presented for spherical organisms display the form of the influence of relative motion on diffusion transport limited uptake rates of phytoplankton.

The fact that shearing motion cannot eliminate diffusion transport entirely may be used to explain the higher value of P Pasciak and Gavis (1975, Fig. 6) needed to fit uptake rate data in a shear field relative to the values that fit their data in quiescent media. If V_{shear} , the uptake rate in a shear field, is lower than $V_{P \rightarrow \infty}$, then the points in their plot have higher ordinate values than they would have had if $V_{\text{shear}} = V_{P \rightarrow \infty}$. This is so because V_{shear} is in the denominator of the ordinate of the plot.

The reason that diffusion transport limitation cannot be completely overcome by relative motion between organisms and the medium in which they are immersed can be given in physical terms. As a small immersed object moves slowly through a fluid, it drags fluid along with it, because the fluid adheres to the object's surface and cannot "slip" past it. The fluid at the surface moves with the velocity of the object, but far from the surface it must remain at rest relative to the object. The Reynolds number ($2Ru/\nu$), a ratio of the inertial forces arising from movement of the object to the viscous drag forces exerted by the fluid on the moving object, is a measure of the distance out from the surface over which the velocity changes. The smaller the Reynolds number, the larger the distance. For phytoplankton cells for which the $Re \ll 1$, the distance is at least of the same order of magnitude as the size of the object.

If a substance is diffusing to a small, immersed, stationary, absorbing object, a region around the object in which the substance is depleted may develop if the absorption rate is rapid with respect to the diffusion rate, as already described. If the object moves slowly, fluid in the depleted region is sheared away. New fluid in which the concentration of diffusing substance has not been decreased takes its place. This decreases the effective size of the depleted region and increases the rate of transport of substance to the object. The magnitude of the increase depends upon the rate at which new fluid replaces depleted fluid. This, in turn, depends upon the velocity of the object and on the distance over which the velocity changes from that at its surface to zero in the fluid bulk. It also depends on the diffusivity of the substance.

The Peclet number ($2Ru/D$), a ratio of the rate of transport when relative motion occurs to that in the absence of motion, is a measure of the increase in transport rate caused by motion. When $Pe \ll 1$, which occurs for slow motion of small objects, e.g., sinking phytoplankton cells, the effective size of the depleted region is of the order of the distance from the surface over which the velocity changes, i.e., of the order of the size of the object itself. It decreases linearly with increase in velocity, and the rate of transport increases linearly with the velocity, as given by equation (10). As the Peclet number increases past unity and becomes large, the size of the depleted region, now smaller than the distance over which the velocity changes and small with respect to the size of the object, changes inversely proportionally to the cube root of the velocity, as given by Friedlander [1957, equation (18)]. The rate of transport then increases proportionally to the cube root of the velocity.

At realizable phytoplankton velocities the nutrient depleted region around a cell is not reduced to zero extent, and limitation of the nutrient uptake rate by diffusion transport is not eliminated completely.

4. Growth

When nutrient concentrations are at steady state, which must occur at least approximately in nature in large water masses, organism growth rate, μ (cell/cell/hr = hr⁻¹), is proportional to nutrient uptake rate. The proportionality coefficient is the yield coefficient, Y (cell/ μ mol). Because this varies with organism growth rate (Droop, 1973; Caperon & Meyer, 1972a), the relationship between growth rate and nutrient concentration differs from that between nutrient uptake rate and nutrient concentration. Therefore, the influence of diffusion transport on growth rate is not described simply by its influence on uptake rate.

The problem of the growth rate dependence of the yield coefficient has been investigated by Fuhs (1969), Droop (1968, 1973), and Caperon and Meyer (1972a). Relationships between growth rate and uptake rate have been developed by Fuhs

et al. (1972), Caperon and Meyer (1972b), Droop (1973), and Eppley and Renger (1974). Droop's exposition is the easiest to adapt for present purposes.

Based on his work on growth and uptake of vitamin B₁₂ by several phytoplankton species, Droop observed a linear relationship between the cell quota, q , the reciprocal of the yield coefficient, Y , and uptake rate. He showed, using the results of others, that the linear relationship was also obeyed for such nutrients as iron, phosphate, and nitrate. The relationship is

$$V = \mu'_m (q - q_0). \quad (17)$$

Here μ'_m represents the slope of the line that results when V is plotted against q ; it is a limiting growth rate reached when the *internal* cell nutrient concentration becomes large. The intercept of the plotted line on the q axis is represented by q_0 ; it is a minimum cell nutrient quota at zero uptake rate or zero growth rate. Equation (17) may be solved for q , and, when combined with the fact that $V = q\mu$, gives

$$q = \mu'_m q_0 / (\mu'_m - \mu), \quad (18)$$

or, in terms of Y ,

$$Y = Y_0 (\mu'_m - \mu) / \mu'_m; \quad Y_0 \equiv 1/q_0. \quad (19)$$

Thus, the yield coefficient decreases linearly with increasing growth rate; the cell quota increases hyperbolically with growth rate.

When equations (17) and (18) are combined there results

$$\mu = \mu'_m V / (V + q_0 \mu'_m) \quad (20)$$

as the equation relating growth rate to uptake rate. Growth rate is proportional to uptake rate at small uptake rates but becomes independent of it as uptake rate increases.

The uptake rate, however, is limited by the nutrient concentration as described by equation (2). When this is inserted into equation (20) the result is an equation for the dependence of growth rate on external nutrient concentration in the form

$$\mu = \mu_m C_0 / (K_g + C_0) \quad (21)$$

where

$$\mu_m \equiv \mu'_m V_m / (V_m + \mu'_m q_0) \quad (22)$$

is the maximum growth rate for large nutrient concentration *external* to the cell and

$$K_g \equiv q_0 \mu'_m K / (V_m + \mu'_m q_0) = \mu_m q_0 K / V_m \quad (23)$$

is the growth rate half-saturation constant. Note that μ_m is smaller than μ'_m , so that q , in equation (18), is always finite.

Both μ_m and K_g are smaller than the corresponding quantities for uptake, V_m and K . In fact, Droop (1973) obtained values of K_g as small as about $1/20 K$ in his experiments. This means that growth rate reaches its maximum at a lower external nutrient concentration than does uptake rate.

The influence of diffusion transport limitation on growth rate is obtained by substitution of C , the nutrient concentration in the medium, for C_0 in equation (21) by means of equation (3). The result is similar in form to the result of substitution of C for C_0 in equation (2) by means of equation (3). In fact, growth rate may be plotted as a function of concentration, C , to give a set of curves, for different values of P , that are identical to those for the plot of uptake rate as a function of C in Fig. 2. Fig. 2 reflects this: the axes are labeled V/V_m or μ/μ_m , and C/K or C/K_g . In order to determine growth rate at a given external nutrient concentration when the uptake rate is diffusion transport limited, it is necessary only to determine P from uptake rate measurements and to obtain μ/μ_m at any C/K_g from the curve of Fig. 2 corresponding to that value of P .

Because, in general, K_g is smaller than K , at least for vitamin B₁₂, iron, phosphate, and nitrate, μ is closer to μ_m at any nutrient concentration than V is to V_m . For uptake V/V_m is given, in Fig. 2, by the intersection of an ordinate erected at C/K and the curve for the given value of P . For growth μ/μ_m is given by the intersection of the ordinate at C/K_g and the curve. The latter ordinate is to the right of the former one and μ/μ_m is closer to unity than is V/V_m . Therefore, *when diffusion transport limits uptake of the nutrients noted above, it causes a smaller change in growth rate than it does in uptake rate.* Organisms slightly diffusion transport limited in uptake rate may exhibit no diffusion transport limitation of growth rate.

Carbon dioxide limited uptake and growth rates constitute an exception to this conclusion. Gavis and Ferguson (1975) have discussed how low CO₂ concentrations that may exist in fresh-water systems at elevated pH may limit the CO₂ uptake rate of those species of phytoplankton able to assimilate inorganic carbon only in the form of dissolved CO₂. Goldman et al. (1974) have observed that Y is independent of uptake rate for CO₂-limited uptake by two fresh-water species. Therefore, μ is proportional to V with a constant Y relating them, and the half-saturation constants are identical while $\mu_m = Y V_m$, and, for this limiting nutrient at least, the influence of diffusion transport limitation on growth rate is the same as its influence on uptake rate.

A complicating factor in the analysis just presented is the fact that V_m may vary as a function of μ . Droop considered V_m constant. Both Caperon and Meyer (1972b) and Eppley and Renger (1974), however, observed that V_m is a function of μ , the former investigators observing that V_m increased proportionally to μ , the latter observing that V_m decreased with increasing μ . Both pairs of investigators worked with the same organism limited by the same nutrient.

Variability of V_m can be included in the derivation of the equations just given. If, as suggested by Caperon and Meyer,

$$V_m = b\mu \quad (24)$$

with b a constant, equation (21) becomes

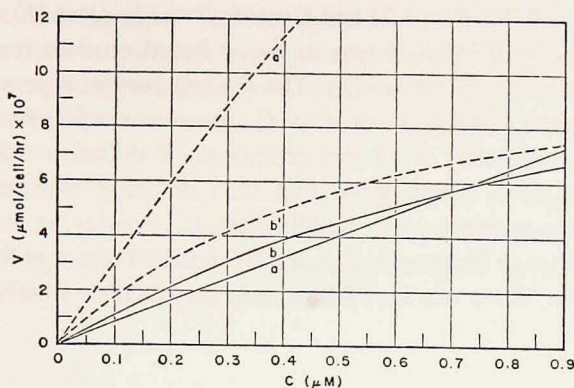


Figure 9. Comparison of uptake rates, V , as functions of concentration, C , at low concentrations between *C. lineatus* and *D. brightwellii*. Solid curves: diffusion transport limited uptake rates, (a) *C. lineatus*; (b) *D. brightwellii*. Dashed curves: non-diffusion transport limited uptake rates, (a') *C. lineatus*; (b') *D. brightwellii*.

$$\mu = \mu'_m (1 - q_0 K/C_0 b) \quad (25)$$

when $q_0/b \ll 1$, as observed in Caperon and Meyer's experiments. While equation (25) differs in form from equation (21), μ is still a hyperbolic function of C ; the shape of the plot of μ/μ'_m against C/K is similar to the plot of μ/μ'_m against C/K from equation (21). Substitution of C from equation (3) for C_0 yields a family of curves similar to the curves of Fig. 2.

Thus, inclusion of variability of V_m , at least in the form of equation (24), leads to results that differ quantitatively from those for constant V_m , but leads to similar phenomenological descriptions. Because there appears to be disagreement on how V_m varies with μ , it is not possible to quantify its effect completely at this time.

5. Competition

Potentially, the most important effect diffusion transport limitation of nutrient uptake rates can have is on the ability of organisms to compete. If diffusion transport limits the growth rate of an organism significantly, it may limit the abundance of that organism relative to others in nutrient poor environments. Organisms that inhabit nutrient poor regions of the oceans are those with small values of their half-saturation constants, K (Eppley et al., 1969). Such organisms are most likely to have small values of P and are most likely to be diffusion transport limited in nutrient uptake rate. It is necessary, therefore, to consider the parameter P in addition to K and V_m in a discussion of nutrient limited competition.

An example taken from previously published data illustrates this. Although the organisms may not actually compete at such low nutrient concentrations in nature, a comparison of rates of uptake of NO_3^- by *Ditylum brightwellii* ($K = 0.6 \mu\text{M}$,

$V_m = 12.5 \mu\text{mol/cell/hr}$, $P = 1.3$) and *Coscinodiscus lineatus* ($K = 2.8 \mu\text{M}$, $V_m = 90 \mu\text{mol/cell/hr}$, $P = 0.34$) is shown in Fig. 9 based on data from Eppley, et al. (1969) and Pasciak and Gavis (1975). The dashed curves, representing non-diffusion-transport-limited uptake, show that *C. lineatus* would absorb NO_3^- more rapidly than *D. brightwellii* at all concentrations, if diffusion transport limitation were absent. The solid curves show that with diffusion transport limitation *D. brightwellii* absorbs nutrient more rapidly than *C. lineatus* at concentrations less than $0.75 \mu\text{M}$, although both organisms absorb nutrient less rapidly than in the absence of limitation. There are insufficient data to establish whether this occurs in nature, however.

6. Size

It appears, in equation (4), that P is proportional to organism size, R . This is misleading because the ratio K/V_m may be a function of R . If V_m is substituted for in terms of μ_m by

$$V_m = 4/3 \pi R^3 \rho \mu_m q_m \quad (26)$$

for a spherical organism, where ρ ($\mu\text{gm/cm}^3$) is the cell density and q_m is the cell nutrient quota at the maximum growth rate, equation (4) for P may be rewritten as

$$P = 10.8 DK/\rho R^2 \mu_m q_m. \quad (27)$$

Laws (1975), based on data published by Eppley and Sloan (1966) for 10 species of marine phytoplankton, showed that μ_m was a function of cell volume, v (μm^3). In the units used here the dependence of μ_m on v may be written

$$\mu_m = 82.1/v^{0.1075}. \quad (28)$$

With the approximation that

$$R^{3(0.1075)} \cong R^{\frac{1}{3}}$$

this becomes, for spherical cells,

$$\mu_m = 51.7/R^{\frac{1}{3}}. \quad (29)$$

Substitution of equation (29) into equation (27) gives

$$P = 0.208 DK/\rho R^{5/3} q_m. \quad (30)$$

For prolate and oblate spheroids this should be multiplied by $\alpha/(1 - e^2)$ and $\alpha/(1 - e^2)^{\frac{1}{2}}$, respectively. Thus, P actually decreases as organism size increases, other factors remaining constant.

Organisms with small values of K , susceptible to diffusion transport limitation of nutrient uptake, could compensate for this by being small since, if q_m is independent of or only weakly dependent on size, small values of K can be compensated for by small size, as the presence of $R^{5/3}$ in the denominator of equation (30) shows.

Although the factors relating P' to P in equations (11) and (15) contain R in the numerators, these are never great enough to overcome the advantage small size allows. This may explain, at least in part, why small size phytoplankton are found in impoverished regions of the ocean (Munk and Riley, 1952; Parsons and Takahashi, 1973).

Although Munk and Riley predicted maximum sizes of organisms from their equations, this cannot be done here, because uptake and growth rates are controlled not only by physical factors but also by biological parameters that cannot *a priori* be related to organism size.

7. Conclusions

a. Although phytoplankton nutrient uptake rates are controlled primarily by biological parameters and concentration, physical parameters associated with nutrient diffusion influence the uptake rates. The dimensionless quantity P [equation (4)] is a quantitative measure of the influence. It determines which curve of Fig. 2 describes the uptake rate as a function of nutrient concentration and enables the uptake rate to be calculated at any concentration for an organism whose biological parameters are known. A quantitative discussion of the role of diffusion transport on growth and adaptation of phytoplankton, therefore, must be based on the three parameters V_m , K , and P and on the nutrient concentration.

b. When relative motion occurs between an organism and the medium in which it is immersed, P' [equations (9), or (11) and (15)] should be substituted for P . For slow rectilinear motion of spherical cells P'/P is plotted as a function of velocity for different size organisms in Fig. 4. Motion decreases the size of the nutrient depleted region about an absorbing cell and thus increases the uptake rate. It cannot completely eliminate diffusion transport limitation, however; motion cannot raise the uptake rate to that which would occur if there were no limitation. Fig. 6 shows how sinking increases uptake rate, Fig. 7 shows how swimming increases it, and Fig. 8 shows how shear motion does likewise.

c. Diffusion transport limits growth rate through its limitation of uptake rate. Because K_g and μ_m for growth are both smaller than K and V_m for uptake, diffusion transport causes smaller changes in growth rate, at any nutrient concentration at which limitation occurs, than in uptake rate, except for uptake of CO_2 . If K_g and μ_m are known, Fig. 2 may be used to obtain growth rates at any C/K_g and P or P' .

d. Decrease of nutrient uptake rate caused by diffusion transport limitation may be so great for an organism with small P relative to other organisms that it may lose the competitive advantage it might otherwise have had.

e. Smaller size leads to larger values of P [equation (30)] and thus decreased in-

fluence of diffusion transport limitation. This may, in part, explain why phytoplankton that predominate in impoverished regions of the oceans have small values of K , and are small in size.

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