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ABSORPTION OF NUTRIENTS BY AQUATIC PLANTS

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ABSTRACT

Formulae are derived for the rate of nutrient absorption by aquatic plants approximating the shapes of spheres, discs, cylinders, and plates. Other parameters are the size and specific gravity of the plant, the nutrient concentration of the medium, and the physical properties affecting the transfer of nutrients toward the plant surface. The formulae allow for convection, i. e., the movement of water relative to the plant. Hence absorption is aided by a current in the case of attached plants and by a rapid sinking rate in the case of plankton. The results are not materially modified by turbulence.

The formulae are applied to problems of diatom growth and adaptation. Any division rate of diatoms corresponds to a certain *minimum* rate of nutrient absorption; this in turn requires a certain sinking rate and therefore a certain excess in specific gravity of the diatoms over that of the surrounding water. In well fertilized laboratory media the excess may be very small, and this is consistent with the slow sinking rates usually observed under laboratory conditions. Under impoverished natural conditions the excess must be much larger, and hence there is a flotation problem. Accordingly, the analysis was extended to take into account sinking rates and vertical overturn in addition to nutrient absorption. The results are realistic with regard to observed division rates and sizes of diatoms, but they indicate an inherent competitive advantage of small diatoms over large ones. The observed size-frequency distribution of diatom species can be accounted for if one introduces an arbitrary predation factor which assumes that small cells are eaten more readily than large ones and that spheres are more acceptable food for small animals than long cylinders and plates.

1. INTRODUCTION

It is commonly stated in the literature that the elaboration of diatoms into flat discs, plates, and more intricate shapes is a flotation device. However, this hypothesis ignores the existence of equally common adaptations that have the opposite effect. For example, the formation of centric diatoms into chains reduces the total surface area

¹ Contribution from the Scripps Institution of Oceanography, New Series No. 584. We are indebted to Marston C. Sargent for proposing the problem and examining the manuscript.

and thereby increases the sinking rate. While the necessity of adequate flotation cannot be denied, we must look further for a logical explanation of the whole array of observed morphological variations.

The absorption of essential nutrients is an aspect of phytoplankton ecology that involves both surface-volume relations and sinking rates. Ecological evidence indicates that the rate of absorption often puts an upper limit on plant growth in the sea. This is most likely to occur in warm and stable waters that are also critical from the standpoint of flotation. If variations in size and shape in the diatoms have survival value, the problem should be analyzed in terms of both sinking rates and absorption.

The coexistence of a variety of forms and sizes of diatoms in nature implies that each variety has a slight advantage over the other in a particular set of circumstances, but no single variety maintains an advantage in all circumstances. It remains to be seen whether slight differences of this sort can be detected experimentally. In the present paper we shall take the obvious preliminary step of investigating the underlying physical principles by theoretical methods. Brief attention will also be given to the related problem of absorption by attached plants.

A small grain of solid material sinking through water will absorb heat by *diffusion* and by *forced convection*. We shall assume that the physical laws governing these two processes give also an adequate description of the processes whereby sinking diatoms absorb nutrients. This permits us to be quantitative, within limits.

Unfortunately the theory of forced convection has not been developed to a point where it can easily be applied to our problem. Our knowledge of this subject rests mostly on experimental evidence guided by dimensional analysis. The experiments have been performed largely on wires, spheres and plates for which the Reynolds numbers are larger by at least one order of magnitude than those applicable to sinking diatoms. In order to extrapolate the experimental results into the region of interest, it is necessary to have some guidance from theory as to what should be expected at very small Reynolds numbers. The associated mathematical problem is surprisingly difficult, and there are several published accounts describing these difficulties without giving solutions. The first adequate approximation² has been found only very recently by Kronig and Bruijsten (1951), and this work makes it possible to discuss with confidence the relationships for the scale with which we are concerned.

The derivation of these relationships are cumbersome and uninteresting and are contained in Appendix I, pp. 235-239.

² See footnote 10 on p. 240.

2. THE ABSORPTION AND SINKING RATES

Consider a diatom of mass m , containing rm grams of phosphate. Thus r designates the fraction in body weight of phosphate. Suppose q grams of phosphate are transferred each second from the surrounding water to the diatom. The relative rate of absorption may then be expressed by

$$\tau^{-1} = \frac{q}{rm}, \quad (1)$$

where τ is a measure of the time required to absorb as many grams of phosphate as are initially contained. The time required for a diatom to split in two cannot be much shorter than τ , but it may be longer because of other limiting factors. We shall call τ the "absorption time."

Different nutrients lead to different absorption times. The nutrient with the largest absorption time imposes the most severe limitation on the possible rate of growth.

The problem is to obtain q . It depends on the dimensions of the plant and on the physical characteristics of the surrounding fluid. It will be much larger if the fluid moves past the plant (or vice versa) and continually renews the nutrients in an impoverished film immediately surrounding the plant than if there is no such relative motion. The effect of the moving water is designated as "forced convection," the remaining part as "diffusion."

The forced convection depends on the velocity v of the fluid relative to the plant. This velocity is measured at some distance, say at least three diameters, from the plant, where the disturbing effect on the flow by the plant itself is negligible. We must distinguish between attached³ plants and freely sinking plants. In the former case the velocity v is an independent variable and is determined by wave action, currents, etc. In the latter case v is dependent only on the properties of the plant and the fluid, provided the effect of turbulence does not have to be taken into account. Apparently this is the case, as will be shown.

The solutions have been derived for five cases: an attached plate, a freely sinking plate, disc, sphere and cylinder. The geometry and dimensions are given in Fig. 1. Such simple geometric arrays are quite inadequate to represent intricate plant forms. All that can be said is that this is the best that can be done and that it is better than making no calculations at all. An indication of the uncertainties arising from the representation of plants by simple geometric bodies

³ The term "attached" has no bearing here on a flow of nutrients through the stem.

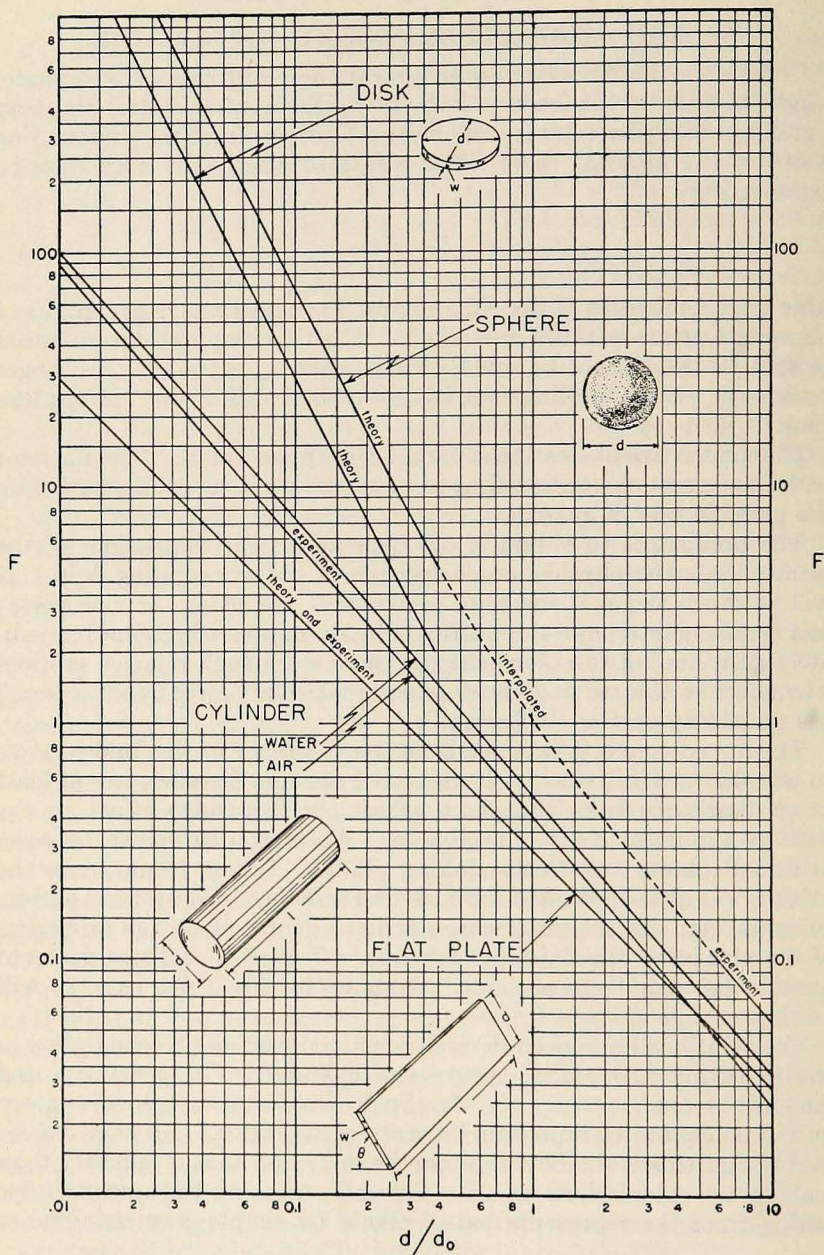


Figure 1. Plot of the relative absorption rate, F , as function of the diameter, d , for various geometric shapes: a flat plate sinking obliquely along a plane inclined by an angle θ , a sphere, disc and cylinder sinking vertically as shown. In the case of a sphere, the theoretical relation for $d/d_0 < 0.4$ can be smoothly joined to the empirical relation for $d/d_0 > 5$. In the case of the flat plate the theoretical relation has been confirmed by experiment. In the case of the cylinder the relation is wholly empirical. In the case of the disc, it is theoretical. The relations hold for water and air, except for cylinders, where separate curves have been constructed.

is found in the variability of the results among the geometric bodies themselves. The terms of the equations are defined as follows:

v in cm sec⁻¹ velocity of fluid relative to plant, at large distance from plant;

ϕ in g cm⁻³ excess in concentration of nutrient at large distances from plant over concentration at surface of plant;

m in g mass of plant;

r mass of nutrient in plant divided by m ;

ρ in g cm⁻³ density of surrounding fluid;

$\Delta\rho$ in g cm⁻³ mean density of plant minus density of fluid.

The absorption rates in sec⁻¹ are given by

$$\text{attached plate:}^4 \quad \tau^{-1} = \frac{\phi}{r\rho} \frac{1}{wd^{\frac{3}{2}}} (k'v)^2; \quad (2)$$

$$\text{sinking plate:}^4 \quad \tau^{-1} = \frac{\phi}{r\rho} \left(\frac{\Delta\rho}{\rho}\right)^{\frac{3}{2}} \tau_0^{-1} \left(\frac{d^2}{w^2} \sin \theta\right)^{\frac{1}{2}} F_p; \quad (3)$$

$$\text{sinking disc:} \quad \tau^{-1} = \frac{\phi}{r\rho} \left(\frac{\Delta\rho}{\rho}\right)^{\frac{3}{2}} \tau_0^{-1} \frac{d}{w} F_d; \quad (4)$$

$$\text{sinking sphere:} \quad \tau^{-1} = \frac{\phi}{r\rho} \left(\frac{\Delta\rho}{\rho}\right)^{\frac{3}{2}} \tau_0^{-1} F_s; \quad (5)$$

$$\text{sinking cylinder:} \quad \tau^{-1} = \frac{\phi}{r\rho} \left(\frac{\Delta\rho}{\rho}\right)^{\frac{3}{2}} \tau_0^{-1} F_c. \quad (6)$$

The sinking rates⁵ in cm sec⁻¹ are

$$\text{plate:} \quad v = v_0 \left(\frac{w}{d} \sin \theta\right)^{\frac{1}{2}} P r^{\frac{1}{2}} F_p'; \quad (3a)$$

$$\text{disc:} \quad v = v_0 \frac{w}{d} F_d'; \quad (4a)$$

$$\text{sphere:} \quad v = v_0 F_s'; \quad (5a)$$

$$\text{cylinder:} \quad v = v_0 F_c'. \quad (6a)$$

We shall also need

⁴ For the plate we have assumed diffusion negligible compared to forced convection, as will be the case except for extremely small values of v .

⁵ The expressions for the sinking rate are more elaborate than ordinarily required in order to make it possible to plot the F and F' function against the same parameter d/d_0 . Thus the diffusivity k enters through v_0 , and hence v_0 on one hand, and through δ_0 , and hence d_0 on the other hand, but actually the sinking rate is independent of k .

$$d_0 = \delta_0(\Delta\rho/\rho)^{-1/2}, \quad v_0 = v_0(\Delta\rho/\rho)^{1/2}. \quad (7)$$

Definitions and values are contained in Table I. Scale factors of time, τ_0 , of diameter, δ_0 , and of speed, v_0 , depend only on the viscosity and diffusivity of the surrounding medium. The effect of size is contained in the F and F' functions. These are plotted in Figs. 1 and 2

TABLE I. DEFINITIONS AND VALUES OF CONSTANTS

			Water	Air
ν	cm ² sec ⁻¹	viscosity at 20° C	0.01	0.15
k	cm ² sec ⁻¹	diffusivity* at 20° C	2x10 ⁻⁵	0.15
k'	cm ² sec ⁻¹	1.8 $k^{4/3} \nu^{-1/3}$	4.5x10 ⁻⁶	0.27
Pr		Prandtl number, νk^{-1}	5.0x10 ²	1.00
τ_0	sec	$(\nu^2/g^2k)^{1/3}$	1.73x10 ⁻²	0.54x10 ⁻²
δ_0	cm	$(72\nu k/g)^{1/3}$	0.24x10 ⁻²	12.0x10 ⁻²
v_0	cm sec ⁻¹	$(k^2 g/72\nu)^{1/3}$	8.17x10 ⁻³	1.27

* The diffusion coefficient may vary by a factor of two depending on the nature of the solute.

against d/d_0 , where d is the diameter (the length in the direction of flow in the case of the plate). Numerical examples are given in Section 4. Table I and Figs. 1 and 2 deal with water and air, but no application will be made to conditions in air.

3. ATTACHED PLANTS

We shall represent a leaf by a thin plate of density ρ and with the dimensions given in Fig. 1. The flow is along d . The surface area on both sides is $s = 2ld$, and the mass $m = \rho ldw = \rho(\frac{1}{2}s)w$. It follows from equation (1) that

$$\frac{q}{s} = \frac{r}{\tau} \frac{m}{s} = \frac{r\rho w}{2\tau}$$

is the absorption per unit surface area. Solving equation (2) for v yields

$$v = \left(\frac{2q}{s}\right)^2 \frac{1}{\phi^2} \frac{d}{k'}.$$

Setting the absorption at $q/s = 10^{-10}$ g sec⁻¹ cm⁻², $\phi = 3.1 \times 10^{-8}$ g cm⁻³ (1 μ g-at P/l), $d = 4$ cm, yields $v = 37$ cm/sec. If the nutrient concentration is reduced to 0.5 μ g-at P/l , $v = 150$ cm/sec. It would appear that attached plants must obtain their nutrients from the sea bottom or a bacterial slime film, or otherwise exist in an environment rich in nutrients and exposed to high velocities such as are found in shallow

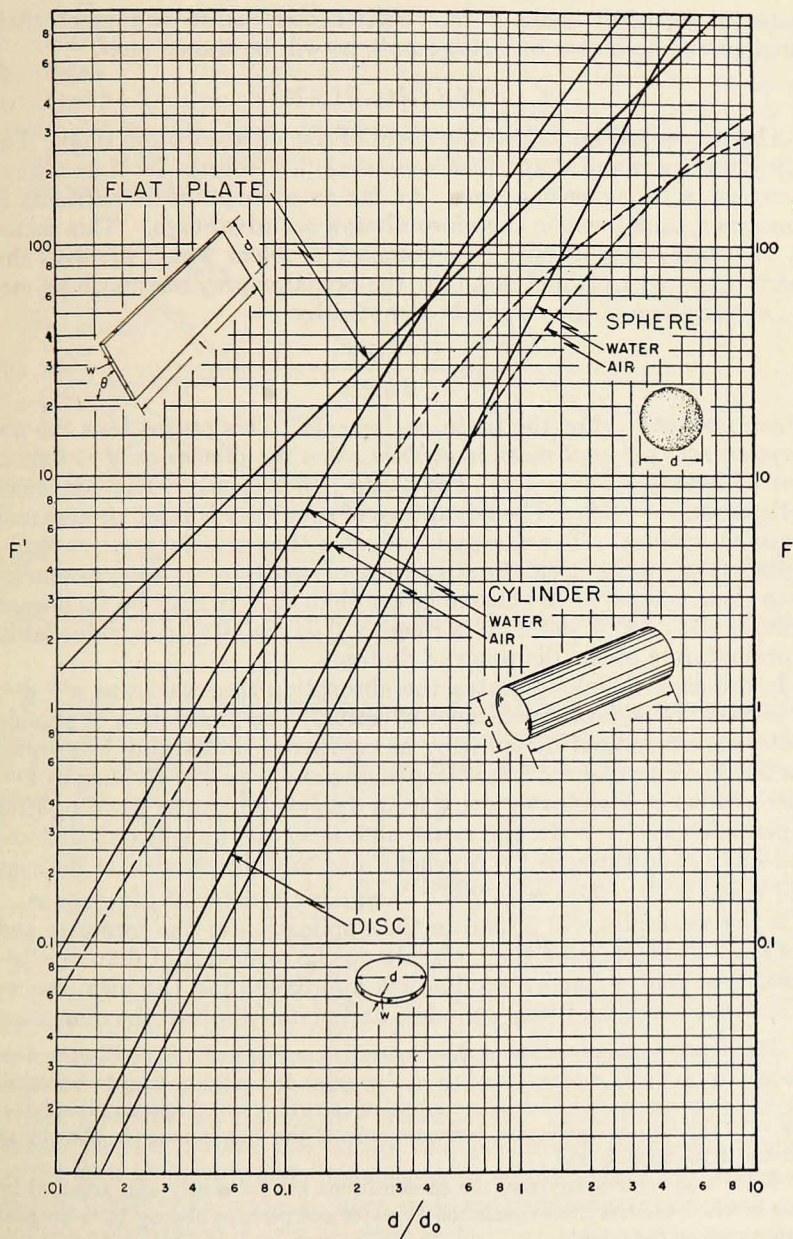


Figure 2. Plot of the relative sinking rate, F' , as function of the diameter, d , for the various geometric shapes considered in Fig. 1. The curves are based on both theoretical and experimental considerations.

water along open coast lines. Unattached plants can meet their nutrient requirements by being small, as will be shown next.

4. SINKING PLANTS

The curves in Fig. 1 show the effect of size on absorption time. For any given form and shape (w/d constant), the absorption time always increases with increasing size. As far as absorption of nutrients is concerned, small size is therefore always an advantage. This factor is, of course, only a part of a complex problem which involves the merits of structural differentiation, the predator-prey relationships, etc.

Let the slope of the curves be denoted by

$$m = \frac{d \log F}{d \log x}, \quad (8)$$

where $x = d/d_0$. For the plate, $m_p = -1$. This means that the absorption rate per unit mass is doubled when the dimension d is halved. For cylinders, $m_c = -1.2$. For large spheres, $m_s = -1.1$; for small spheres, $m_s = -2.0$. The advantage of small size is most pronounced for small spheres. The change in slope⁶ of the curve for spheres represents a marked change in the advantage of small size for spheres smaller than d_0 as compared to spheres larger than d_0 . It may be significant that, in the case of water, d_0 is roughly 0.01 cm (100 μ), a value fairly representative of the diameter of diatoms.

In the case of sinking plates, the absorption time varies as $w^{2/3} d^{1/3}$. It is remarkable how much more effectively the production of organic material is increased by splitting as compared to dividing lengthwise (in the direction of flow). Splitting increases τ^{-1} by $2^{2/3}$, dividing by $2^{1/3}$. The number of diatoms resulting from a single diatom by dividing after n generations is 2^n . In the same time interval the splitting diatoms will have gone through $2^{1/3} n$ generations, and the number of diatoms will equal $2^{2^{1/3}n}$. The ratio $2^{(2^{1/3}-1)n}$ equals 100 after 25 generations.

A few examples will illustrate the application of the formulae and the kind of information they provide on the problems of diatom existence. Assume an array of diatoms approximating the ideal shapes of spheres,⁷ discs, and long cylinders and plates in which the dimension

⁶ The physical interpretation of this change in slope is that for $d \ll d_0$ absorption is largely by diffusion, whereas for $d \gg d_0$ absorption is largely by forced convection. An increase in size leads to a smaller surface/volume ratio, and this is always unfavorable. In the case of convection, however, some of the disadvantage is offset by an increase in the sinking rate.

⁷ While true spheres are rare, the specifications will be closely approximated by discs in which the thickness equals the diameter and perhaps also by more irregular shapes such as *Biddulphia*.

d (Fig. 1) ranges from .0005 to .03 cm (5 to 300 μ). Let the ratio of diameter to thickness in the discs be 3:1 and of width to thickness in the plates 5:1. The angle of the plate is 10° . Phosphorus is designated as the limiting nutrient, and its concentration r in the diatom is assumed to be .001 (based on the estimate that phosphorus constitutes about 1% of the total organic matter and that the latter is about 10% of the wet weight).

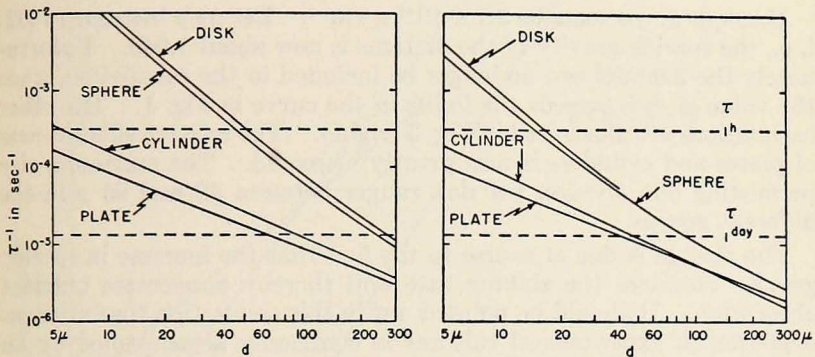


Figure 3. Absorption rates τ^{-1} (in sec^{-1}) for bodies of various sizes d (in μ) corresponding to example 1 (left) and example 3 (right).

Example 1. In well fertilized laboratory media, diatoms generally have a nearly negligible sinking rate. A similar condition may exist in the sea during flowerings. To simulate this condition in the model, let $\Delta\rho/\rho = .0001$; $\phi = 3.1 \times 10^{-8} \text{ g cm}^{-3}$ (1 $\mu\text{g-at P/l}$). This gives $d_0 = 0.052 \text{ cm}$, $v_0 = 3.8 \times 10^{-4} \text{ cm sec}^{-1}$, according to equations (7). For a sphere in water with $d = 0.01 \text{ cm}$ (100 μ), we find $d/d_0 = 0.19$, and hence $F_s = 19$, $F_s' = 1.5$, according to Figs. 1 and 2 respectively. From equation (5) we obtain $\tau^{-1} = 7.1 \times 10^{-5} \text{ sec}^{-1}$, or $\tau = 4$ hours; from (5a) $v = 5.6 \times 10^{-4} \text{ cm sec}^{-1}$, or 2 cm/hour. The computed absorption rates are plotted in Fig. 3 (left). They set a maximum limit to the size of diatoms that can absorb sufficient phosphorus to maintain an adequate division rate. For example, one division per day ($\tau^{-1} = 1.16 \times 10^{-5}$) requires that the width of a plate shall not exceed 76 μ and that the diameter of spheres, discs and cylinders shall not be greater than 260, 300, and 105 μ respectively. More than 90% of the marine diatom species fall within the prescribed maximum limits. Larger sizes require further reductions in specific gravity in order to maintain negligible sinking rates, and nutrient absorption then requires an increase in ϕ or a decrease in r .

Example 2. If ϕ is reduced to $3.1 \times 10^{-9} \text{ g cm}^{-3}$ ($0.1 \text{ } \mu\text{g-at } P/l$) and other conditions remain the same, the value of τ^{-1} in Fig. 3 (left) will be reduced one order of magnitude. Plates and cylinders capable of maintaining one division per day will then have a maximum dimension d of less than $10 \text{ } \mu$. Spheres and discs will have maximum diameters of 61 and $65 \text{ } \mu$ respectively. These are unrealistic results, particularly for plates and cylinders. Larger species have been observed in the sea under conditions of severe nutrient depletion.

Example 3. ϕ remains $3.1 \times 10^{-9} \text{ g cm}^{-3}$. Let $\Delta\rho/\rho$ increase to $.02$; i. e., the specific gravity of the diatoms is now about 1.045 . Unfortunately the flat disc can no longer be included in the calculation, since the value of d/d_0 exceeds the limits of the curve in Fig. 1. The other calculations are illustrated in Fig. 3 (right). The relative effectiveness of plates and cylinders is now greatly increased. The maximum size permitting one division per day ranges between 48 and $95 \text{ } \mu$ in the different groups.

The change is due of course to the fact that the increase in specific gravity increases the sinking rate and thereby accelerates nutrient absorption. It should be pointed out in this connection that nutrient depletion in experimental cultures is commonly accompanied by an increased sinking rate. The same phenomenon may occur in the sea toward the end of a flowering and perhaps throughout the summer. There may be an increase in specific gravity due to the accumulation of storage products that cannot be used for reproduction because of nutrient deficiency. If so, we can postulate a self-regulatory device, since the accumulation of storage products will automatically increase the rate of nutrient absorption. However, the value of such a device is limited. It serves no useful purpose if the sinking rate is rapid enough to carry the diatoms below the euphotic zone before the necessary cell divisions occur. The calculated sinking speeds shown in Fig. 4 are by no means negligible for the larger size categories. Thus it becomes necessary to include the problem of flotation in the solution of the example.

It should be pointed out that values for $\Delta\rho/\rho$ have been so chosen as to yield realistic results with regard to absorption rates. These values of $\Delta\rho/\rho$ may be regarded as minimum values; if they were smaller it would be impossible to reconcile the computed absorption rate with the observed rate of division. In this regard it can be noted that the minimum value under natural conditions (example 3) is several hundred times the value corresponding to well fertilized laboratory media (example 1). Values of $\Delta\rho/\rho$ can be larger than those given. In that case conditions other than nutrient absorption must be limiting the

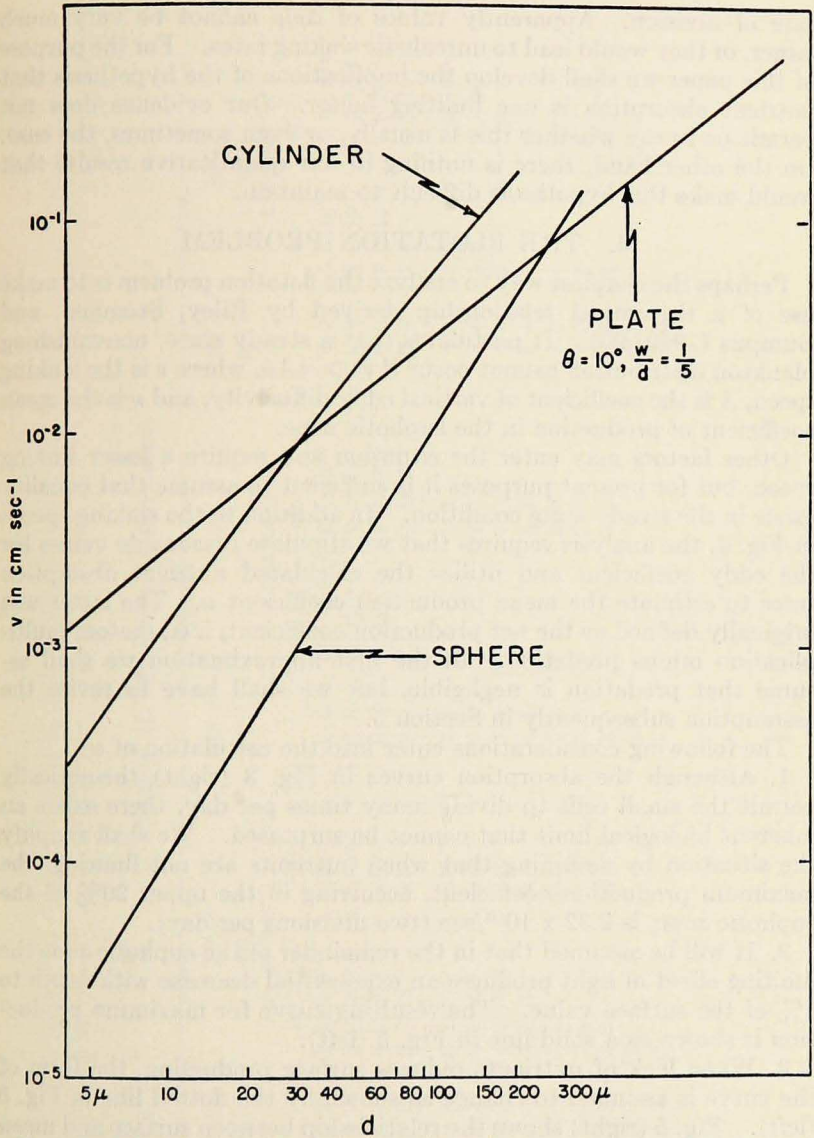


Figure 4. The sinking speed v (in cm sec^{-1}) for bodies of various sizes d (in μ), corresponding to example 3, with $\Delta\rho/\rho = 0.02$.

rate of division. Apparently values of $\Delta\rho/\rho$ cannot be very much larger, or they would lead to unrealistic sinking rates. For the purpose of this paper we shall develop the implications of the hypothesis that nutrient absorption is one limiting factor. Our evidence does not permit us to say whether this is usually, or even sometimes, the case. On the other hand, there is nothing in our quantitative results that would make this hypothesis difficult to maintain.

5. THE FLOTATION PROBLEM

Perhaps the simplest way to analyze the flotation problem is to make use of a theoretical relationship derived by Riley, Stommel, and Bumpus (1949: 90). It postulates that a steady state, nonvanishing plankton distribution cannot occur if $v^2 > 4A\omega$, where v is the sinking speed, A is the coefficient of vertical eddy diffusivity, and ω is the mean coefficient of production in the euphotic zone.

Other factors may enter the situation and require a lesser sinking speed, but for present purposes it is sufficient to assume that equality exists in the steady state condition. In addition to the sinking speeds in Fig. 4, the analysis requires that we stipulate reasonable values for the eddy coefficient and utilize the calculated nutrient absorption rates to estimate the mean production coefficient ω . The latter was originally defined as the net production coefficient, i. e., diatom multiplication minus predation. In the first approximation we shall assume that predation is negligible, but we shall have to revise the assumption subsequently in Section 6.

The following considerations enter into the calculation of ω :

1. Although the absorption curves in Fig. 3 (right) theoretically permit the small cells to divide many times per day, there exists an inherent biological limit that cannot be surpassed. We shall simplify the situation by assuming that when nutrients are not limiting, the maximum production coefficient, occurring in the upper 20% of the euphotic zone, is $2.32 \times 10^{-5}/\text{sec}$ (two divisions per day).

2. It will be assumed that in the remainder of the euphotic zone the limiting effect of light produces an exponential decrease with depth to 1% of the surface value. The resulting curve for maximum production is shown as a solid line in Fig. 5 (left).

3. When lack of nutrients reduces surface production, the form of the curve is assumed to change as shown by the dotted line in Fig. 5 (left). Fig. 5 (right) shows the relationship between surface and mean production that results from these assumptions.

Thus Figs. 3 (left) and 5 (left) may be used to estimate the mean production coefficient ω for various sizes and shapes of cells. Examples are given in Table II, which also lists a critical coefficient ω' :

TABLE II. PRODUCTION COEFFICIENTS

d μ	Sphere			Cylinder			Plate		
	$10^6 \omega$ sec ⁻¹	$10^6 \omega'$ sec ⁻¹ A (cm ² sec ⁻¹)		$10^8 \omega$ sec ⁻¹	$10^6 \omega'$ sec ⁻¹ A (cm ² sec ⁻¹)		$10^6 \omega$ sec ⁻¹	$10^6 \omega'$ sec ⁻¹ A (cm ² sec ⁻¹)	
		10	50		10	50		10	50
5	9.2	1.8x10 ⁻⁵	3.6x10 ⁻⁶	9.2	4.2x10 ⁻³	8.4x10 ⁻⁴	9.2	5.6x10 ⁻²	1.1x10 ⁻²
10	9.2	3.0x10 ⁻⁴	6.0x10 ⁻⁵	9.2	4.9x10 ⁻²	9.8x10 ⁻³	9.2	2.2x10 ⁻¹	4.4x10 ⁻²
20	9.2	4.8x10 ⁻³	9.6x10 ⁻⁴	9.2	5.1x10 ⁻¹	1.0x10 ⁻¹	9.2	9.0x10 ⁻¹	1.8x10 ⁻¹
30	9.2	2.5x10 ⁻²	5.0x10 ⁻³	8.9	2.2	4.4x10 ⁻¹	7.8	2.0	4.0x10 ⁻¹
40	9.2	8.1x10 ⁻²	1.6x10 ⁻²	7.3	5.6	1.2	6.6	3.6	7.2x10 ⁻¹
50	9.2	2.0x10 ⁻¹	4.0x10 ⁻²	6.1	11	2.2	5.6	5.6	1.1
60	9.2	4.2x10 ⁻¹	8.4x10 ⁻²	5.3	20	4.0	4.9	8.1	1.6
70	8.0	7.8x10 ⁻¹	1.6x10 ⁻¹	4.7	32	6.4	4.4	11	2.2
80	7.0	1.3	2.6x10 ⁻¹	4.2	48	9.6	4.1	14	2.8
90	6.3	2.2	4.4x10 ⁻¹	3.9	73	15	3.8	18	3.6
100	5.6	3.3	6.6x10 ⁻¹	3.5			3.5	22	4.4
150	3.7	17	3.4	2.5			2.6	50	10
200	2.9	58	12	1.9			2.0		

$$\omega' = \frac{v^2}{4A}.$$

When ω exceeds ω' , the cells will increase unless predation is equal to the difference between the two quantities. When ω is less than ω' , the species must vanish. Lines in Table II indicate approximately the maximum size of cells that can exist in a steady state condition ($\omega = \omega'$).

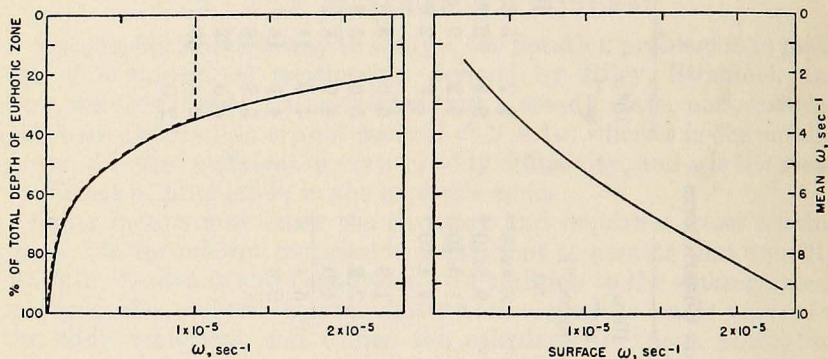


Figure 5. Left: Production coefficient as function of depth. Dashed line illustrates case where nutrient absorption limits production to 1 division in 10^5 seconds in upper 35% of euphotic zone, and the light intensity limits production in lower 65%. Solid line represents conditions for unlimited nutrient supply. Right: Relationship between surface production and mean production in euphotic zone.

The results serve only to specify maximum size limits. They reveal no good reasons for the evolution of the diatoms into a variety of shapes and sizes. Fig. 3 and Table II indicate that it is an advantage for them to be small. In all size categories, a primitive centric type approximating a sphere appears to be slightly superior to the more elaborate shapes.

6. THE GRAZING FACTOR

The fact that neither flotation nor nutrient absorption imposes severe limits upon cells of less than 20μ must mean that some other factor is decidedly unfavorable. Otherwise the larger species would not be able to compete with the small cells. Predation is a possible explanation. Although it has been demonstrated (Harvey, 1937) that a large copepod such as *Calanus finmarchicus* feeds most effectively on large cells, it seems likely that the small animals which constitute the major bulk of the zooplankton population would have definite limits as to the size of the food they encompass. Therefore, two hypotheses are proposed: (a) The average predation coefficient decreases with an

increase in the size of the food species; (b) the coefficient of predation on a sphere is larger than for a cylinder of the same diameter or for a plate of the same width.

An analysis of the hypotheses may be developed as follows:

1. Assume a diatom population of spheres, cylinders, and plates of varying sizes up to the maximum size that can maintain a steady state (cf Table II). In each size category, let the number of spheres, cylinders, and plates be initially equal.

2. Further assume that the total number of cells in the population has a steady state existence. This does not necessarily imply that any particular shape of cell exists in a steady state, but if, for example, the number of spheres of a particular size increases, there must be a corresponding decrease of plates or cylinders. The requirements of the first two assumptions will be fulfilled if, in each size category, the production coefficient equals the mean value of ω' (Table II) for the three shapes. This in turn requires that the predation coefficient equal the mean value of $\omega - \omega'$. The latter decreases with increasing size of the cells in accordance with hypothesis (a).

3. To fulfill hypothesis (b), a modification must now be introduced. It is arbitrarily assumed that the coefficient of predation on a cylinder of a given diameter and on a plate of the same width will be equal to the predation on a sphere with a diameter three times as large. This is readily accomplished in the model by comparing 10 μ cylinders and plates with 30 μ spheres, etc.

Thus in the two examples in Table II ($A = 10$ and $A = 50 \text{ cm}^2 \text{ sec}^{-1}$), positive values of $\omega - \omega'$ are averaged for each of the stipulated size groups. For each shape, the deviation of $\omega - \omega'$ from the mean is plotted in Fig. 6. Within the limits of the simplified assumptions, the deviations of each shape from the steady state existence of the population as a whole are indicative of the competition pressure exerted by a particular size and shape of diatom.

Cells of less than 20 μ show no striking differences in ability to compete. Within this range, competition must depend primarily upon factors that are not considered in the present analysis, namely inherent biological potentialities and reactions to the physical variations of the environment. In the larger size categories, cylinders appear to be particularly effective in the size range of 20 to 55 μ , plates from 30 to 95 μ . The spheroidal type appears to have a wider range of effectiveness than the other two shapes. In the present example it is not excessively dominant in any size category, but the form of the curve can be altered by changing assumption 3. If the spheres are compared with other shapes of half the size, instead of one-third, there is a strong peak of effectiveness centered at 60 μ .

7. COMPARISON WITH OBSERVED SIZE-FREQUENCY DISTRIBUTIONS

To determine whether these results have any meaning, we must inquire as to whether they bear any relation to observed diatom speciation. A list of species was prepared, more or less approximating the ideal shapes under consideration. The list will not be reproduced in detail, but the following genera were included:

Spheroids	Cylinders	Plates
<i>Thalassiosira</i>	<i>Rhizosolenia</i>	<i>Eucampia</i>
<i>Coscinodiscus</i>	<i>Lauderia</i>	<i>Climacodium</i>
<i>Hyalodiscus</i>	<i>Schroderella</i>	<i>Streptotheca</i>
<i>Lauderia</i>	<i>Dactyliosolen</i>	<i>Hemiaulis</i>
<i>Stephanodiscus</i>	<i>Leptocylindricus</i>	<i>Striatella</i>
<i>Biddulphia</i>	<i>Guinardia</i>	<i>Plagiogramma</i>
	<i>Ditylum</i>	<i>Pseudoeunotia</i>
	<i>Cerataulina</i>	<i>Achnathes</i>
22 species	31 species	11 species

Lauderia glacialis is placed among the spheroids, *L. borealis* with the cylinders.

The size limits of each species as listed by Cupp (1943) were then used to determine the size-frequency distribution of each shape, expressed as the percentage of the total number of species occurring in each size category. The results, plotted in Fig. 6, show that frequency modes of observed speciation correspond with favorable portions of the theoretical curves.

The large and important genus *Chaetoceros* is not included in the analysis. The individual species intergrade between plate-like and cylindrical form. The effect of the spines on its behavior is uncertain. However, examination of the genus shows a mode in the number of species at 12 μ , with less than 20% of the species in any size category above 35 μ . It could be placed with plates or cylinders without producing serious discord.

A small number of spheroids and cylinders (primarily *Coscinodiscus* and *Rhizosolenia*) greatly exceed the maximum size limits predicted by the example. They probably represent a special case that does not meet the initial assumptions. *Coscinodiscus* in particular has an unusually large vacuole, which probably gives it an abnormally low specific gravity and nutrient content. This appears on theoretical grounds to be virtually a necessity for large diatoms occurring in stable waters deficient in nutrients. For example, the 200 μ sphere in Table II requires an eddy coefficient of 200 $\text{cm}^2 \text{sec}^{-1}$ in order to maintain

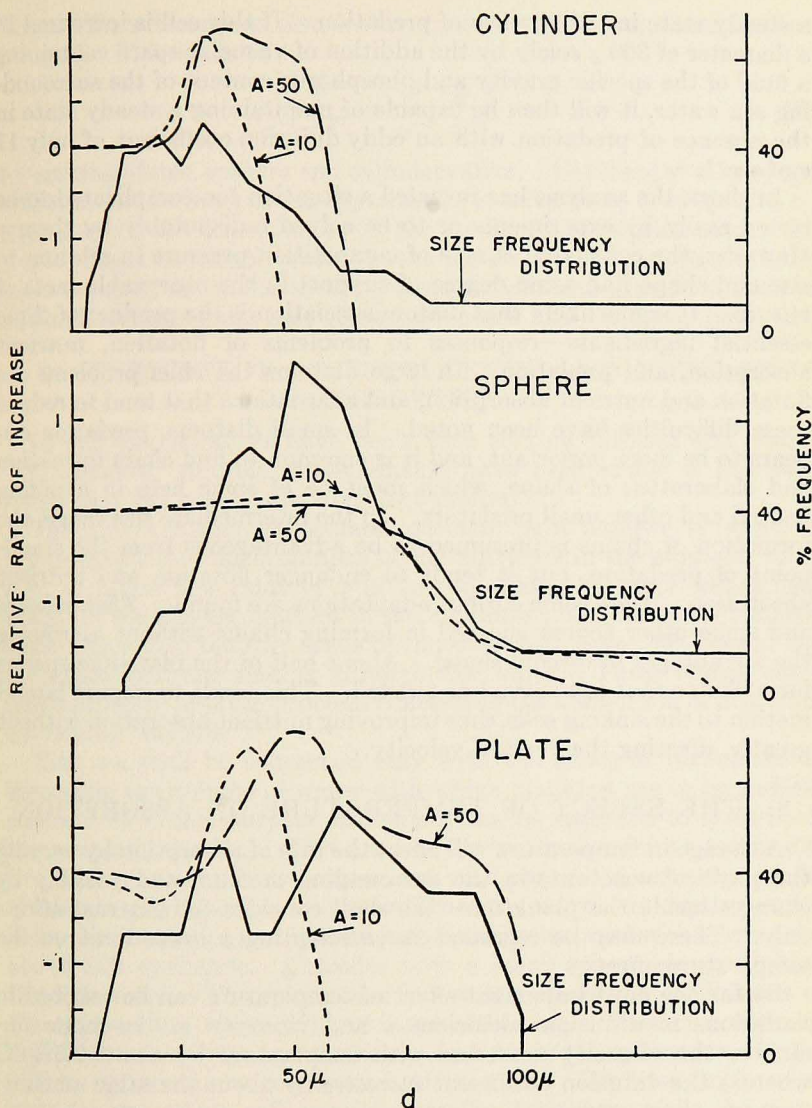


Figure 6. The dashed lines, corresponding to eddy viscosities of 10 and 50 $\text{cm}^2 \text{sec}^{-1}$, are indicative of the "competition pressure" exerted by diatoms of stated shapes and sizes. These curves are based on an analysis which takes into account nutrient absorption, the flotation problem (including sinking rates and vertical overturn), and the grazing factor. The solid curves give the observed size-frequency distribution for species resembling spheroids, cylinders, and plates, respectively.

a steady state in the absence of predation. If this cell is increased to a diameter of 300μ solely by the addition of vacuolar space containing a fluid of the specific gravity and phosphorus content of the surrounding sea water, it will then be capable of maintaining a steady state in the absence of predation with an eddy diffusion coefficient of only $17 \text{ cm}^2 \text{ sec}^{-1}$.

In short, the analysis has revealed a situation too complicated to be tested easily by experiments or to be solved indisputably by theory. However, the calculated curves of competition pressure in relation to size and shape find some degree of support in the observable facts of nature. It seems likely that diatom speciation is the product of three essential ingredients—responses to problems of flotation, nutrient absorption, and predation. In large diatoms the chief problems are flotation and nutrient absorption, and adaptations that tend to reduce these difficulties have been noted. In small diatoms, predation appears to be more important, and it is common to find chain formation and elaboration of shape, which must be of some help in avoiding nauplii and other small predators. In the intermediate size range, the formation of chains is presumed to be advantageous from the standpoint of predation, but it tends to endanger flotation and nutrient absorption. Here some curious adaptations are found. *Thalassiosira* and some other genera succeed in forming chains without sacrificing the advantages of discoid shape. About half of the plate-like species form chains that are curved or twisted. This tends to impart lateral motion to the sinking cells, thus improving nutrient absorption without greatly affecting the vertical velocity.

8. THE EFFECT OF TEMPERATURE ON ABSORPTION

A change in temperature will effect the rate of absorption by varying the physical constants in the surrounding medium and possibly by changes inside the plankton. We shall consider the external effects only. These may be regarded as constituting a lower limit on the temperature effect.

By far the most important effect of temperature can be ascribed to variations in diffusion coefficient k and viscosity ν . In most substances the viscosity decreases with temperature by about $2.5\%/^{\circ}\text{C}$ whereas the diffusion coefficient *increases* by about the same amount:

$$\alpha = \frac{1}{k} \frac{dk}{dT} = - \frac{1}{\nu} \frac{d\nu}{dT} = 0.025 \text{ } (^{\circ}\text{C})^{-1}.$$

The coefficients appear in the combination $(\nu k)^{1/3}$ in the parameter d_0 , and the temperature effects of ν and k cancel in the first approximation.

The coefficients appear also in the constant τ_0^{-1} in the combination $k^{1/3} \nu^{-2/3}$. This leads to

$$\frac{1}{\tau^{-1}} \frac{d\tau^{-1}}{dT} = \frac{1}{\tau_0^{-1}} \frac{d\tau_0^{-1}}{dT} = \alpha \quad (9)$$

for sinking plates, spheres and cylinders alike. Goldberg's⁸ very rough estimate on the basis of his experiments is a factor of 5-10%/°C, i. e., from 2α to 4α . According to (9) the maximum absorption rate in the tropics might be roughly twice that in the arctic. Similar results have been obtained in studies of the photosynthesis and growth of natural phytoplankton populations (Riley, Stommel and Bumpus, 1949: 94).

9. THE EFFECT OF TURBULENCE AND NOISE ON ABSORPTION

In our discussion we have dealt with sinking through still water. Yet whenever suitable measurements have been made, it has been found that the ocean is in turbulent motion.

Turbulence enters the general problem in a number of ways: it brings about the replenishment of the nutrients in the euphotic zone, i. e., it affects the value of ϕ in our equation (1); large eddies help maintain the sinking diatoms in the euphotic zone (Section 5); turbulence also erases the tiny trails of impoverished water left behind the individual diatoms sinking through the water. These effects enter only indirectly into the problem concerning the absorption of nutrients by sinking diatoms.

Here we shall be concerned only with the effect of turbulence in increasing the volume of water with which plankton are in immediate contact. For this purpose turbulence can be regarded to include all the unsteady motion. This motion can be resolved into many different frequencies. Low frequencies, with periods of, say, 10 seconds, are due largely to ocean waves (whether the waves are regular or not is of no consequence here); noise in the sea is associated with frequencies above 100 cycles/sec. Consider now a small sphere slowly sinking through water. The sphere can follow low frequency oscillations of the surrounding water without appreciable lag. However, with increasing frequency a condition is reached where the sphere is no longer able to follow the water motion without lag. For even higher frequencies the sphere will remain virtually stationary, while the water will wash back and forth along its sides. Such high frequency turbulence is therefore associated with a "forced draft" which can be expected to increase the nutrient made available to plankton.

⁸ Personal communication.

For any *fixed* amplitude of oscillation, the most effective forced draft is associated with the highest frequencies, i. e., acoustic noise. However, it is found that amplitude of oscillations in the ocean drops off so rapidly with increasing frequency that the most effective portion of the turbulence spectrum lies in the low frequencies. Even there, as will be shown, the effect is quite small.

TABLE III. VALUES OF PERTINENT PARAMETERS

	Surface waves	Sound waves	
Frequency $\sigma/2\pi$ in cycles per second	10^{-1}	10^2	10^4
Wave length L in cm	15,000	1500	15
β for $d = 10^{-2}$ cm (100 μ)	2×10^{-6}	2×10^{-5}	2×10^{-3}
γ for $d = 10^{-2}$ cm (100 μ)	0.03	0.9	9

The theory is rather involved. Fortunately it is closely related to the problem of the attenuation of sound by fog, which has received the attention of the mathematicians and experimentalists (Epstein, 1941). Let us define the ventilation

$$h = \frac{v_{\text{water}} - v_{\text{sphere}}}{v_{\text{Stokes}}}$$

as the ratio between the mean slippage through the water associated with turbulence, and the sinking velocity v_{Stokes} according to Stokes' law. The slippage depends on three dimensionless quantities,

$$\frac{\Delta\rho}{\rho}, \quad \beta = \frac{\pi d}{L}, \quad \gamma^2 = \frac{\sigma d^2}{8\nu},$$

where L is the wave length, σ frequency, and $C = L\sigma/2\pi$ the wave velocity. Some values of β and γ are given in Table III. It appears that γ may be large or small compared to unity but that $\beta \ll 1$. In addition $(\Delta\rho/\rho) \ll 1$. With these approximations it can be shown (Appendix 2) that

$$h = \frac{48\nu}{\pi g d^2} f(\gamma) V, \quad (10)$$

where

$$f = \gamma^2/3,$$

$$f = 1/2,$$

according to whether the frequency is small ($\gamma \ll 1$) or large ($\gamma \gg 1$). Here V is the amplitude of the velocity of oscillation of the water.

Surface Waves. For very low frequencies equation (10) gives the ventilation arising from the viscous effects only. This can be used to analyze the effect of surface waves whose height H equals $2V/\sigma$, and wave length $L = 2\pi g/\sigma^2$. Equation (10) then becomes simply

$$h = 2H/L.$$

The theoretical maximum for H/L equals $1/7$ and leads to $h = 0.28$. This value is attained only under extreme conditions; furthermore it applies only to a thin upper layer of thickness, say $L/10$, and diminishes rapidly with increasing depth. Thus under extreme conditions the absorption may be increased by something like 25% in the upper 10 or 20 feet.

Noise. For ambient sound it is convenient to convert the amplitude of oscillation to pressure amplitude P and express these in the customary units (see, for example, Knudsen and Harris, 1950). Thus

$$V = \frac{P}{\rho C}, \quad P = \frac{1}{5000} 10^{L'/20},$$

where L' is the sound level in db 's above 0.002 dynes cm^{-2} . Measurements of ambient noise (Knudsen, et al., 1948) are well represented by straight lines on a graph L' against $\log \sigma$, such as

$$L' = 20 a - 20 b \log(\sigma/1000).$$

This leads to

$$\delta h = \frac{48 \nu f(\gamma)}{5000 \pi \rho g C d^2} 10^{a+3b} \sigma^{-b} \delta \sigma$$

for each frequency band $\delta \sigma$. We shall overestimate the effect by setting $f(\gamma) = 1/2$. Integrating from σ_1 to σ_2 , this gives

$$h = h_0 \frac{10^{a+3b}}{1-b} \left(\sigma_2^{1-b} - \sigma_1^{1-b} \right),$$

where

$$h_0 = \frac{24 \nu}{5000 \pi \rho g C d^2}$$

equals 10^{-9} for $d = 0.01$ cm (100μ).

For ordinary water noises from 100 to 25,000 cycles, $a = 2.25$, $b = 0.8$. Since $1 - b$ is positive, the larger contribution is made by the higher frequencies. Between the stated limits, this gives $h = 10^{-3}$.

In a very noisy croaker bed one may set $a = 4$, $b = 0$ from $\sigma = 10^2$ to 10^3 sec^{-1} , and $a = 4$, $b = 3$ from 10^3 to 10^4 sec^{-1} . These values lead to $h = 10^{-2}$ for either range of frequencies. The effect of ambient noise is therefore negligible.

APPENDIX I: DERIVATION OF ABSORPTION RATES

The three nondimensional numbers that are encountered in problems of forced convection are the Reynolds, Prandtl, and Nusselt numbers

$$Re = \frac{vd}{\nu} \quad Pr = \frac{\nu}{k} \quad Nu = \frac{9d}{ks\phi} \quad (11)$$

In some texts the Péclet number $Pe = Re Pr$ is referred to. Here v is the velocity at large distances, ν the kinematic viscosity, k the diffusivity, q the grams of a concentrate transferred each second to an immersed body of surface area s , ϕ the concentration at large distances over that at the surface of the body (in g cm^{-3}), and d a representative dimension of the body. Let p be the volume, ρ the density, and $m = \rho p$ be the mass of the body. Then equation (1) can be written

$$\tau^{-1} = \frac{\phi}{r\rho} \frac{ks}{vd} Nu = \frac{\phi}{r\rho} \left(\frac{\Delta\rho}{\rho} \right)^{2/3} \tau_0^{-1} GF, \quad (12)$$

where

$$G = sd/cp \quad (13)$$

depends on the geometric dimensions, and

$$F = 72^{-2/3} c Nu(d/d_0)^{-2}. \quad (14)$$

The constant c is so chosen as to make G a ratio of dimensions only.

With regard to sinking rate, it is convenient to define a quantity $u_0 = k/d_0$. Then it follows from (11) that

$$\frac{u}{u_0} = \frac{Re Pr}{d/d_0}. \quad (15)$$

Attached Plate. This problem has been studied theoretically by Pohlhausen with regard to a flat plate thermometer oriented parallel to flow (Goldstein, 1938: Chap. 14). For one side of the plate

$$Nu = 0.67 Pr^{1/2} Re^{1/2}, \quad (16)$$

where d in the Reynolds number now represents the length of a thin plate in the direction of flow. The equation has been verified experimentally. For the dimension as given in Fig. 1, substitution of (16) into (1) leads at once to equation (2).

Sinking Plate. The quantity v is no longer an independent variable but equals the sinking speed. Consider the plate slicing obliquely downward and forming an angle θ with the horizontal (Fig. 1). Then after the plate has reached its terminal velocity, the frictional forces on its sides is balanced by the pull of gravity:

$$2Tld = g \sin \theta \Delta\rho lwd,$$

where T is the frictional stress per unit surface area and $\Delta\rho$ the density of the diatom minus the density of the surrounding medium. The stress can be equated to

$$T = \nu \rho \left(\frac{dv}{dy} \right)_{y=0} = 2\nu \nu \rho \frac{2}{5.83} \sqrt{\frac{v}{\nu d}}$$

according to Von Kármán's boundary layer theory (Goldstein, 1938: Chap. 4). This leads to the dimensionless expression

$$Re^{3/2} = 0.73(\Delta\rho/\rho)g \sin \theta w d^2 \nu^{-2} \\ = (0.73)(72) \sin \theta (w/d) Pr^{-1}(d/d_0)^3 \quad (17)$$

for the sinking rate $v = Re \nu/d$ along an axis inclined by an angle θ . Combining equations (13) to (17) leads to

$$G_p = (d^2 \sin \theta/w^2)^{1/3}, \\ F_p = (1.34)(0.73)^{1/3}(72)^{-1/3}(d/d_0)^{-1} = 0.29(d/d_0)^{-1}, \\ F_p' = (0.73)^{2/3}(72)^{2/3}(d/d_0) = 14(d/d_0).$$

Sinking Sphere. For Pr from 0.7 to 400 and Nu from 10 to 40, the following relationship is in agreement with experimental evidence and dimensional considerations (Kramer, 1946):

$$Nu = 2.0 + 1.3 Pr^{0.15} + 0.66 Pr^{0.31} Re^{0.15}. \quad (18)$$

Note the combination $Pr^{0.31} Re^{0.5}$, which is similar to the one encountered for the flat plate. For water and air this becomes, respectively

$$Nu = 5.3 + 4.6 Re^{0.5} \quad (18w)$$

$$Nu = 3.3 + 0.66 Re^{0.5}. \quad (18a)$$

In these experiments the rate of flow past the sphere, as expressed by Re , could be varied independently. For freely falling spheres, it is already determined by the balance between the gravitational force and the drag:

$$\frac{1}{6} \pi \Delta \rho g d^3 = \frac{1}{2} C_D \rho v^2 \left(\frac{\pi d^2}{4} \right).$$

The drag coefficient in the range over which Stokes' law is applicable equals $C_D = 24 Re^{-1}$. We shall write, in general,

$$C_D = 24 Re^{-1} f_s, \quad (19)$$

where the function $f_s(Re)$ can be taken from experimental data (Goldstein, 1938: 493). This leads to the dimensionless expression

$$f_s Re Pr = 4(d/d_0)^3 \quad (20)$$

for the sinking rate $v = \nu Re/d$ of a freely falling sphere. Thus $F_s' = 4(d/d_0)^2/f_s$. The absorption rate for the sphere (eq. 5) is now obtained

in the following manner: in eq. (13) we set $s = \pi d^2$, $p = \pi d^3/6$, and $c = 6$. This leads to $G_s = 1$, and

$$F_s = 6 \times 72^{-2/3} Nu(d/d_0)^{-2} = 0.345 Nu(d/d_0)^{-2}. \quad (21)$$

We then substitute for Nu in terms of Re according to (18) and for Re in terms of d/d_0 according to (20).

For small values of $Pe = Re Pr$, Kronig and Bruijsten (1951) obtain from theory⁹

$$Nu = 2 + \frac{1}{2} Pe + \frac{581}{1920} Pe^2 + \dots \quad (22)$$

The empirical and experimental curves are shown in Fig. 1.

Sinking Disc. According to Oberbeck (Lamb, 1932: 597-604), $Nu = 8/\pi$ for a disc at rest. This compares to $Nu = 2$ for a resting sphere. Setting $s = \pi d^2/2$, $p = w\pi d^2/4$, and $c = 2$ gives $G_a = d/w$ and $F_d/F_s = 4/3\pi$. This ratio applies only to small discs (Fig. 1). We know of no empirical or theoretical evidence which would permit us to extend these calculations into a more pertinent range.

In computing the sinking rate of a small disc, we note that, according to theory and observations, small (but not too small) objects sink with the flat side horizontal. Equating the resistance to the force of gravity,

$$6\pi \mu \left(\frac{4d}{3\pi} \right) v = \pi \left(\frac{d}{2} \right)^2 w \Delta \rho g$$

leads to

$$Re Pr = \frac{9\pi w}{4 d} \left(\frac{d}{d_0} \right)^3$$

for the sinking speed. This yields $F_d' = (9\pi/4)(d/d_0)^2$.

Sinking Cylinder. Because of the relative ease with which measurements can be made with fine wires, the empirical evidence is more complete than for other shapes. For $Re > 50$, Ulsamer (Kramer, 1946) finds

$$Nu = 0.60 Pr^{0.31} Re^{0.5}. \quad (23a)$$

The occurrence of $Pr^{0.31} Re^{0.5}$ should be noted. For Re from 0.1 to 50, Ulsamer finds, on the average,

$$Nu = 0.91 Pr^{0.31} Re^{0.385}. \quad (23b)$$

At $Re = 0.1$, $Nu \sim Re^{0.3}$ approximately. There is also some theoretical evidence that, for very small Reynolds numbers, Nu should be a function of $(Pr Re)$ only, hence the exponent of Re would approach 0.31. Apparently we shall not be far amiss if we set

⁹ See footnote 10 on p. 240.

$$Nu = 0.8 Pr^{0.31} Re^{0.31} \quad (23c)$$

for $Re \ll 1$. For the long cylinder (unlike the sphere), Nu must approach zero as Re approaches zero, in agreement with the foregoing type of equations. These three equations (23) define the relationship $Nu(Re)$ with sufficient accuracy for our purposes.

We can again express the sinking rate in nondimensional form. Using the relationships given by Lamb (1932: 616) we obtain

$$\frac{Re f_c Pr}{\kappa - \ln Re} = \frac{9}{2} \left(\frac{d}{d_0} \right)^3,$$

where

$$C_D = \frac{8\pi f_c}{Re(\kappa - \ln Re)}$$

is the drag coefficient, and $f_c(Re)$ can again be determined from empirical data (Goldstein, 1938: 16). For $Re \ll 1$, Oseen's investigations (Lamb, 1932: 616) lead to $f_c(Re) = 1$. Here $\kappa = 0.5 + \log 8 - \eta = 2.00$, and $\eta = 0.577$ is Euler's number. Setting $s = \pi d$, $p = \pi d^2/4$, and $c = 4$ gives $G_c = 1$, and

$$F_c = 4 \times 72^{-2/3} Nu (d/d_0)^{-2} = 0.23 Nu (d/d_0)^{-2}. \quad (25)$$

We then substitute for Nu in terms of Re according to (23) and for Re in terms of d/d_0 according to (24).

APPENDIX II.

The ratio "R" between the displacement of a rigid sphere of density $\rho + \Delta\rho$ to that of the water (density ρ) at the position of its center when the sphere is absent is given by (Lamb, 1932: 659-661)

$$R = 1 - \frac{\Delta\rho}{\rho f' + \Delta\rho}, \quad (26)$$

where

$$f' = \frac{3}{4\gamma^2} \left[2\gamma^2 + 3\gamma - i(4\beta\gamma + 3\gamma + 3) \right]. \quad (27)$$

According to Table II, $\beta \ll 1$. Furthermore, $\beta \ll \alpha$, provided $2\nu\sigma/C^2 \ll 1$ or $\sigma \ll 10^{12} \text{ sec}^{-1}$. The simplifications resulting from these approximations have been incorporated in equations (26) and (27).

The following extreme cases should be noted:

1. The sphere oscillates essentially with the surrounding water ($R = 1$) (a) if its density equals that of the surrounding water ($\Delta\rho = 0$), (b) for low frequencies ($\sigma = 0$, $\beta = 0$), (c) for small spheres ($d = 0$, $\beta = 0$), and (d) for very viscous fluids ($\nu = \infty$, $\gamma = 0$).
2. The sphere does

not partake in the oscillation of the surrounding water ($R = 0$) if its density is large ($\Delta\rho = \infty$).

If $\Delta\rho \ll \rho$, $R = 1 - \Delta\rho/\rho f'$, then the mean value of $v_{\text{sphere}} - v_{\text{water}}$ equals

$$\frac{2}{\pi} V \frac{\Delta\rho}{\rho} (f_r'^2 + f_i'^2)^{-1/2},$$

where f_r' and f_i' are the real and imaginary parts of f' . Combining this with Stokes' equation for a small sinking sphere leads to

$$f(\gamma) = \gamma^2(4\gamma^4 + 12\gamma^3 + 18\gamma^2 + 18\gamma + 9)^{-1/2}. \quad (28)$$

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Footnote 10 (added in page proof). Prof. Paul Epstein has just drawn our attention to the fact that the method used by Kronig and Bruijsten (1951) leads to a divergent series, and that only the first two terms in equation (22) of Appendix I, p. 238, are correct. The third term should be $-\frac{1}{4} Pe^2 \ln(\frac{1}{2}\Gamma e^{1/4} Pe)$ instead of $+(581/1920) Pe^2$, where $\Gamma = 1.781$ is Euler's number. Actually the numerical values and the curve in Fig. 1 are not appreciably affected by this correction.