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DEPTH RELATIONSHIPS OF PLANKTON DIATOMS IN SEA WATER*

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For more than twenty years I have been directly interested in the space relationships of marine plankton organisms. Not least among the unsolved problems of these relationships is that of the maintenance of residence at appropriate depths by microscopic creatures, e. g., the plankton diatoms. Even the questions concerning the fate of the dead bodies, empty frustules, or other remains of these tiny plants have considerable importance not only for the marine biologist but also for the marine hydrologist, or physicist, or chemist. Such problems are difficult enough if presented in the simplest form for a particular kind of particle of designated shape, density, dimensional limits, frictional characteristics, solubility, etc. They are far more difficult in Nature because of the endless complications and modifications introduced by biological influences of many kinds.

Still, I believe that there exist certain major tendencies of behavior of microscopic particles in respect to maintenance of level or change of levels in natural waters which might be worked out if a well-organized program of investigations were carried over a period of time and a wide extent of observable conditions. However, I do not believe that the rate of settling of marine plankton diatoms, or of their frustules (the kinds of small particles most familiar to me) can ever be expressed dependably by a mathematical formula because, at any given point in the sea, sinking may occur according to formula today and not tomorrow, the difference being due to influences added, subtracted, or modified in ways not open to prediction.

While a study of marine deposits shows that plankton diatoms are represented in them, this representation is much less than might be expected from our knowledge of excessive abundances in many seas. The reasons for this condition are probably to be found mainly in the characteristics fitting the plankton forms for a suspended existence and in the influences contributing to their suspension. Consequently, there are interesting relationships between the problems of suspension

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and of deposition as well as between those of suspension and maintenance of life.

There are recorded nearly two hundred species of marine diatoms which seem to spend most of their active existences adrift. For all such it appears that suspension must be an advantage and that they must possess some means of regulating it within necessary limits. For them the primary need is to keep suspended at the levels which are favorable for their growth and development. Confronted with the endless vagaries of waves, currents and other disturbances, this often proves to be impossible. On the other hand, the vast numbers in which these tiny plants appear from time to time in many parts of all oceans show that they have some means for keeping contact with tolerable if not with favorable conditions. Needless to say, these powers of holding an acceptable level add indefinitely to the difficulty of measuring or of describing their powers of suspension and of distinguishing between physical and biological causes of the phenomena of suspension or of deposition in any particular case.

In the discussion of ability to keep adrift considerable stress is rightly given to the production of gases and oils by the living substance. Since the microscopic plant has nearly the same specific gravity as ordinary sea water, it seems to be certain that a slight change in relative volume of either gas or oil would suffice to make the diatom either lighter or heavier, and so capable of shifting position slightly in either the downward or upward direction. Since it is improbable that for any individual diatom this power of adjustment would be worth much in relation to change in level, it seems probable that its value would lie in approximate maintenance at a tolerable or favorable level.

A less changeable feature in relation to suspension is that of structure of the frustules, the walls being thinner and lighter in all floating diatoms and showing highly modified protuberances in many forms. In the genus Chaetoceros these protuberances have the shape of delicate hairs many times longer than the main body and so presenting a relatively enormous expanse of surface to delay sinking. Some kinds of plankton diatoms get similar relative expanse of surface by merely lengthening the whole frustule into a thread, without much development of protuberances. Reduction in size of the body would have a similar effect but it is not clear that this would be likely to occur in a way to promote suspension at a favorable level.

Formation of mucous threads or films might be expected to give material aid to suspension by increase of friction over larger and moving surfaces, but since the diatoms of colder seas exhibit these developments more generally, it may be doubted that they have high value in
that way. Still, it may be that they do and that they are more prominent in colder seas because of some coincidental condition.

In some species it seems probable that the extrusion of protoplasmic threads or streams aids in suspension, partly by exerting stream friction against the surrounding water and partly by increase of surface.

If suspension is really promoted by this means it can be more directly controlled than by any of the others mentioned. While, at first, it may seem improbable that the effect of protoplasmic extensions would be great enough to have appreciable effect on suspension, this improbability tends to disappear when one recalls that for the living diatom very little influence is needed to tip the balance of adjustments to favor suspension.

For the sake of clarity most of the foregoing discussion has been written as though the surroundings of marine plankton diatoms were fairly constant, as they are not even at a single chosen depth. Various features in the ordinary relationships of these surroundings may or may not aid in suspension at a favorable level. In many cases suspension is promoted by slight (unobservable) movements of small water masses either horizontal, vertical, or irregular. No trustworthy data exist from which to estimate the importance of this influence but that it must be considerable is indicated by the movements of diffusion and of mixing of minute and microscopic particles often observable in small masses of water and in air. On the other hand, it is still more certain that such movements may carry certain diatoms or certain populations to a lower or higher level or to some lateral point which is less favorable for suspension or maintenance.

Still more indefinite and elusive would be the effects of movements of vigorously swimming animals which must be directly disturbing to suspension of diatoms in any certain relation but which indirectly constitute aid to suspension by changing gaseous and organic content of the water and by promotion of vigor in all functions of the microscopic plant. This indirect effect might include removal of particular diatoms to levels extremely favorable, in which their increasing numbers and more vigorous growth would aid materially in securing suspension although the general alteration of relationships may have been considerable.

Ordinarily conditions of viscosity may be supposed to favor suspension of diatoms which have adjusted themselves to conditions at a particular depth in the sea, because viscosity is understood to increase with increase of pressure and with decrease of heat. But nearly all diatoms are active only at depths less than seventy meters, in all cases
being confined to levels within reach of numerous causes of disturbance of water masses. For such reasons it appears that viscosity does not bear a constant relation to level and that it is subject to considerable variation at different points in any level, depending upon more or less immediate influences of wind, wave, and of bottom topography. The same is true of a number of other physical and chemical conditions which may have possibilities of influence on flotation.

In harmony with the foregoing suggestions it seems fair to assume that in ordinary conditions of all seas there is little tendency for plankton diatoms to settle to the bottom so long as they are in vigorous activity, either photosynthetic or assimilative. It is probable that those forms having heavier and smoother frustules are able to offset their greater tendency to sink by developing some peculiarity in this activity, for example, special formation of oils or frequent division to produce smaller cells.

At any rate, it seems to be certain that most of those tending to deposition are moribund, dead, or otherwise inactive. The more common forms of individual cells in plankton diatoms are smooth discoid, rough or spinose discoid, heavily setose discoid, cylindrical, spindle shaped, and filamentous. Many of them unite into chains so that they behave more or less like filaments. Even when the living matter has disappeared and only the bare frustules are left the chains are often prominent in a plankton catch and they are probably much more prominent in the undisturbed condition in the sea. This is especially true of smaller forms in the genus *Chaetoceros* which often appear in large numbers in the dead or cleaned (empty frustule) condition near the surface of the sea, indicating that sinking may be a long and highly variable process for many plankton diatoms.

Judging from the rate at which diatoms sink through a distance of several centimeters in a container in the laboratory one might conclude that they may sometimes settle from higher to lower levels in the sea at a rate of several meters per day, perhaps as many as twenty or thirty meters. However, no reliable data concerning the rate of sinking exist, not even as to the laboratory differences in rates shown in relation to the different species. Therefore, it seems highly probable that laboratory observations lack dependability as a basis for estimating or understanding the actual rates of sinking in the ocean, just as they do for so many other natural phenomena.

For one thing, the mere increase in viscosity as successive lower levels are reached in descending from the surface in many instances would be sufficient to materially change the rate of sinking, perhaps almost stopping descent below the hundred meter level for delicate frustules. This, together with slight movements of surrounding
water particles might result in an empty frustule remaining afloat for so long that it would disintegrate or redissolve into a colloidal or other state in which its substance would remain suspended without ever being deposited. There seems to be a reasonable probability that this actually happens and that the lack of abundance of plankton forms in marine sediments is due to the ordinary tendency of sea water to reduce their delicate frustules to solution. That is to say, the problem of suspension or of sedimentation is intimately related to the problem of disintegration.

Lest it appear that I have merely succeeded in making the situation seem to be hopeless so far as the study of microscopic particles in the sea is concerned, let me say in conclusion that any addition to reliable information is helpful and important, no matter if it may fall short of full solution of the problems involved. Essential approximations to correct solutions may come later.