FACTORS AFFECTING THE RETENTION OF

EUKARYOTIC PHYTOPLANKTON WITHIN

THE EUPHOTIC ZONE

by

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A CRITICAL ESSAY

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ABSTRACT

Phytoplanktonic species face a serious problem in balancing photosynthetic light requirements with nutrient needs. Optimal light intensities are found toward the surface, while nutrients are usually in greater concentrations below the epilimnion. Motile species, such as the flagellates or gas vacuolate blue-green algae, collect at depths which optimize these needs, or migrate vertically to take maximal advantage of each in turn. Phytoplankton, with few exceptions, are denser than their media and without various internal and environmental suspension factors, non-motile species sink irrevocably from the euphotic zone.

The subject of phytoplanktonic suspension has been reviewed by Hutchinson (1967), who dealt with limnetic species, and Smayda (1970), who considered the problem in marine organisms. Research published after these papers appeared has added new dimensions to our understanding of the problem, and has stimulated the writing of this critical review. Since many of the suspension factors recognized are employed by both marine and fresh water species, it is convenient and useful to combine them into one paper. The prokaryotic phytoplankton are not considered here for a current and detailed analysis of gas vacuoles, the

floatation bodies of prokaryotes, has been prepared by Walsby (1978).

Many factors, both physical and biological, are implicated in maintaining epilimnetic populations of non-motile phytoplankton. The primary mechanism is wind-induced turbulence. Even fairly light winds create Langmuir spirals which circulate and retain motile and non-motile cells in an even distribution throughout the upper waters. Non-motile cells are dependent upon turbulence, and normally bloom only when a substantial mixing of nutrients and cells occurs in the euphotic zone. Motile cells lose positional control in turbulence but may become dominant in calm, stratified conditions. The many mechanisms which reduce sinking rates in still laboratory media become effective in nature only as turbulence decreases. These secondary retention factors include cell size, shape, density, colony formation, mucous secretion, age, selective ion accumulation, fat storage, light, nutrient availability, etc. Each of these mechanisms are discussed and where possible their values to different groups of phytoplankton are compared.

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INTRODUCTION

It is readily apparent that phytoplanktonic species must spend sufficient time within the euphotic zone to satisfy photosynthetic requirements. The amount of time is determined by the combined energy needs of daily respiration, growth and reproduction, which, if not consistently met, will result in death. Continuous euphotic residence is not usually necessary.

Flagellated eukaryotes and gas vacuolate cyanobacteria (blue-green algae) have little difficulty fulfilling their photosynthetic requirements, but nonmotile species which are, almost without exception, denser than their media, have a more serious problem. This paper seeks to identify and critically discuss the various factors which affect the retention of eukaryotic phytoplankton within the euphotic zone. Much work has been done since Hutchinson's 1967 treatment of the limnetic phytoplankton, and Smayda's 1970 review of marine suspension mechanisms. It is hoped that this new analysis, which incorporates and emphasizes recent work, and combines limnetic and marine "floatation" factors, will prove useful. The blue-green algae and purple and green photosynthetic bacteria are not considered here, for Walsby's (1978) publication on the gas vacuoles of prokaryotes is current and very comprehensive. Other recent

works dealing with the blue-green algal phytoplankton are by Reynolds (1973), Reynolds and Walsby (1975) and Porter and Jost (1976). At the risk of extreme oversimplification, the function of gas vacuoles is briefly stated.

In a system unique to the prokaryotes, gas filled vacuoles composed of constituent gas vesicles are synthesized. These reduce cell density, causing the organism to rise. Destruction of vesicles occurs near the surface at light intensities which stimulate high rates of photosynthesis and the subsequent buildup of osmotically active substances. The resultant increase in turgor pressure collapses some of the vesicles which raises cell density and leads to sinking. By this process cells are able to maximize photosynthesis, but the very high light intensities which would inhibit photosynthesis or cause photooxidation are usually avoided.

Traditionally, the majority of thought and research has been directed toward understanding what was felt to be the most critical problem of non-motile phytoplankton, the reduction of sedimentation rates. Of special interest were cells with particularly excessive densities, such as diatoms.

The more recent recognition that phytoplankton must move through the medium to assimilate sufficient nutrients, has led to the understanding that sinking or swimming (or for a few species, floating) is essential. Species dependent

upon sinking do so at the risk of loss from the euphotic zone, while floating organisms risk damage from exposure to full sunlight.

The apparent failure of early workers to appreciate the substantial contribution of turbulence to vertical positioning may have been perpetuated by laboratory research which did not, and for the most part still does not, take natural conditions into consideration. As will be demonstrated, even slight turbulence is enough to override most of the factors carefully detailed by laboratory workers.

Much laboratory work is dealt with in this paper as it forms a large part of the information available. Such work does help to round out the overall picture, particularly during periods of low turbulence. It should however be borne in mind throughout the reading, that factors manipulated in the laboratory normally play a very secondary role, relative to turbulence, in determining the depth of a cell in natural waters.

Phytoplankton utilize various mechanisms to give them a depth range or migrational range in which all their needs may be met. A balance must be struck between photosynthetic light requirements, photooxidative light avoidance and the motion needed for nutrient absorption. The features discussed are generally biological or environmental in nature. The biological factors include cell size, shape, age, motility, colony and sheath formation, ionic composition,

and lipid levels. Environmentally, the factors discussed will include light, viscosity and density of the medium, and especially, nutrient availability and water turbulence.

The multiple factors involved in sedimentation are superimposed on each other in nature. In order to quantify and determine the impact of each, at least in the laboratory, Stokes' Law (or modifications of it) for bodies falling through a liquid medium is used. The sinking rate or velocity is:

$$V_a = \frac{2\ gr^2}{9} \times \frac{p'-p}{N-\emptyset_r}$$

where g = gravitational acceleration; r = radius; p' = the densities of the cell and the medium, respectively; N = the viscosity of the liquid; and $\emptyset_r$ is the coefficient of form resistance. The latter coefficient is a correction factor for nonspheroidal cells. In many situations the sinking factors determined by Stokes' equation are in good agreement with observed values, while in others, Stokes' calculations do not match experimental results. The equation will be referred to where relevant throughout the critical analysis.

The critical review is divided into three sections. The first part discusses the planktonic Bacillariophyceae, or diatoms, which are essentially non-motile. The second part covers the Dinophyceae, or dinoflagellates, and is subdivided into motile and non-motile species. The third section is a "catch-all" dealing with groups which have not

been studied in much depth. These are largely chlorophytes, or green algae, but chrysomonads, haptomonads, and crypto-monads, are also discussed.

CRITICAL REVIEW

A. <u>The Bacillariophyceae - (diatoms)</u>

The planktonic diatoms are a very widespread group
which contribute to the primary productivity of marine
and fresh waters alike. An interesting and difficult
problem arises when one considers the maintenance of posi-
tion within the euphotic zone. Diatom frustules are com-
posed of silica and are relatively heavy, having a density
of 2.6 (Strickland, 1965). The siliceous material may
comprise up to 63% of the dry weight of a cell (Lund, 1965).
Direct measurements of cell densities for most diatoms are
lacking, but Bellinger (1977) estimated the density of an
average cell to be almost 1.19 while the density of sea
water is 1.021 to 1.028. Since the vegetative cells of
diatoms do not possess any means of locomotion which would
be of use in the water column, their negative bouyancy
causes them to sink. Limnetic diatoms have even greater
negative buoyancy due to the very low density of fresh water,
i.e., only 0.01% greater than that of distilled water (Lund,
1959).

Mechanisms exist which provide a sinking rate rapid
enough to prevent the buildup of low nutrient boundary layers

around the cells while allowing diatoms to reside in the euphotic zone for a sufficient time to grow and reproduce successfully. This section outlines and discusses these mechanisms and seeks explanations for anamolous situations such as the positive buoyancy observed in Ditylum bright-welli (Anderson & Sweeney, 1978; Eppley et al., 1967) and Chaetoceros armatum (Lewin, 1975).

In this section, more than any other, laboratory research is cited. One is again reminded that experiments isolating a single physical or physiological parameter do not reflect the highly complex conditions in situ, and care must be exercised in the application of such results to limnetic or marine environments.

During the microscopic study of diatoms one is struck by the array of sizes, shapes, exotic extensions and sculpturing of the frustules. The selective advantage of such features is not clear but various researchers have related some of these morphological characteristics to suspension, nutrient absorption and protection from preda-tion in the planktonic environment.

Cell Size

It is expected that the larger a cell grows, the smaller the surface area to volume ratio will become, thus reducing the effect of frictional drag. Smayda (1970) compiled and graphed data from Smayda and Boleyn (1965,

1966a, b) and Eppley, Holms and Strickland (1967) showing sinking rates versus surface area to volume ratios for solitary cells of several species of the three centric diatoms, Coscinodiscus, Cyclotella and Thalassiosira, which are geometrically similar but which differ in size. There was a general decrease in buoyancy with increasing size but not nearly of the magnitude which Stokes' equation would predict. By calculation, the large diatom Coscinodiscus wailesii would have a sinking rate of 40 m day^{-1}, a rate at which it could not possibly survive photosynthetically. Smayda (1970) commented that the densities of large cells must be much less than the densities of small cells.

An interesting contradiction to the inverse relationship noted for size relative to sinking rate is seen in actively growing cultures of Thalassiosira nana and Rhizosolenia setigera. Rhizosolenia has a volume 3200 times that of Thalassiosira but a roughly equivalent sinking rate (Smayda, 1970). A possible explanation for the unexpectedly low settling rates of large cells is discussed on page 13.

Gelatin Secretion. The ability to secrete a gelatinous sheath provides a means of altering cell size. Various limnetic species of unicellular diatoms such as Stephanodiscus and Cyclotella are surrounded by well developed gelatinous sheaths while colonial diatoms such as Tabellaria and Asterionella may have a gelatinous webbing stretching

between elongate cells. The external gel or mucilage would tend to reduce the relative surface area and the frictional drag, thus increasing the settling rate. This, however, is not the effect observed, for such cells sink more slowly. The mucilage was then suspected to be of very low density. Hutchinson (1967) calculated from Stokes' Law that the density difference between the organism and its mucilage must be at least twice the density difference between the mucilage and the medium to reduce the sinking speed. If the gel is of the same density as the medium then the sinking rate may be controlled by adding or shedding it. To date, the density of mucilage has not been analyzed and the sinking rates of diatoms with and without the gelatinous sheath have not been compared, so Hutchinson's calculations lack experimental verification.

With few exceptions, the production of gel is restricted to limnetic phytoplankton. This adaptation may be a mechanism which compensates for the accentuated suspension problems created by the very low density of the fresh water medium. Further research may show mucilage production to be a more important factor in planktonic existence than is presently recognized.

Hutchinson (1967) evaluated the advantages of large size in planktonic diatoms. He claimed that if the difficulties of a low relative surface area for nutrient absorption and a high sedimentation rate could be overcome, large

cell size would be selectively favored by the avoidance of small predators.

Culture Age

Another problem which clouds the issue, is the difficulty of separating the effects of culture age from the effects of cell size. The peculiar method of cytokinesis employed by diatoms means that as cells divide, the average cell size decreases to the point where auxospores may form or where cell division is inhibited. Post-auxospore cells are very large relative to pre-auxospore cells.

Data compiled on ten different diatom species from four sources by Eppley et al. (1967b) showed roughly a four-fold increase in the sinking rates of non-dividing older cultures over the actively dividing younger cultures of each species. Additional data showing the tendency of senescent cells to sink more rapidly have been collected by Smayda (1970) and Bellinger (1977), however, the relative proportions of small, average, and post-auxospore cells were not reported. One expects that older, non-dividing cells would, on the average, be quite small, a deduction supported by Bellinger's (1977) report that small cells predominate in older blooms. This idea again conflicts with the theory that smaller cells should be more buoyant. The large post-auxospore cells of Rhizosolenia setigera did show an increased sinking rate over that of pre-auxospore cells, but an

unexplained ascending motion was also reported in a large number of these cells (Smayda & Boleyn, 1966a). These facts lead one to conclude that suspension is controlled largely by physiological mechanisms which fail with age.

An exception to the effect of senescence is seen in Chaetoceros lauderi in which settling rate showed no obvious relationship to culture age (Smayda & Boleyn, 1966b). The behavior of Chaetoceros armatum, discussed in some detail on page 20, is relevant to this problem.

An increased sinking rate in older cultures is thought to be an adaptation designed to increase exposure to nutrients which have become limiting at shallow depths. Sinking increases nutrient uptake by forced convection, and moves cells to new, possibly nutrient rich areas. This theory is covered in more detail with the effects of nutrients.

Colony Formation

In the case of colony formation, intraspecific comparisons of sinking rates between cells which are solitary and those which are aggregated can easily be made. For nearly all species there is an obvious correlation between an increase in chain length and an increase in sinking rate. This has been reported in Nitzschia, Rhizosolenia, Bacteriastrum, Chaetoceros and two species of Thalassiosira by Smayda and Boleyn (1965, 1966a, b), and for a different

species of <u>Thalassiosira</u> by Eppley <u>et al</u>. (1967b). There
was a pronounced increase in fragmentation of the chains
of <u>Nitzschia</u> <u>setigera</u> with age. In this instance, the
tendency towards an increased sinking rate with senescence
was counterbalanced by the reduction in colony size so that
a constant mean sinking rate was maintained irrespective
of colony age (Smayda & Boleyn, 1965). These events have
been explained by the decrease in surface area to volume
ratio which accompanied colony formation and which reduced
frictional drag. The outstanding exception to this
correlation is <u>Skeletonema</u> <u>costatum</u> in which the sinking
rate was decreased by chain formation (Smayda & Boleyn,
1966a). Smayda and Boleyn suggested that the thin silica
rods extending between the cells created sufficient micro-
turbulence to increase frictional drag.

Comparisons of sinking rates versus cell diameters
were made for the seven genera of colonial diatoms studied
by Smayda and Boleyn (1965, 1966a, b) and Eppley <u>et</u> <u>al</u>.
(1967b). The results confirmed that cell diameters were
reflected in the settling rates of chain formers.

Cell Shape

By measuring the settling rates of inanimate wires,
spheres and plates of different sizes, Monk and Riley (1952)
demonstrated that the shape of a body falling through a
liquid affected its velocity. Their work also showed that

the velocities of different shapes were size dependent.
It should be kept in mind that the objects which were used
were at least one order of magnitude greater in size than
the average diatom and that complex corrections were made
before the results could be applied to phytoplanktonic
cells. For large cells with diameters of about 500 μm the
sinking velocity decreased from cylinders to spheres to
plates, and for diameters of 5 μm the rate decreased from
plates to cylinders to spheres. These tests attempted to
isolate the single effect of cell shape, a feature which
often is not highly significant in nature. For instance,
the application of Monk and Riley's findings to cylindrical
cells the size of Rhizosolenia and Coscinodiscus give
impossibly high sinking rates (Hutchinson, 1967). Hutchin-
son postulated that if the large vacuoles present in these
species were of a density equal to sea water, the low net
density might compensate for the rapid sinking expected for
large cylinders, giving the moderate rates actually
measured. Such a mechanism would not be so effective in
fresh water diatoms since it is improbable that vacuoles
could attain a density as low as or lower than that of the
medium. It is perhaps telling that large-celled species
are not usually found in the plankton of limnetic environ-
ments.

Many diatoms have bizarre spines and protruberances
and irregular shapes which have been postulated to reduce

sinking rates by increasing the frictional drag. For
these and all nonspherical organisms the term "coefficient
of form resistance" is used to refer to the change in set-
tling speed of a nonspherical cell relative to a spherical
body. This coefficient (ϕ_r), is used in Stokes' modified
equation.

A particularly good example of the effect of irregular
processes is seen in Thalassiosira fluviatalis which bears
extended chitinous fibers. Cells treated with chitinase
to remove the fibers sank 1.7 times faster than cells with
fibers (Walsby & Xypolyta, 1977). Dead cells were used in
each case to eliminate physiological complications. The
2.8 fold increase in surface area contributed to the 1.9
fold increase in form resistance. Smayda and Boleyn (1966a)
reported that spineless Rhizolenia setigera sank up to three
times more rapidly than normal cells with apical spines.
The altered sinking rates observed in these two species
is not solely a result of the change in form resistance,
for loss of weight is also a factor. Corrections could
be made, using Stokes' equation, which would isolate the
effects of form resistance to show even greater sinking
rates.

The theory that spines may also function to orient
the largest surface area perpendicular to the direction
of gravity, was put forth by Smayda and Boleyn (1966a)
after their work with Rhizosolenia. Few data are available

for the evaluation of this idea. Lund (1959) made "casual observations" that in static water, algae took up a position presenting the least surface area to the direction of rise or fall. The opposite view was expressed by Riley (personal communication, Hutchinson, 1967) who noted that elongate diatoms tended to take up a position normal to the gravitational force, and to fall with a zigzag motion. Experiments with asymetrical metal bodies falling in liquids (McNoun & Malaika, 1950) support the ideas of Smayda and Boleyn and of Riley.

Trainor (1969) noted that spines might also act to increase surface area for absorption. Numerous species of Chaetoceros bear long, hollow spines containing cytoplasm and chloroplasts which would serve well in nutrient assimilation.

<div align="center">Fat Storage</div>

For a long time the physiological mechanism of storing fat was thought to be a significant factor in diatom settling rates. This possibility was investigated for the massive surface blooms of Coscinodiscus concinnus in the North Sea. Smayda (1970) calculated the net density of cells with the maximum fat content (40%). The reduced density of 1.157 was still considerably greater than that of sea water, and this alone could not account for the apparent floatation of the blooms.

Anderson and Sweeney (1978) have shown that in Dity-lum brightwelli, a species capable of daily vertical migration, the maximum amount of lipid per cell was present at the end of the lighted period, a time when the settling rate was greatest. Ackerman, Toches and McLachlen (1968) also noted an increase in fat accumulation with senescence, when sedimentation increased. At present, all evidence indiates that an elevated fat content is not significant in reducing the sinking rate of diatoms.

Selective Ion Accumulation

In theory, floatation, or at least reduced settling, can occur as a result of the active accumulation of the light monovalent ions, Na^+ and NH_4^+, and the exclusion of the heavier ions such as monovalent K^+, and divalent SO_4^{2-}, Ca^{2+} and Mg^{2+}. Ion selection was postulated by Gross and Zeuthen (1948) as a factor which might control the sedimentation rate of marine diatoms, but subsequent studies by Beklemeshev et al. (1961) and Kessler (1967) were rather inconclusive. It was not until the Anderson and Sweeney paper (1978) on Ditylum brightwelli that really substantial evidence was presented to support the ion shift theory. Measurements of settling rates and ion concentrations were taken throughout the 8:16 hour light:dark cycle and compared. After 8 hours of light the mean sinking rate was at a maximum and the concentration of heavy ions K^+, Cl^- were high,

Mg^{2+} and Ca^{2+} were moderately increased, and the lighter Na^+ ions were low. At the end of the dark period the cells were buoyant, the relative ion concentrations were reversed, and there was an 80% reduction in the dry weight. The concentration of SO_4^{2-} might also be of interest since it is important in other types of phytoplankton.

In order to determine whether the differences in density caused by ion shifts could account for the measured changes in suspension, Anderson and Sweeney (1978) used the observed velocities in Stokes' equation to find the densities by calculation. The net increase in cell density calculated for the two settling rates agreed remarkably well with the differences calculated from the ion shifts. It appears that the movement of ions alone is sufficient to account for the alternate floatation and sinking observed in Ditylum brightwelli.

Changes in the size of the vacuole accompanied the ion and density shifts. At the end of the dark period, all cells had small vacuoles and after several hours of light, as K^+, Cl^-, Mg^{2+}, and Ca^{2+} entered, the vacuoles grew to occupy nearly the whole interior of each cell (Anderson & Sweeney, 1978). These observations correspond with the low settling rates seen in actively growing, small vacuolated cells of some other types of diatoms. Complications arise if, as Anderson and Sweeney suggested, there is also an outer vacuole between the cell membrane and

another membrane adjacent to the cell wall. Questions arise regarding the movement through, or collection of ions in this peripheral vacuole.

The idea that there is a straightforward relationship between the presence of ions controlling the sedimentation rate and the size of the vacuole is dispelled somewhat by observation of the resting cells of Ditylum and the large cells of Rhizosolenia and Coscinodiscus. The "spheroid" cells, presumably resting cells of Ditylum noted by Boleyn (1972), had essentially no vacuole and yet sank very rapidly. The corollary to this situation was seen in Coscinodiscus and Rhizosolenia which had large vacuoles and very low sinking rates for their size. In contrast to the Anderson-Sweeney theory for Ditylum, that vacuoles concentrate heavy ions, Gross and Zeuthen (1948) proposed that for the species they observed, the vacuolar sap had a very low specific gravity which gave lift to the cells. Furthermore, those cells which could not retain the sap would sink rapidly. To test this idea Anderson and Sweeney used Boleyn's settling velocities to calculate the density differences or loss of lift necessary to cause such high velocities in the resting cells of Ditylum. These changes in density matched the density differences calculated from loss of vacuolar sap and supported Gross and Zeuthen's theory. Analysis of the vacuolar contents of Coscinodiscus and Rhizosolenia must be made before this theory can

confidently be used to explain the slow sinking rates.

If both theories are correct then the function of the vacuole must vary from species to species. The organelle must concentrate heavy ions in some species and selectively exclude heavier ions in others.

It is obviously desirable to extend studies on selective ion shifts to many other species of diatoms to determine the extent and general importance of this mechanism. In the dinoflagellates Noctiluca and Pyrocystis (considered in section B), the selective inclusion and exclusion of appropriate ions was found to correlate closely with floatation and sinking. The accumulation of NH_4^+, an ion of lower specific gravity than sea water, when in isotonic concentrations, was important in holozoic organisms but it is not likely to be significant in diatoms which are often limited by nitrogen.

It is of interest that one diatom besides Ditylum is known to exhibit periods of buoyancy during its diel vertical migration, but that this organism, Chaetoceros armatum, does not appear to use selective ion concentration (Lewin & Rao, 1975). Chaetoceros collects in the surface waters of the surf zone in daylight and disperses at night. Samples removed from the turbulent water at all times sink rapidly indicating that the buoyancy is not due to a reduction in density. The most buoyant period, dawn, coincided with mitosis, cell division without silica deposition and

a slight increase in cell length. These features would normally decrease the surface area to volume ratio and increase the settling rate. During the late afternoon, when a new silica valve formed on each daughter protoplast, bristles developed on some valves separating the filaments into 2 or 3-celled chains which began to sink. Again, reduction in colony size normally has the reverse effect on sedimentation. To date, no theories have been proposed to explain the anomalous settling behaviors observed in this organism.

Lewin and Hruby (1973) noted that at dawn, diatomaceous materials changed surf bubbles to a stable foam. It may be that this high surface tension foam held Chaetoceros at the surface, but since Asterionella socialis, the second most abundant planktonic diatom in the area, remained evenly dispersed, it seems unlikely.

With mitosis and increased buoyancy, Lewin and Rao (1975) noted the production of mucous, an unusual feature for a marine diatom. If the mucous was copiously produced and of low specific gravity, the buoyancy might be explained. During the afternoon as the chains separated, the mucous coating was interrupted, perhaps enough to account for the cells sinking. A density analysis of the gel would support or refute this theory.

An obvious objection to the mucoid theory of floatation is is that supposedly buoyant surface samples of Chaetoceros

armatum sink rapidly when held in still water, implying a
high density unaltered by biological mechanisms such as
mucous. A useful observation comes from cells cultured in
still media. These cells have no mucous coating and have
lost the strong rhythmicity of cell division seen in
turbulent conditions (Lewin & Rao, 1975). Unfortunately,
changes in settling rates were not reported. Lewin and
Rao interpreted the constant high number of cells undergoing
division (40%), and the absence of a night time buildup
of shorter chains to mean that the cells were behaving at
all times like illuminated cells in nature. Instead, one
could construe the data to mean that in calm water Chaeto-
ceros behaves quite differently than surf populations and
that one physiological change is the loss of mucous. If
such a response to nonturbulent water occurred rapidly the
apparent sedimentation of surf samples on collection would
be explained. Aerated deep tank experiments, with attention
given to mucous production, appear necessary for the further
elucidation of the diel migrations of Chaetoceros.

Many biological features of diatoms which independently
or cooperatively affect settling rates have now been dis-
cussed. Certain environmental factors such as water vis-
cosity, light intensity, the availability of nutrients and
water turbulence are also known to affect diatom suspensions
and will now be considered.

Viscosity

Water viscosity is an important consideration for viscous drag may reduce the settling rate of a diatom significantly. This effect is particularly critical for tropical species since the viscosity of water at 25° C is about one half that at 0° C, and suspension problems are doubled (Wetzel, 1975). Smayda (1970) calculated by Stokes' Law that the sinking rate of an average sized cell would increase by 4% per degree rise in termperature from 0 to 25° C. Interestingly, there are relatively few tropical planktonic diatoms. Changes in salinity have little effect on the viscosity of water.

Light

For organisms capable of regular vertical migration it was suspected that the response was "tuned" to take advantage of photosynthetic light intensity optima and was light controlled. However, Chaetoceros armatum cells rose in darkness just prior to dawn (Lewin & Hruby, 1973), indicating that light did not directly trigger the floatation mechanisms.

Somewhat conflicting evidence has been reported for Ditylum brightwelli. Eppley et al. (1967a) found in still deep tank cultures that during the dark period cells first sank, then became buoyant and then sank again, implying

floatation mechanisms independent of light. In contrast, Anderson and Sweeney (1978) found that normally migratory Ditylum cells kept in dim light failed to migrate and did not alter their buoyancy. The latter observation suggests that the floatation cycle is not endogenous and depends upon a light stimulus.

Some organisms which do not undergo diel migrations exhibit relevant reactions when exposed to light. Smayda and Boleyn (1966a) reported an erratic positive buoyancy response in illuminated post-auxospore cells of Rhizosolenia cells which normally sink very rapidly. On one occasion they noted buoyancy in lighted pre-auxospore cells as well. Steele and Yentsch (1960) observed a much sharper decrease in the settling rates of darkened over lighted cultures of Skeletonoma costatum when nutrients were added. The influence of light on diatom suspension must be tested in more detail before any generalizations may be made.

Nutrients

Probably the major advantage of the movement of phytoplankton relative to the medium is the increase in the availability of nutrients. Both the movement out of nutrient depleted areas and the prevention of the localized depletion of the boundary layer of each cell, enhance nutrient assimilation. The benefits of sinking are to a greater or lesser extent balanced by the loss of cells from the euphotic

zone.

The sinking rates of some diatoms become slower when nutrient concentrations are increased. A high percentage (35%) of the cells in cultures of both Ditylum brightwelli and Stephanopyxis turris, grown in von Stosch's medium, were neutrally buoyant over several hours of observation (Eppley et al., 1967b). This phenomenon was not seen in the alternate IMR and $\frac{IMR}{2}$ media. Differences in the specific gravity of the media were not reported. Steele and Yentsch (1960) reported a nutrient factor in Skeletonoma sedimentation rates. Both 3-4 day old and 7-8 day old cultures exhibited a rapid decrease in sinking and an increase in cell division when enriched with 4B medium. Smayda (1970) demonstrated a nutrient effect which was age-dependent in Rhizosolenia. Nutrient supplemented cultures up to six days old sank much less rapidly than similar but non-enriched cultures. With age, both cultures sank at similarly rapid senescent rates.

The physiological mechanism for reducing density and settling rates by concentrating ions of low specific gravity in vacuoles was proposed earlier. It might reasonably follow that insufficiently nourished or senescent cells lose the ability to selectively retain or exclude the appropriate ions and therefore sink rapidly.

It would be highly beneficial to malnourished cells which were sinking from a nutrient poor, shallow environment

to darker depths and eventual death to have a "second chance" in slightly deeper nutrient rich waters. These nutrients would only be useful if the rapid sinking rates were reduced to allow the cells an extension of their time in the euphotic zone. The data cited for Rhizosolenia and Skeletonema showed that additional nutrients did in fact slow settling rates under the consistent light conditions of the laboratory. In situ, of course, the depth of the euphotic zone becomes critical and in this situation the survival of any species will depend upon its ability to photosynthesize at reduced light intensities.

Canelli and Fuhs (1976) reported an increased uptake of labelled phosphate as the rate of water flow past cells of two species of Thalassiosira on a filter increased. The assimilation rate at least doubled as the flow increased from 0.5 to 15 mm/min.$^{-1}$ Vigorously stirred cultures required a much longer time than the flowing media cultures to absorb an equal amount of phosphate.

Stirring, like turbulence in nature, tends to carry phytoplankton cells with the surrounding water molecules, and the replacement of boundary layer nutrients is slow and still partially dependent upon diffusion gradients. In the laboratory, medium flowing past cells, or in nature, a cell moving relative to the medium gives a much more efficient replacement of boundary nutrients. For some diatoms, the reduction of sinking rates to zero may well be a charac-

teristic selected against, and some of the emphasis given to floatation mechanisms might be, at least partially, misplaced.

Turbulence

A vast majority of the observations and experimental work done with diatoms have been carried out in laboratories where nutrient absorption, sinking rates, etc., are not complicated by the realities of water motion. In nature, nonturbulent situations rarely exist, particularly in marine environments.

Wind, and to a lesser extent, solar radiation, transfer energy to water surfaces where it is expressed as waves and vortices, deeper Langmuir spirals and thermal convection cells (Owen, 1966). A common secondary factor which generates turbulence is the effect of bottom friction on tides and currents, especially near shore. Small particles such as non-motile phytoplankton are greatly affected by these forces.

Smayda (1970) has made an interesting comparison between the settling rates of the seven diatoms studied by Smayda and Boleyn (1965, 1966a, b), and the vertical velocities of water which accompany moderate, 3.3 to 6.6 m sec^{-1}, winds. Langmuir convergence velocities were found to be 2 to 3 orders of magnitude greater than the average maximum sinking rates of the diatoms. These figures rather strongly

suggest that very light winds would be sufficient to keep the majority of cells in a population in a circulating suspension, even though they are constantly sinking relative to the medium.

Short periods of calm weather may have significant effects in limnetic situations, particularly in small well protected lakes. In temperate mono- or di-mictic lakes, spring thermal stratification may occur rapidly, sealing any cells below the thermocline barrier into the hypolinmion. Furthermore, a few days of static water would allow even many actively growing, relatively light cells to descend below the thermocline permanently or until the next overturn.

One example of diatom dependence upon mixing was reported by Lund (1971). Melosira italica maintained large populations in Blenham Tarn, England during the winter isothermal period but were only found in a resting state in or on the mud after summer stratification. An artificial destratification of the Tarn in summer was accompanied by a large bloom of Melosira which was undergoing rapid cell division. Since the Tarn is only 6 m in depth it is likely that even the resting cells on the bottom were receiving some light, but required turbulence and suspension for growth. Pollingher (1978) gave further support to the dependence of Melosira upon wind turbulence. Melosira flourished in Lake Kinneret only during the windy period through January and

February, but the numbers dropped immediately with the on-
set of the spring calm period when the dinoflagellate
Peridinium became dominant.

Other diatom populations appear to be independent of
turbulence. In Asterionella (Lund, 1971) and Stephano-
discus (Pechlaner, 1970) population densities could not be
related to wind turbulence.

Stommel (1949a) mathematically determined the trajec-
tories of cells with sinking velocities which were less
than, more than, or equal to the velocity of the water. He
diagrammed these pathways into Langmuir spirals. More
detailed treatment of this theory is found in Stommel (1949a),
Riley et al. (1949), and in Hutchinson (1967). Briefly, in
circulation created by gentle winds, cells which are less
dense than water will tend to collect in windrows or
slicks at the lines of convergence. Cells with a density
equal to that of water will tend to follow the streamlines
of that water flow. If such neutrally buoyant cells are
in the proximity of a divergent upwelling, they may be
constantly recirculated in "regions of retention" within
the Langmuir spirals. If the cells enter the area of
maximum convergent downwelling they may pass out of the
base of the spiral by eddy diffusion and then remain sus-
pended below the depth of the Langmuir spiral. Species
which are even slightly denser than the medium will con-
stantly sink relative to it. Cells with a relatively low

sinking rate will tend to be moved in much the same manner as the cells of neutral buoyancy. Species which have a moderate sedimentation rate will be less influenced by normal turbulence, but their descent will be slowed. Phytoplankton which is much denser than water, or which has a settling rate greater than the upward water velocity, will tend to sink out of the turbulence, but usually with a lateral trajectory. Depending upon the balance between a cell's inherent sinking rate, its initial position in a spiral and the water's vertical velocity, a diatom's downward progress may be enhanced, slowed or prevented altogether. As winds and turbulence increase, Langmuir spirals become deeper, circulate more rapidly and retain greater numbers of increasing heavy cells within the surface waters.

To summarize, most diatoms are denser than water and tend to sink continuously, a feature which is useful in nutrient assimilation. Retention within the euphotic zone depends basically upon two different types of mechanisms. The major factor is water turbulence which is caused mainly by wind, but also by currents and overturns, etc. The effects of the secondary group of factors may become apparent as agitation weakens. These physical and physiological factors, in combination, determine the net settling rate of an organism as seen in Stokes' equation. The size, shape and density of a cell or its parts may be measured to calculate the net density and form resistance of a cell.

As density decreases and form resistance increases, the
position of a cell is controlled almost completely by the
motion of the water. In the reverse situation, as density
becomes greater, form resistance decreases and turbulence
weakens, diatoms will tend to sink out of the euphotic zone
and even massive blooms will cease rapidly.

B. The Dinophyceae

The Motile Dinoflagellates

Although various types of phytoplankton possess flagella, studies to date indicate that dinoflagellates are the most significant group both in terms of numbers and in their effect on the environment. For example, Peridinium forms 90% of the phytoplankton in Lake Kinneret (Sea of Galilee) from January to June, other species dominate most alpine lakes and blooms of the red tide species, Gonyaulax and Gymnodinium often have drastic consequences.

The possession of a flagellum confers a great advantage upon a planktonic organism if the motility is sufficient to overcome normal turbulence so that the cell controls its vertical position in the water column. Such control is demonstrated by the many dinoflagellates which make diel migrations to depths of 10-20 m. Presumably the cells optimize light intensities for photosynthesis at one time of the day and conditions for nutrient assimilation at another. Horizontal distribution is, as seen in other phytoplankton, mostly a function of winds and currents which override swimming motions. Research information on flagellated dinoflagellates which do not undergo diel migration is scarce.

First, data describing the phenomenon of vertical diel migration of varied species in marine and fresh water systems will be cited, then, factors which influence and direct the motion will be discussed.

Vertical Migration

In situ studies of a bloom off Seal Beach, California by Eppley et al. (1968) clearly showed diel migration in Ceratium furca. During the afternoon the dinoflagellates were massed at the surface, while at 1900 and 2100 they were seen as bands at progressively greater depths. This downward migration was at about 2 m hr^{-1}. Other dinoflagellates, Peridinium depressum and Ceratium fusus, also rose to the surface during the day but were seen to disperse somewhat at night, and distinct bands were not apparent at depth.

Deep tank laboratory experiments with Gonyaulax polyedra and Cachonina niei showed obvious vertical migration (Eppley et al., 1968).

Similar diel and temporal migrations have been observed in the fresh water dinoflagellate, Peridinium cinctum, in Lake Kinneret from 1969 to the present. Several 24 hour depth profiles were constructed in May 1967 by Berman and Rodhe (1971). Between midnight and sunrise, little aggregation occurred. Shortly after sunrise, Peridinium moved

upward and peak surface concentrations were seen from 700 to 900. The peak then began its descent until, at 1500, it was at 6 m and a second prominent peak had formed at 11 m. These studies do not report the night time distributions which would likely provide depth maxima.

Work by Eppley et al. (1968), Hasle (1950) and Kamykowski (1977) show normal swimming rates of 1-2 m hr^{-1} for various dinoflagellates--a remarkable speed considering their size. These rates are sufficient to account for the distances covered in any of the migrations observed.

Temperature and Salinity

Hand et al. (1965) have studied the effects of temperature and salinity on the swimming rates of dinoflagellates. Tolerance to varied environmental conditions is important to organisms which migrate vertically. Gonyaulax and Gyrodinium were able to maintain high swimming rates at alinities from 20-40% and over wide temperature ranges as well.

The question arises as to whether dinoflagellates can migrate through a thermocline or halocline to take advantage of nutrients below. Kamykowski (1977) found that Cachonina niei would descend only 6 m in a darkened thermally stratified tank (11°-17°C), to the level of its minimal growth temperature of 12°C. The descent rate was 0.5 m hr^{-1}. Eppley et al. (1966) also monitored the migration of Cachonina niei, but in a dark, unstratified 10 m tank at 22°C.

At that temperature, <u>Cachonina</u> descended to the bottom at a rate of 1-2 m hr^{-1}. <u>Cachonina</u> demonstrated the ability to cross a gradient of 5° C (17°-12°C) but its maximum depth appeared to be temperature limited. The reduced swimming rate in the cooler tank indicated that temperatures below optimal growth temperatures of 19°-23° C (Loeblech, 1975) do affect swimming ability. Other examples of phytoplankton crossing temperature gradients of 2-10° C <u>in situ</u>, are cited by Kamykowski (1977).

Kamykowski has cautioned against the direct application of deep tank results to natural situations where thermoclines may be very sharp and where the dynamic aspects of light intensity, temperature, salinity, nutrients, zooplankton grazing and turbulence came into play. He does, however, believe that most of the observed behavior is likely to occur <u>in situ</u>.

Regular migrations to depths where growth is inhibited must confer some selective advantage to the organism. Eppley <u>et al</u>. (1968) formulated the hypothesis that downward migration and nutrient assimilation in darkness were required to account for the amount of nitrogen found in surface blooms of dinoflagellates. They were considering N limited marine dinoflagellates but the same theory would apply equally well to fresh water species limited by N or other nutrients. There are no data at this time which prove that rising cells contain nutrients which were assimi-

lated at depth. Deep tank experiments introducing labelled
nutrients below a thermocline, but within growth range
temperatures, would provide evidence for or against the
Eppley et al. hypothesis. If temperature is a factor which
limits the depth of migration and the need for more nutri-
ents make such motion advantageous, what factors trigger
and control migration?

Light

One is tempted to label the migration responses as
obviously phototactic, however, the deep tank experiments
with Gonyaulax polyedra and Cachonina niei by Eppley et al.
(1968) showed that the cells began their descent before
the light was extinguished. When the lights were kept on
all night, Cachonina completed its downward migration nor-
mally. Cachonina was also able to carry out a normal
migration cycle in 24 hours of total darkness. Furthermore,
for some species migration in the dark is highly directed,
not random, and thus cannot be explained by negative photo-
taxis. An endogenous rhythm is clearly indicated here.

In an attempt to explain such data, Eppley et al. (1968)
have postulated a geotactic response, where a circadian
shift of organelles within a cell changes the center of
gravity so as to direct the cell up or down as the flagella
beat. Some support for this theory is claimed by the ob-

servation that another dinoflagellate, Pyrocystis, shows a circadian shift of plastids (Swift & Taylor, 1967). However, Pyrocystis does not migrate daily and this "evidence" cannot be given much credit.

Despite evidence that vertical distribution is not directly light controlled, the migration must be and is timed, at least indirectly, to the light cycle for the purposes of photosynthesis. Berman and Rodhe (1971) have demonstrated, using C^{14} inoculated subcultures that Peridinium does not position itself for optimal photosynthesis. The photosynthetic maximum was generally 1-3 m above the peak concentration of cells. Thus, they suggested that sensory mechanisms were not reacting to peak photosynthetic wavelengths and intensities of light, but perhaps to lower values of green light which are more available and penetrate deeper.

Further indications of the reaction to light and/or heat are seen on the temporal changes in vertical distribution profiles of Peridinium. From January through July the peak concentration of cells deepens as light intensity increases (Pollingher & Berman, 1976). This may be a direct response to photooxidative damage to the cell, or may be due to other, as yet undetermined, stimuli.

All these various pieces of data may be accomodated if one theorizes that the light cycle "conditions" or

"sets" some internal cellular rhythm, and that the effective wavelengths are in the green range.

This does not account for the observation by Eppley et al. (1968) that cloudy weather lessens the intensity of migration. If, however, such overcast could be correlated with wind, mixing such as demonstrated by Serruya et al. (1978) could be responsible for the reduced surface concentration of cells.

Nutrients

The role of nutrients in migration, specifically nitrogen and phosphorus compounds have been studied in some dinoflagellates. Laboratory work with Gonyaulax (Eppley et al., 1968) showed that normal vertical migration was possible only with sufficient Nh_4-N present. With NO_3-N only, upward migration was delayed for 7 hours beyond the start of illumination. N-starved Gonyaulax did not show any significant migration. It has not been reported whether flagellar motion was impaired or whether perhaps the sensory system was affected by the low concentration of NH_4. Microscopic observation of the N-starved cells might provide useful information.

Interestingly, similar experiments with N-starved Cachonina showed vigorous migration for 5 days, though by the 4th day of starvation the band was somewhat more diffuse.

Both Cachonina and Gonyaulax recovered their migrational
abilities rapidly and completely when NH_4-N was reintroduced.
The role of N in migration appears to be species dependent.

Interpretation of nutrient data for Peridinium in Lake
Kinneret poses some interesting problems. Serruya and
Berman (1975) indicated that N was not a limiting factor,
but phosphorus was under suspicion since 90% of the P
entering the lake sedimented rapidly. Studies by Halman
(1972) showed P to be the sole limiting factor in his cul-
tures. Serruya and Berman's studies contradict Halman's
and they note that his cultures were not pure. Peridinium
can grow exponentially even with very high intracellular
C:P ratios (450:1). In contrast, blooms have ceased when
internal P levels were still moderate. Laboratory tests
with samples collected from lake blooms and enriched with
P and N did not show increased growth. It is now believed
that luxury storage of P occurs during the spring overturn
when cells newly emerged from cysts, accumulate sufficient
P at depth to support a bloom of many generations in low
P surface waters.

If in contrast to Gonyaulax, N and P are not limiting
for Peridinium, of what advantage is it to expend the energy
to migrate to depths of 10-12 m daily? Avoidance of photo-
oxidative light intensities would not require movement to
such depths, nor would it be a factor in the evening or at

night when the downward migration was greatest.

After years of study of Lake Kinneret, no solid con-
clusions have been reached about the advantages of the
deep vertical migration in Peridinium. Perhaps as yet
unidentified deep water nutrients are limiting near the
surface. Vitamin B_{12}, a scarce nutrient needed by almost
all motile dinoflagellates may be a prime candidate for
further testing.

Turbulence

The effects of wind and turbulence on the growth of
Peridinium in Lake Kinneret have been reported in a recent
paper by Serruya et al. (1968). At least some of the
motile cells are present in the water at all times, but
they become dominant (90% of the biomass) only during the
stable, generally windless period from February to June.
During high wind periods (average 8 m s^{-1}) in winter and
summer, the number of cells dividing dropped to an average
of 10%, but during the spring calm (average 2 m s^{-1}) the
number of cells undergoing division averaged between 30-40%.
Brief windy periods during the spring also reduced division
rates significantly, a minimum recorded value being 2.5%.

Distribution data add further support to the growth-
turbulence pattern. During winter isothermal mixing, motile
and non-motile phytoplankton were evenly distributed with
only 44% of the dinoflagellates in the upper 10 m of water

in daylight. Through March more than 80% of the Peridinium population was in the upper layer in the daytime.

It is clear that calm periods allow the flagellated cells to migrate to upper waters where photosynthetic light intensities are optimal, division rates increase, competition is reduced, and blooms occur. The selective advantage of control of vertical position is lost during windy turbulent periods and diatoms, chlorophytes or other algae become dominant.

In summary, we can only state that some marine and fresh water dinoflagellates do carry out substantial diel vertical migration and that the survival value of such movement may involve increased availability of limiting nutrients, optimization of light for photosynthesis and perhaps the avoidance of photooxidative damage or death.

The Non-Motile Dinoflagellates

Research has been carried out on the floatation mechanisms of two large, essentially non-motile marine dinoflagellates, Noctiluca militaris (Kessler, 1966) and Pyrocystis noctiluca (Kahn & Swift, 1978). Both are positively buoyant and have vacuoles which make up more than 95% of their volume, but Noctiluca being holozoic and non-photosynthetic, will not be discussed in detail with phytoplankton.

Selective Ion Accumulation

As noted in some large diatoms, the sizeable vacuole of Pyrocystis contained ions giving a density lower than sea water at concentrations which were isotonic to it (Kahn & Swift, 1978). The buoyancy is relatively constant and there is no daily rhythmic change in ion composition as was noted in the vertically migrating diatom Ditylum (Anderson & Sweeney, 1978). Significant vertical movements do occur and are the subject of this discussion.

Kahn and Swift found that the cell sap of Pyrocystis contained decreased amounts of heavy divalent ions relative to sea water. SO_4^{2-} was at 1/8 the concentration of the medium, and Ca^{2+} and Mg^{2+} were each at 1/3 to 1/2 its concentration. They proposed that Cl^- replaced SO_4^{2-} while Na^+ replaced Ca^+ and Mg^{2+}. Another source of lift which is available only when nitrogen is adequately supplied, is NH_4^+. Aqueous ammonium solutions are less dense than sea water at isotonic concentrations. NO_3^- may also be stored in the vacuoles but at about 1/10 the concentration of NH_4^+. The holozoic dinoflagellate, Noctiluca, is able to concentrate large amounts of NH_4^+ due to the protein-N content of its prey.

Nutrients

The availability of nutrients plays an important role in buoyancy. Nutrient-replete cells concentrated NH_4^+ in cell sap by a factor of 7×10^3. Nutrient-deplete cells lost positive buoyancy and became neutrally buoyant (Kahn & Swift, 1978). Corroborating the effect of nutrient depletion in sinking rate was the observation that vacuoles of neutrally buoyant, nutrient-deplete cells had shrunk slightly to 80-90% of the cell volume. Cells which were dividing or dead had little or no vacuole and sank rapidly.

Light

Light intensity was reflected in both sinking rates and ion concentrations. Highly illuminated cultures were less buoyant than dimly lit cultures and contained more of the heavy ions K^+ and Mg^{2+}. The most buoyant Pyrocystis cells were found in dimly lit nutrient-replete cultures.

A general picture emerged from the data. Cells which were beginning to divide became negatively buoyant and sank. The new vegetative cells produced were exposed to the dim light and high nutrients of deeper water, became buoyant, and floated upward. In situ studies by Sukhanova and Rudyakov (1973) supported this pattern. They found peak populations of vegetative cells at 65 to 70 m and population

maxima of reproducing cells at 100 to 110 m depth. Swift
et al. (1976) noted that Pyrocystis thrived and divided
most rapidly in deep water where there was a light-nutrient
optimum.

Cell densities were calculated by Stokes' equation
from the floatation rates of living and dead cells, and
compared with the densities calculated from the ionic make-
up of the cell saps. Close agreement between these two
sets of values support the theory of vacuolar ion control
as the floatation mechanism.

Although Pyrocystis did not migrate daily it was clear
that selective inclusion and exclusion of vacuolar ions
occurred in response to nutrient supplies, light intensity
and the physiological condition of the cells. This mechanism
appeared to position the cells so that their immediate needs
were best met.

C. The Chlorophyceae and Other Algae

Relatively little research has been carried out on
the suspension mechanisms of phytoplanktonic groups other
than the blue-green algae, diatoms and dinoflagellates.
This third section deals with studies of some chrysomonads,
haptomonads, cryptomonads and especially of chlorophytes.

Temporal Distribution Patterns

Certain generalizations may be made regarding phyto-
plankton motility and the temporal sequence of dominant
limnetic species. Population studies of Abbot's Pond, England
(Happey-Wood, 1976a, b) and Tilzer's (1973) alpine lake showed
that flagellated phytoplankton tended to have an advantage
during calm weather and stratified conditions, while non-
motile species peaked when turbulence returned.

Abbot's Pond is sheltered, shallow (3.5 to 4 m) and is
stratified and the epilimnion is depleted of PO_4^{-3} and NO_3^{-1}
in summer. These conditions favor motile species which can
select optimal photosynthetic light intensities, avoid
photooxidative intensities, and migrate down through the
steep nutrient gradient at 2-3 m depth to richer water. Of
the nine species described it is interesting that seven were
flagellated and five made regular diel migrations. One of
the non-motile species, Chlorococcum, showed a population

peak in late July and a second peak after the fall overturn.
A greater proportion of these cells were found in the tur-
bulent October water than during the summer peak. It is
not known how the non-motile cells thrived in the calm,
nutrient-deplete summer epilimnion. The diffusion of nutri-
ent from hypolimnion upward suggested by Happey-Wood would
be low during stratification.

Tilzer's study of a high Austrian lake showed that
flagellated phytoplankton dominated the lake. The dino-
flagellate Gymnodinium was the most important species through-
out the year, followed by two species of chrysomonads, a
haptomanad and a cryptomonad. All of these species were
flagellated and underwent diel migrations. The extreme
conditions of the lake, i.e., great changes in light and a
severe scarcity of nutrients except at depth, etc., strongly
favored these motile species.

The general pattern was an upward migration during the
late afternoon or night, and a gradual sinking through the
morning as light intensities increased to damaging levels.

There was a light turbulence through the summer suffi-
cient to suspend some of the non-motile cells, but no blooms
occurred. Tilzer suggested that non-motile species "seemed
to prefer" periods of low light since they would be less
subject to photooxidation. He did not mention that it was
only during the spring and particularly the strong fall

overturn that such cells could thrive. The overturn mixing of more cells and nutrients into the epilimnion would stimulate photosynthesis and growth.

Temporal distribution in marine situations tend to be less dependent upon seasonal, wind induced turbulence since current, tide, and wind initiated water motions are more constant features in the ocean.

The physical effects of turbulence were covered in some detail in the diatom section, and the same principles follow for the non-flagellated phytoplankton of other groups. Flagellates too are controlled by turbulence unless it is very gentle.

Size

Little reference has been made to size relative to suspension in these algae. However, Tilzer (1973) does note that cell size has no observable effect on the speed of migration.

Density

The coccolithophoids have density problems somewhat similar to the diatoms. Calcium carbonate coccoliths have a density of 2.70 to 2.95 and can form up to 25% of the dry weight of the cell, giving a net density of 1.27 (Eppley et al., 1967b). The effects of coccoliths were well demon-

strated by Eppley et al. who bubbled acidifying CO_2 through the medium of Coccolithus huxleyi to dissove the $CaCO_3$. Non-treated cells sank five times more rapidly than the "bald" cells.

The negative "survival value" of these structures, as regards retention in the euphotic zone for photosynthesis, is puzzling. Smayda (1970) suggested that coccolithophorids might regulate their density by shedding coccoliths or contolling the size of them. Except for the variety of naked and plated cells seen in nature there is no evidence to support this idea; however, careful observation of laboratory cultures in media of varied densities may verify or refute it. The secretion of mucous is a common process in many limnetic phytoplankton particularly blue-green algae, diatoms and some green algae. When the mucous is of sufficiently low density, as discussed under diatoms, sinking rates are reduced. Mucous secretion in marine species is rare, however, cells of the chlorophyte Phaeocystis are imbedded in an acrylic acid gel. Density analyses of the gel of Phaeocystis and other chlorophytes have not been reported so it is impossible to evaluate the effectiveness of this suspension mechanism. Much research remains to be done in this area.

Form Resistance

A discussion of the meaning and use of the term form resistance may be found in the section on diatoms. Conway and Trainor (1972) carried out experiments with the chlorophyte, <u>Scenedesmus</u> to determine whether the bristles effectively increased form resistance and frictional drag and thus reduced the sinking rate. Cells which were gently centrifuged to remove bristles, and those which were naturally bristle-free showed a sinking rate which was substantially greater than that of bristled forms. The microturbulence and drag created by such extensions did affect sedimentation.

Fat Accumulation

Perhaps the only species of phytoplankton for which fat storage is an accepted method of reducing sedimentation is the green algae, <u>Botryococcus</u> <u>braunii</u>. Older cultures of this chlorophyte accumulate up to 40% of their dry weight as lipids. This storage reduces their density enough to enable them to float (Fogg, 1965). Other species which collect fat do not have reduced sinking rates since they tend to be senescent cells in the process of breakdown or have heavy silica walls.

Selective Ion Accumulation

The preferential storage of low molecular weight ions in the vacuolar sap of the dinoflagellates, Noctiluca and Pyrocystis, and of the diatom, Ditylum, was demonstrated and discussed earlier. This mechanism has also been shown to occur in Chlorella. Shieh and Barber (1971) determined that in Chlorella pyrenoidosa light stimulated the internal accumulation of K^+ over Na^+, but that exchange was much reduced in darkness. Evidence suggested that this active process was respiration dependent. Though sinking rates were not reported, a high $K^+:Na^+$ ratio during daylight would increase the sinking velocity, an advantage if photooxidation is a danger but a disadvantage at low light intensities. A nighttime reduction in the $K^+:Na^+$ ratio would reduce the sinking rate but likely not cause a return to the surface. Chlorella likely depends upon turbulence for retention within the euphotic zone.

Nutrients

Relatively little direct information is available regarding the effects of nutrients on sedimentation rates of these "section C" algae. The accumulation of sufficient fat to result in buoyancy was observed only in mature nutrient-deplete cultures of Botryococcus (Fogg, 1965). Conway and Trainor (1972) determined that Scenedesmus sank more slowly

when NH_4NO_3-Bristol's medium was used instead of normal Bristol's medium. Surprisingly, the vacuoles of cells in normal Bristol's were larger than those grown in NH_4 Bristol's. More research is required to explain the apparent influence of N on the suspension of this organism. A vacuolar ion analysis would be most useful.

Flagellated species generally have an advantage in nutrient-deplete waters. They can migrate to depths where nutrients are often more available, and their motion, relative to water, prevents low nutrient boundary layers from forming. This generalization is not absolute as seen by the early cessation of Pandorina blooms in Abbot's Pond. Despite its deep diel migrations, this highly motile colonial flagellate is reported to have become N-limited. Interestingly, Chlamydomonas and even non-flagellated Chlorococcum were able to succeed it. It is probable that its colonial form of a sphere of adjacent cells embedded in mucilage, greatly reduced its efficiency of assimilation. The surface area for absorption is severely reduced while the mucilage "halo" would increase diffusion time. The ability to migrate partially counteracts these problems, and without it, Pandorina might not have dominated at any time. The small non-mucilaginous cells of Chlamydomonas and Chlorococcum do not have such limitations. Pandorina may have the additional disadvantage of a high assimilation constant (K_s) for NO_3

uptake, but such data are not available.

Light

All phytoplankton are tied to light for photosynthesis but only motile cells can show distinct phototactic responses. The advantage of accumulation at the depths where photosynthetically optimal light intensities occur depends upon the reception of and directed response to light. Hand (1970) observed the orientation and positive phototactic responses of Pandorina noreum and Volvox aureus and proposed a model to fit the reactions. For these species he suggested a receptor field of anterior cells and a shade field of posterior cells. Only the anterior cells showed differential activity and effected orientation through movement or non-movement of their flagella. An intercellular communication system was not required in this model.

An extensive treatment of Euglena motility can be found in Buetow (1968). Briefly, Euglena exhibited a positive phototactic response, even if bleached of chlorophyll, as long as the photoreceptor (paraflagellar swelling) and shading stigma were intact. Euglena cultured on a 12:12 hour light: dark cycle showed no photoresponse when light was introduced during the dark period (Jahn & Bovee, 1968). The endogenous cycle was gradually eliminated by continuous light.

For the variety of flagellated phytoplankton studied in Abbot's Pond, Happey-Wood (1976a, b) suggested that the

observed vertical distribution resulted largely from the different light intensity optima of each species. To cite extremes, Pandorina both rose and sank earlier than the other species indicating a high sensitivity to light, while Cryptomonas migrated vertically within the deepest meter of the water column at the limit of the euphotic zone. The species in Tilzer's (1973) alpine lake also showed differences in the timing and extent of their migrations, but these were not nearly so extreme as those seen in Abbot's Pond.

The light response was not direct, for, as Happey-Wood and Tilzer noted, most organisms began their upward migration before dawn, again implying an endogenous rhythm.

The aspects of suspension studied in the chlorophytes and other algae have conformed fairly well with results reported in the diatoms and dinoflagellates.

GENERAL CONCLUSIONS

Two critical factors determine the success of any phytoplanktonic organism, (a) sufficient light for photo-synthesis and (b) an adequate supply of the appropriate nutrients. The depth at which photosynthetic light inten-sities are optimal does not usually correspond with the area of greatest nutrient availability.

Flagellates and vacuolate cyanobacteria are observed to change positions to take best advantage of first one factor and then the other, while non-motile cells can do relatively little to select or adjust their position. Most cells are denser than their medium and, unless motile, will tend to sink not only away from their photosynthetic optima, but out of the euphotic zone altogether.

The role of environmental factors was not recognized as important in vertical positioning until the long ignored factor of turbulence was analyzed. Langmuir (1938) charac-terized the universal Langmuir spiral, and later Stommel (1949a) mathematically determined the trajectories of cells of different densities trapped in such convection spirals. Smayda (1970) determined that the veolcity of water in Langmuir cells normally exceeded the sinking rates of the seven diatoms he was considering, by 2-3 orders of magnitude!

Such turbulence tends to circulate and retain lighter cells
in the surface layers for very extended periods of time,
and heavier cells for lesser but still sufficient lengths
of time to complete their life cycles.

Nearly all non-motile phytoplankton bloom during turbu-
lent conditions and die back in periods of calm, as Lund
(1971) and Pollingher (1978) observed for Melosira. Turbu-
lent mixing suspends such cells in the surface layers where
they may photosynthesize efficiently, and brings nutrients
up from depths which stimulate growth.

Motile cells such as the flagellated cryptomonads,
chlorophytes, chrysomonads, haptomonads and dinoflagellates
tend to dominate in calm stratified waters where they are
able to position themselves to maximize light conditions and
nutrient assimilation. This is a feature which they share
with gas-vacuolate cyanobacteria. Turbulent conditions tend
to override the action of flagella and gas vacuoles, mixing
the motile cells with other cells randomly throughout the
water column. When motile cells lose the photosynthetic
and nutrient advantage over non-motile cells, diatoms or
green algae usually become dominant.

Only recently has an understanding been gained of the
adaptations and limitations brought about by the problems
of nutrient assimilation. While it has long been known that
non-motile cells which sink very rapidly cannot survive,

photosynthetically, it is now also recognized that cells
which are of neutral buoyancy, or which sink very slowly,
will succumb to starvation. The upper layers of stratified
water rapidly become nutrient-poor due to high population
densities, and organisms which are stationary develop even
greater local depletions in their individual boundary layers.
It is essential that cells move relative to the media to
displace boundary layers and to find more nutrient-rich
waters. Turbulence does little to displace boundary layers.

In theory, the relative motion requirement may be met
either by sinking or rising, but given the low density of
most aqueous environments, particularly fresh water, it is
natural that the majority of organisms maximize nutrient
assimilation by moving downward. Only flagellates, vacuo-
lated blue-green algae and a few anomolous species can en-
hance assimilation by rising. These species are believed
to take in most of their nutrients during migration to depths
where nutrients are normally more abundant.

Selection in non-motile species has been for cells which
sink at a rate that balances the photosynthetic need for
light with satisfactory nutrient assimilation. The sinking
of phytoplanktonic cells should not be viewed as a failure
to develop efficient floatation mechanisms, but as an adap-
tation to the nutrient requirements of plants living in an
aquatic environment.

The most critical aspects of the vertical positioning of phytoplankton, turbulence and the cellular motions of swimming, sinking, and floating, have been discussed, but the numerous secondary factors remain to be summarized. Treatment of these will be brief, but, where data are sufficient, comparisons of the value of each mechanism to the different groups will be made. It is emphasized that in nature the isolated effects of any one factor are rarely seen, and that the depth of a cell at any moment is the result of a complex interaction of variables.

Detailed studies of cell size relative to sinking rate have been carried out only on the diatoms, however, it is suspected that other non-motile cells act similarly. For species of a given shape there is an inverse relationship between the sinking rate and the surface area to volume ratio. Large cells of regular shape have a relatively small surface area, and must sink more rapidly than smaller cells to obtain sufficient nutrients. The loss of such cells to deep water is often high as water stratifies. Flagellated species show no size/velocity correlation (Tilzer, 1973).

The shape of a cell determines its form resistance which is reflected in the frictional drag and subsequent sinking rate. However, the relationship between shape and sinking rate is observed to be size dependent. The sinking order of a disc, a sphere and a cylinder of an equal nominal radius

depends upon which size range the radius falls into.

The orientation of a cell relative to its direction of fall is also determined by shape. Even small asymmetries cause cells to fall more slowly, since the greatest surface area will be normal to the direction of motion.

An increase in form resistance and frictional drag is noted in a variety of spined or bristled species of planktonic diatoms and green algae. The careful removal of the siliceous, chitinous, cellulose, or carbonate spines of such organisms, significantly increases sinking rates. These projections also discourage small predators.

Colony formation, with one explainable exception, increases the sedimentation velocity in all species observed. The aggregation of cells reduces the total surface area to volume ratio and associated frictional drag. Loss of relative surface area would also impede absorption.

Generally, as cells age the sedimentation rate increases, even if dimensions remain constant. This trend has been reduced temporarily in some species by the addition of nutrients. It is strongly suspected that certain physiological mechanisms may be responsible for senescent sedimentation. For instance, selective ion concentration is nutrient dependent and also subject to deterioration with age.

The secretion of mucous is a feature of many limnetic diatoms and chlorophytes, and may be a mechanism which com-

pensates for the extremely low density of fresh water. The reduction in net cell density becomes significant only when the density difference between the mucous and the cell is more than twice the density difference between the mucous and the medium (Hutchinson, 1967). The fact that the unusual marine diatom, Chaetoceros, which makes regular vertical migrations, secretes mucous as it divides and rises, strongly suggests that the substance may be a factor in floatation.

Convincing evidence for the selective inclusion or exclusion of heavy vacuolar ions has been presented for certain diatoms, dinoflagellates and chlorophytes. While this general feature spans all the groups considered, the specifics of its operation vary within and between groups. Anderson and Sweeney (1978) clearly demonstrated that changes in the buoyancy of Ditylum could be accounted for by the cyclic uptake and exclusion of the heavy ions K^+, Mg^{2+}, Ca^{2+}, and Cl^-. The sap vacuoles were largest when these ions were present at the end of the day and sinking was rapid. By contrast, the vacuoles of certain other diatoms and dino-flagellates contain low density sap and are most expanded when the cells are lightest. The "light" ions concentrated in these saps may be Na^+, NH_4^+ and possibly H^+. A light-mediated ion exchange has been demonstrated in Chlorella, but a suspension pattern is not yet clear (Shieh & Barber, 1971). A loss of ion selectivity occurs with nutrient-deplete media.

The photosynthetic requirement for light in phyto-
plankton is not disputed, however, tactic responses to light
are not constant. It appears that for a majority of flagel-
lated phytoplankton the tactic response is not direct.
Vertical migration is controlled endogenously with most
species rising at night or in the predawn darkness, and de-
scending gradually during the morning. Light intensities
through midday tend to be photoinhibitive and even photo-
oxidative in summer. A long term photoresponse is indicated
in most species, for a change in the light cycle is followed,
within a few days, by an adjustment of migrational rhythm.
A number of species do show a direct phototactic response
or an immediate change in migration when the illumination
is altered.

This paper has reviewed and critically discussed the
various inherent and environmental factors which allow a
diverse collection of phytoplankton to satisfy their nutri-
ent and photosynthetic requirements. Motion within a suit-
able area of the water column is essential to fill the special
needs of each species. A large number of secondary mechanisms
may influence the location of a cell, but the motility or
buoyancy of certain species and the wind-induced turbulence
of the medium, remain the prime factors which determine the
vertical position of phytoplankton.

BIBLIOGRAPHY

Ackman, R. G., Tocher, C. S. and McLachlan, J. 1968.
Marine phytoplankton fatty acids. J. Fish. Res. Bd.
Can. 25: 1603-1620.

Anderson, Lars W. J. and Sweeney, B. M. 1978. Role of
inorganic ions in controlling sedimentation rate of a
marine centric diatom Ditylum brightwelli. J. Phycol.
14(2): 204-214.

Beklemishev, C. W., Petrikova, M. N. and Semina, G. I.
1961. The cause of buoyancy of planktonic diatoms.
Trudy Inst. Okeanol. 51: 33-36.

Bellinger, E. G. 1977. Seasonal size changes in certain
diatoms and their possible significance. Br. Phycol. J.
12: 233-239.

Berman, T. and Rodhe, W. 1971. Distribution and migration
of Peridinium in Lake Kinneret. Mitt. Internat. Verein.
19: 266-276.

Buetow, D. E. 1968. The biology of Euglena. Academic
Press. New York. Vol. 1: 361 pp.

Canelli, E. and Fuhs, G. W. 1976. The effects of the
sinking rate of two diatoms (Thalassiosira, spp.) on up-
take from low concentrations of phosphate. J. Phycol.
12: 93-99.

Conway, K. and Trainor, F. R. 1972. Scenedesmus morphology and floatation. J. Phycol. 8: 138-143.

Eppley, R. W., Holm-Hansen. O. and Strickland, J. D. H. 1968. Some observations on the vertical migration of dinoflagellates. J. Phycol. 4: 333-340.

Eppley, R. W., Holmes, R. W. and Paasche, E. 1967. Periodicity in cell division and physiological behavior of Ditylum brightwelli, a marine planktonic diatom, during growth in light-dark cycles. Arch. für Mikrobiol. 56: 305-323.

Eppley, R. W., Holmes, R. W. and Strickland, J. D. H. 1967. Sinking rates of marine phytoplankton measured with a fluorometer. J. exp. mar. Biol. Ecol., Vol. 1: 191-208.

Fogg, G. E. 1965. Algal cultures and phytoplankton ecology. 2nd ed. University of Wisconsin Press. Madison, Wisconsin. 175 pp.

Gross, F. and Zeuthen, E. 1948. The buoyancy of planktonic diatoms: a problem of cell physiology. Proc. R. Soc., B 135: 382-389.

Halman, M. 1972. Chemical ecology. Evidence for phosphate as the only factor limiting algal growth in Lake Kinneret. Israel J. Chem. 10: 841-855.

Hand, W. G. 1970. Some studies concerned with photoorientation and phototaxis in solitary and colonial flagellates. Ber. Dtsch. Bot. Ges. Bd. 83: 181-184.

Hand, W. G., Collard, P. A. and Davenport, D. 1965. The effects of temperature and salinity change on swimming rate in the dinoflagellates, Gonyaulax and Gyrodinium. Biol. Bull. 128: 90-101.

Happey-Wood, C. M. 1976a. Vertical migration patterns in phytoplankton of mixed species composition. Br. phycol. J. 11: 335-369.

Happey-Wood, C. M. 1976b. Influence of stratification in the growth of planktonic Chlorophyceae in a small body of water. Br. phycol. J. 12: 371-381.

Hasle, G. R. 1950. Phototactic vertical migration in marine dinoflagellates. Oikos 2: 162:175.

Hutchinson, G. E. 1967. A Treatise on Limnology. Vol. 2. New York. 1115 pp.

Jahn, T. L. and Bovee, E. C. 1968. Locomotive and motile response in Euglena. In, The Biology of 'Euglena'. Academic Press. New York. pp. 45-99.

Kahn, N. and Swift E. 1978. Positive buoyancy through ionic control in the nonmotile marine dinoflagellate Pyrocystis noctiluca Murray ex Schuett. Limnol. Oceanogr. 23(4): 649-658.

Kamykowski, D. and Zentara, S. 1977. Diurnal vertical migration of mobile phytoplankton through temperature gradients. Limnol. Oceanogr. 22(1): 148-151

Kesseler, H. 1966. Bietrag zur Kenntnis der chemischen und physikalischen Eigenschaften des Zellsaftes von Noctiluca militaris. Veroeff. Inst. Meeresforsch. Bremerhaven 2: 357-368.

Langmuir, I. 1938. Surface motion of water induced by wind. Science, New York. 87: 119-123.

Lewin, J. and Hruby, T. 1973. Blooms of surf-zone diatoms along the coast of the Olympic Peninsula, Washington. II. A diel periodicity in buoyancy shown by the surf-zone diatom species, Chaetoceros armatum. T. West. Estuar. and Coast. Mar. Sc. 1(1): 101-105.

Lewin, J. and Rao, V. N. R. 1975. Blooms of surf-zone diatoms along the coast of the Olympic Peninsula, Washington. VI. Daily periodicity phenomena associated with Chaetoceros armatum in its natural habitat. J. Phycol. 11: 330-338.

Loeblech, A. R. III. 1975. A seawater medium for dinoflagellates and the nutrition of Cachonina niei. J. Phycol. 11: 80-86.

Lund, J. W. G. 1957. Buoyancy in relation to the ecology of freshwater phytoplankton. Brit. Phycol. Bull. 1(7): 1-17.

Lund, J. W. G. 1965. The ecology of the freshwater phytoplankton. Biol. Rev. 40: 231-293.

Lund, J. W. G. 1971. An artificial alteration of the seasonal cycle of the planktonic diatom *Melosira italica* subsp. *subarctica* in an English Lake. J. Ecol. 59: 521-533.

McNoun, J. S. and Malaika, J. 1950. Effects of particle shape on settling velocity at low Reynolds' numbers. Trans. Am. geophys. Un. 31: 74-82.

Munk, W. H. and Riley, G. A. 1952. Absorption of nutrients by aquatic plants. J. Mar. Res. 11: 215-240.

Owen, R. J. 1966. Small-scale horizontal vortices in the surface layer of the sea. J. Mar. Res. 24: 56-65.

Pechlaner, R. 1970. The phytoplankton spring outburst and its condition in Lake Erken (Sweden). Limnol. Oceanogr. 15: 113-130.

Pollingher, U. 1978. In *Lake Kinneret*. The planktonic community. ed. C. Serruya; Dr. W. Junk Publishers, The Hague. 219-291.

Pollingher, U. and Berman, T. 1975. Temporal and spatial patterns of dinoflagellate blooms in Lake Kinneret, Israel (1969-1974). Verh. Internat. Verein. Limnol. 19: 1370-1382.

Porter, J. and Jost, M. 1976. Physiological effects of the presence and absence of gas vacuoles in the blue-green alga, *Microcystis aeruginosa*. Kuetz. emend. Elenkin Arch. Microbiol. 110: 225-231.

Reynolds, C. S. 1973. Growth and buoyancy of Microsystis aeruginosa Kütz emend. Elenkin in a shallow eutrophic lake. Proc. of the Soc. London. B 184: 29-50.

Reynolds, C. S. and Walsby, A. E. 1975. Water blooms. Biol. Rev. 50: 437-481.

Riley, G. A., Stommel, H. and Bumpus, D. F. 1949. Quantative ecology of the plankton of the Western North Atlantic. Bull. Bingham Oceanogr. Coll., 12. No. 3, 169.

Serruya, C., Serruya, S. and Pollingher, U. 1978. Wind, phosphorus release and division rate of Peridinium in Lake Kinneret. Verh. Internat. Verein. Limnol. 20: 1096-1102.

Serruya, C. and Berman, T. 1975. Phosphorus, nitrogen and the growth of algae in Lake Kinneret. J. Phycol. 11(2): 155-162.

Shieh, Y. J. and Barber, J. 1971. Intracellular sodium and potassium concentrations and net cation movements in Chlorella pyrenoidosa. Biochem. et Biophys. Acta. 233: 594-603.

Smayda, T. J. 1970. The suspension and sinking of phytoplankton in the sea. Oceanogr. & Mar. Biol. Rev. 8: 353-414.

Smayda, T. J. and Boleyn, B. J. 1965. Experimental observations on the floatation of marine diatoms. I. Thalassiosira c.f. nana, Thalassiosira rotula and Nitzschia seriata. Limnol. Oceanogr., 10: 499-509.

Smayda, T. J. and Boleyn, B. J. 1966a. Experimental observations on the floatation of marine diatoms II. Skeletonema costatum and Rhizosolenia setigera. Limnol. Oceanog. 11: 18-34.

Smayda, T. J. and Boleyn, B. J. 1966b. Experimental observations on the floatation of marine diatoms. III. Bacteriastrum hyalinum and Chaetoceros lauderi. Limnol. Oceanogr., 11: 35-43.

Steele, J. H. and Yentsch, C. S. 1960. The vertical distribution of chlorophyll. J. Mar. Biol. Ass. U. K. 39: 217-226.

Stommel, H. 1949a. Trajectories of small bodies. J. Mar. Res., 8: 24-29.

Strickland, J. D. H. 1965. Production of organic matter in the primary stages of the marine food chain. In, Chemical Oceanography. ed. J. P. Riley and G. Skirrow, Academic Press. New York. Vol 1: 477-610.

Sukhanova, I. and Rudyakov, Y. 1973. Population composition and vertical distribution of Pyrocystis pseudonoctiluca (W. Thomson) in the western equatorial Pacific, p. 218-228. In M. Vinogradov, ed., Life activity of pelagic communities in the ocean tropics. Isr. Program Sci. Transl.

Swift, E., Stuart, M. and Meunier, V. 1976. The in situ growth rates of some deep-living oceanic dinoflagellates, Pyrocystis fusiformis and Pyrocystis noctiluca. Limnol. Oceanogr. 21: 418-426.

Swift, E. and Taylor, W. R. 1967. Biolumniescence and chloroplast movement in the dinoflagellate Pyrocystis lunula. J. Phycol. 3: 77-81.

Tilzer, M. 1973. Diurnal periodicity in the phytoplankton assemblage of a high mountain lake. Limnol. Oceanogr. 18: 15-30.

Trainor, F. R. 1969. Scenedesmus morphogenesis. Trace elements and spine formation. J. Phycol. 5: 185-190.

Walsby, A. E. 1977. The gas vacuoles of blue-green algae. Sc. Am. 237(2): 90-97.

Walsby, A. E. and Xypolyta, A. 1977. The form resistance of chitin fibers attached to the cells of Thalassiosira fluviatalis Hustedt. Br. Phycol. J. 12: 215-223.

Walsby, A. E. 1978. The gas vesicles of aquatic prokaryotes. Symposia of the society for general microbiology. Number XXVIII: 327-358.

Wetzel, R. G. 1975. Limnolgy. W. B. Saunders Company. Philadelphia. 743 pp.