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delft hydraulics laboratory

Amsterdam university
limnological laboratory

phytoplankton cells, their nutrient contents, mineralisation and sinking rates

R 1310

September 1978

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Preface

This report deals with the results of an extensive literature research to the contents of nitrogen, phosphorus, silicon and chlorophyll in phytoplankton cells, the mineralization rates of nitrogen, phosphorus and silicon from phytoplankton cells and the sinking rates of phytoplankton cells.
The literature research was performed by Mrs. M. Lingeman - Kosmerchock of the Limnological Laboratory of the University of Amsterdam, in co-operation with Mr. F.J. Los of the Delft Hydraulics Laboratory.
This research project is part of an extensive assignment by the Environmental division of the Delta Department to Delft Hydraulics Laboratory in order to develop ecological models, which can serve as tools in providing adequate guide-lines for environmental management in the (future) water basins in the Delta area.
This multidisciplinary project, called Water Basin Model (WABASIM) is carried out in close co-operation between the Environmental division of the Delta Department and the Environmental Hydraulics Branch of the Delft Hydraulics Laboratory.

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1 The contents of nitrogen, phosphorus, silicon and chlorophyll in phytoplankton cells

The cellular content of nitrogen, phosphorus, silicon and chlorophyll of some species of phytoplankton is summarized in Table 1. The weight values are on a dry weight basis and have been standardized to picograms (10^{-12}) per cell. In a few cases values were given in terms of µmole/cell and these values have also been converted to picograms. Frequently in the literature, the values have been given as percentage of dry weight/cell. For cases where a dry weight value was not given, or could not be found in any other sources the composition of that particular species is given only in terms of percentage of dry weight.

There is a great deal of variation in content not only between species but also among a species as reported by various investigators. It is somewhat difficult to compare these values to one another since the cellular content is effected by amounts of nutrient in the medium, light and also temperature. In the laboratory these conditions are generally optimum and thus caution should be taken when applying these laboratory culture values to a natural population.

There is a general lack of information concerning the chlorophyll content in an individual cell. Data for chlorophyll are usually given in terms of an entire population with no additional data which can be used to calculate it on a cellular basis. Perhaps this topic has not been pursued in detail due to the great variation in the content of chlorophyll throughout the day. Those values which have been found (Table 1) exhibit considerable variation in cellular content.

Silicon is the major component of the diatom cell walls. Certain diatoms vary considerably in their content of silicon (Jørgensen 1953, Lewin 1961). Others, including some of the important planktonic forms, show relatively little variation (Einsele & Grim 1938). The amount of silicon also varies in relation to the mode of reproduction. Many diatoms undergo a unique and gradual diminuation in cell size with continual asexual cell division (Lund 1965). The silica content of living cells can be caused to vary by at least five different factors which have been listed by Werner (1977):

1. Limitation of silica supply in the medium.

2. Variation of other culture conditions such as light, temperature, pH, nutrient concentrations, and population density.
3. The variation of the valve diameter and thereby the cell surface area.
4. The stage in the mitonic life cycle.
5. Variation in the formation of special silica containing structures such as spines and processes.

Under (si$(OH)_4$ limitation the silicon content per cell decreases in some species such as Skeletonema costatum and Thalassiosira pseudonana (Harrison 1974, Paasche 1973c). These species can still divide after the cessation of $Si(OH)_4$ uptake at which time they develope very thin shells (Braarud 1948). Other species, such as Cyclotella crypta will not divide when they are silica deficient (Werner 1966).

Nitrogen and phosphorus are necessary elements for all algae as they are major components of proteins, nucleic acids, and lipids. The measured content of cellular phosphorus can be quite variable since it has been shown by Mackereth (1953), Kuenzler & Ketchum (1962), and Reynolds & Walsby (1975) and others that many algae exhibit luxury uptake. This is the ability of the cell to absorb far more phosphorus than their immediate needs when the phosphorus is readily available. Cell phosphorus content is thus effected greatly by the availability of phosphorus in the medium and the rate of uptake.

The uptake of phosphate by algae is generally stimulated, but not dependant on, light. Observations on natural populations have shown a diurnal periodicity in phosphorus uptake with greater rates during some parts of the day than at night (Eppley et al 1971, Overbeck 1962). The maximum rates of phosphate uptake by various algae are also dependant on the simultaneous presence of sodium (Simonis & Urbach 1962), potassium (Scott 1945), or magnesium (Healey 1973). If these ions are required for uptake of phosphorus or for polyphosphate synthesis, however, has not yet been determined.

The polyphosphate appears to be the principle form of storage in most algae. Besides being able to use inorganic phosporus a variety of algae can use phosphorus in the form of some organic esters (Galloway & Krauss 1963, Kuenzler 1965).

The nitrogen content of algae is much higher (often ten fold) than the phos-

phorus content. The amount of cellulair nitrogen at which growth ceases is low. Aach (1952) found growth of Chlorella pyrenoidosa until there was only 0.16 μg N/10^6 cells. Fogg et al (1973) have found that the nitrogen content of healthy blue-green algae is within 4-9% on a dry weight basis. The exact amount was found to depend upon the growth stage. The highest content is found in exponentially growing cells.

Generally algae have the ability to use nitrogen in the form of nitrite, nitrate, or ammonia. The ability of algae to use a variety of organic nitrogen compounds as the sole source of nitrogen is also wide spread among algae. When taken up in the oxidized form as nitrate or nitrite the nitrogen must be reduced before it can be incorporated into organic molecules. The ability to take up and reduce nitrite and nitrate is widely affected by several aspects of their previous history such as the availability of nitrogen during cell growth, the form of nitrogen and whether it is reduced or not, as well as the availability of certain metals required for the operation of the nitrite and nitrate reducing systems.

The uptake and assimilation of inorganic nitrogen compounds by algae is also affected by several aspects of the immediate environment such as light, pH and temperature. Light generally stimulates the uptake and reduction of nitrite and nitrate by algae. A diurnal periodicity in rates of nitrate, nitrite, or ammonia uptake has been reported for both natural phytoplankton populations (Prochazkova et al 1971, McCarthy & Eppley 1972) as well as for algae cultured in a light-dark cycle (Ohmori & Haltori 1970, Kanazawa et al 1970, Eppley et al 1971b).

2 The mineralization rates of nitrogen, phosphorus, silicon and carbon from phytoplankton cells

2.1 Phosphorus

A considerable proportion of the organic matter produced during photosynthesis by phytoplankton may be released in a soluable form by actively growing populations. Some of this released material undoubtly consists of compounds of phosphorus (Corner & Davis 1971).

Early studies involving the release of phosphorus from the cell consisted of monitering the increase in dissolved organic phosphorus (DOP) in the culture medium, after algae had been quickly killed. This procedure was used by Golterman (1960) to measure what he considered to be mineralization of phosphorus (this was a measure of the rate or extent of phosphorus release from dead rather than living cells). He observed that 70-80% of the phosphorus leaves *Scenedesmus* cells during autolysis in a few days. The first product liberated is PO_4-P which is upto 5% of the total cellular phosphorus. Next comes an enzymatic breakdown of phospholopids which account for 10-20% of total cellular phosphorus. These values differ slightly from those of Hoffman (1965) who found 20-25% of inorganic phosphorus and 30-40% of organic phosphorus was liberated from algae shortly after death.

Overbeck (1962) studying natural plankton populations of an open water basin dominated by *Scenedesmus quadricauda* observed that amounts of DOP and plankton phosphorus were inversely proportional to one another and sights this to be evidence that cells are secreting organic phosphorus in the daytime.

The regeneration of phosphorus by algae *in situ* was studied by Anita and coworkers (1963). The natural population of phytoplankton consisted chiefly of six species of diatoms and one dinoflagellate. They found the regeneration of phosphorus to have an initial mean rate of 0.13 µgat P/L/day, which then slowed down by day 40 when 50% of the particulate phosphorus was returned to solution. Gill & Richards (1964) followed the regeneration of phosphorus in a culture of phytoplankton (chiefly centric diatoms) which had been incubated in the dark. The increase in particulate carbon continued for 8 days after which a sudden increase in DOP and a decrease in particulate phosphorus occurred.

Kuenzler (1970) has shown that dissolved organic phosphorus in cultures of marine phytoplankton reaches a maximum unit of 12-25% of total phosphorus present when cultures are entering the stationary phase. Cyclotella cryptica was found to reassimilate this during the stationary stage but in the case of Thalassiosira fluviatilis the level increased with age of the culture. Kuenzler makes the statement that DOP released by phytoplankton in the euphotic zone maybe as important as that excreted by zooplankton and that relative abilities to utilize the organic phosphate could provide some species with a competitive advantage over others.

Under selected laboratory circumstances a periodic release of phosphate was demonstrated with synchronous cultures of Chlorella fusca by Soeder et al (1971). The maximum phosphorus released corresponded to 2×10^{-7} µg P/cell/hr. They conclude that if periodic excretion of phosphate were a more widely distributed phenomenon it could first induce slight changes in the phosphate concentration of natural waters and secondly the exchange of phosphorus from one cell to another could be possible and might have some influence in producing limiting levels of phosphorus.

A different approach was taken by Lean & Nalewajko (1976) who used a radioactive tracer, ^{32}P, to follow the uptake and release of phosphorus compounds by four fresh water species of algae. In their experiments DOP was excreted when phosphate in the medium was nearly depleted. This is similar to results of Kuenzler (1970) who found the maximum accumulation of the isotope in DOP form occurred when inorganic phosphorus was low and often less than 1% of the original concentration and also when biomass was approaching the stationary stage.

Fogg (1971) in a review of the literature on formation of DOP concluded that release was most likely to occur during periods of maximum growth when inorganic phosphorus is abundant while DOP utilization may be expected when inorganic phosphorus is scarce. The relative contribution of living algae to the rapid turnover of phosphate in lake water still remains rather incertain, however, Lean & Nalewajko (1976) have demonstrated that algae as well as bacteria can account for this phenomenon which occurs at phosphate concentrations less than the sensitivity of the molybdate test for orthophosphate.

A summation of the values for the release of phosphorus by algae as found by various investigators is given in Table 2.

2.2 Nitrogen

Very little information is available on the actual mineralization of nitrogen from phytoplankton cells (Table 3). What information is available is concentrated in the area of extracellular products which are secreted by the cell. The work of Hellebust (1965) has shown that nitrogenous substances are liberated by algae. The liberation of substantial amounts of soluble nitrogenous substances from cells of healthy cultures of blue-green nitrogen fixing algae have been recorded several times and mostly in the form of polypeptides and amino acids (Fogg 1952, 1962, Magee & Burris 1954).

The amount of nitrogenous substances excreted depends upon: 1. the stage of growth, 2. the environmental conditions, and 3. the strain of algae. Fogg (1952) found the amount of extracellular combined nitrogen to increase during the growth of Anabaena cylindrica. From 5-60% of the fixed nitrogen was excreted with the highest amount during the lag and stationary phases. In later experiments Fogg (1962) found 20-40% of the nitrogen assimilated appeared in the form of extracellular products. Walsby (1965, 1970) found that a substantial portion of nitrogenous material is released initially in the form of small molecules containing a small number of serine and thrionine residues.

Undoubtly much of the confusion and controversy which surrounds the origins and functions of extracellular substances has arisen because although many studies have been made on the classes of compounds (e.g. combined nitrogen, amino acids, sugars, peptides, carbohydrates, and mucilages) only in a few cases have the exact identities of compounds been made.

2.3 Silicon

In diatoms the biological mineralization of silica occurs during cell wall formation. At this time the cells polymerize silicic acid $Si(OH)_4$ to form a morphologically complex and species specific silica shell. This formation is dependant on the transport of $Si(OH)_4$ from the external environment to the intracellular environment and the manner in which silicic acid is then polymerized to multimeric forms such as dimers, trimers etc. (Sullivan 1976).

The classical method to determine silicon is the hydrolysis of the polymer silica to monosilicic acid and its reaction with molybdate followed by a

reduction to a blue complex (Mullin & Riley 1955, Engel & Holzapfel 1960, Strickland & Parsons 1968). Newer methods for silica analysis include mass spectroscopy (Goering et al 1073) and the use of radioactive tracers (Coombs & Volcani 1968, Azam et al 1973, Werner et al 1975). The use of radioactive tracers has increased the analytical sensitivity by several orders of magnitude. ^{31}Si has a disadvantage of a half life of only 2.6 hours, thus, it is useful only in short term experiments. However, a discovery of Mehard and coworkers (1974) which uses $^{68}Ge(OH)_4 + Si(OH)_4$ as a tracer for silica increased the analytical accuracy. Improvements of their technique have been made by Azam et al (1973) and Sullivan (1976) which now make detailed investigations of the properties of silica possible.

When conducting experimental studies on the dissolution of silica from the algal cells in laboratory cultures many factors should be taken into account. Werner (1977) has summarized some of these important factors. They include:

1. Species size
2. Diameter of valve
3. Stage in life cycle
4. Growth rate and phase of cells
5. Average thickness of the cell wall
6. Average surface area of the cells
7. Temperature at which the cells are grown
8. Silicon concentration of medium
9. Other mineral concentration of medium
10. Light conditions (solid light or light/dark periods)
11. Relative proportion of parts of the cell (valves, girdle, bands)
12. "Cleaning methods" used to separate the organic matter from the frustules (acid, heat, enzyme).

In one of the earliest experiments involving silicon dissolution Jørgensen (1955) found the liberation of silicon to be dependant on the pH and the rate of dissolution to be different for different species. The percentage dissolution was found to increase with an increase in pH of the medium for both Nitzschia linearis and Thalassiosira nana. At pH 10 Nitzschia dissolved only 20% in 40 days whereas in the same time period Thalassiosira cells were completely dissolved. The rate of dissolution was linear throughout the experiment with Thalassiosira whereas the rate for Nitzschia fell off abruptly after a certain period.

The mineralization of silica from diatoms was found by Golterman (1960) to be a slow non-enzymatic process. He observed that only 20-30% of the silica in Stephanodiscus hantzschii was liberated after a period of several weeks.

Lewin (1961) observed that the dissolution of silica from living freshwater diatoms in the laboratory was extremely slow, much slower than the rate of dissolution from dead cells. She concluded that the silica in the walls of living cells are protected by a "physico-chemical" system which is disrupted when cells die allowing for more extensive dissolution.

A completely different approach was taken by Anita and coworkers (1963) who attempted to measure the extent of mineralization in situ with the use of large volume plastic bags. Experiments were 100 days in duration using the natural plankton population which consisted mainly of diatoms. The change in the dissolved silica content of the water was used as a measure of the extent of dissolution. After 55 days 40% of the plant silica had been mineralized. At the conclusion of the experiment (100 days) a total of 53% was mineralized.

No detectable dissolution of silica from the crops of Asterionella in Lake Windemere were observed by Lund and his co-workers (1963). However, Kamatani (1969) found mineralization in sea water at 30°C to be 50% and more within 10 days in cultures of Skeletonema costatum and Chaetoceros gracilis but less than 10% with Thalassiosira deciphiens.

Plankton samples from a shallow, eutropic lake consisting chiefly of diatoms (Cyclotella, Stephanodiscus, Asterionella) were concentrated and used by Baily-Watts (1976) in laboratory experiments to determine rates of mineralization of silica. The concentrated plankton samples were placed in plastic bottles and filled with filtered sea water. They were then placed at different temperature and different light-dark regimes. An increase in the dissolved silicon (taken to represent mineralization) was observed with both living and dead cells, and in constant light and constant dark. In one experiment after 38 days at 20°C and in the light 36% of the silica had dissolved.

Another experimental approach was taken by Parker and co-workers (1977) in Lake Michigan. Theymeasured the diatom frustules and the Si/gm dry wt. of sediment at 5 meter intervals in the upper water column (0-40 m), in sediment traps at 37 and 60 meters, and in a sediment core. The vertical distribution of diatom frustules and the Si/unit dry wt. showed a considerable fraction of

the silica in euphotic zone was decomposed before it was incorporated into the sediment. Experiments revealed an average loss of 0.0016 mg Si/day.

The ^{30}Si tracer technique was applied to laboratory batch cultures of the marine diatom Thalassiosira pseudonana by Nelson et al (1976). They found the v_{dis}/hr = 0.0020-0.0085 pg Si/cell/hr. Although incubation time was short it was evident that there was dissolution from the population when they were growing exponentially. Their data supports the assumption of Paasche's (1973b) that the dissolution rate of dead but physically intact diatom cells is also characteristic of living cells, from which dissolution can not be measured by observing the changes in silicic acid concentrations.

Lewin (1961), as previously stated, detected little or no dissolution from living cells and suggested that living cells have some mechanism to prevent dissolution. She did, however, recognize that the masking of dissolution by Si uptake was a possible explanation for her experimental results. This assumption is consistant with the direct measurement of simultaneous uptake and dissolution of Nelson et al (1976).

Information on the dissolution of silicon from algal cells as observed by various investigators is given in Table 4. From this information one can conclude that dissolution from living cells does occur, however, it varies considerably from one species (or community) to another and also is dependant upon environmental conditions. The role of silica dissolution as a source of elemental silica availability for the plankton growth in a natural environment should not be overlooked.

2.4 Carbon

Extracellular products, defined as soluble organic substances liberated from healthy as distinct from injured or decomposing cells, are produced in a greater variety and amount than has generally been realized (Fogg 1966). It seems likely that a large proportion of the products of phytoplankton photosynthesis are liberated in this way thus, extracellular products are of considerable importance as metabolites and a source of energy for the aquatic emvironment. This phenomenon has been studied mostly in laboratory cultures. Conditions in natural environments are likely to be rather different and these differences must be taken into account when accessing the ecological significance of the data.

To obtain sufficient material for direct determination of extracellular products it has been necessary to use large populations in long time periods and therefore the results may be of little significance. However, the use of the ^{14}C radioactive tracer method has greatly increased the sensitivity of the results.

Eppley and Sloan (1966) studied extracellular products released in 8 species of marine phytoplankton by three different methods and concluded that the radio-carbon method is most reliable. They found extracellular products varied from 0.5-34% of the total photosynthetic production with no consistant difference between groups of algae. Hellebust (1965) studied 22 marine species and found most to excrete 3-6% of their photosynthetically fixed carbon. He also found no difference between groups of algae. Nalewajko (1966) experimenting with 23 fresh water species of algae found the range to be 0.2-19.4% of total assimilated carbon with the diatoms having slightly higher values than other groups. A summary of the percentage assimilated carbon excreted under laboratory conditions is given in Table 5.

In situ determinations with ^{14}C have been made in various lakes by Fogg (1958), Fogg & Nalewajko (1963), Fogg, Nalewajko & Wall (1965), Nalewajko & Marin (1968), Nalewajko & Lean (1972), Nalewajko & Schindler (1976) and Storch & Saunders (1978). The results revealed that between 7-50% of the total carbon fixed in the photic zone of a water column was released into the water in extracellular forms. There was a tendency for release to be greater in low light. The amount increased as the population became less dense. Some experimental values of extracellular release in natural populations are summarized in Table 6.

3 Sinking rates of phytoplankon

The mechanisms by which non-motile phytoplankton achieve suspension within the euphotic zone has long intrigued aquatic biologists. The sinking rates are of potential importance in determining the vertical distribution of phytoplankton biomass and productivity as well as contributing to the movement of organic carbon from the surface waters. Sinking rates have been studied in relation to physical characteristics of the cell, such as age (Smayda and Boleyn 1965 , 1966a, 1966b), size and morphology (Ostwald 1902, Munk & Riley 1952 , Smayda & Boleyn 1965 , 1966a, 1966b), on physiological phenomena which effect cell density (Gross & Zeuthen 1948 , Smayda & Boleyn 1965, 1966a, 1966b, Smayda 1970, Boleyn 1972) as well as environmental factors such as mixing of the water column (Lund 1959, Smayda 1970), light (Steele & Yentisch 1960, Epply, Holmes, Paasche, 1967). The potential effects of sinking on the vertical transfer of biomass is also accounted for in many production models (Riley, Stommel & Bumpus 1949, Rhyter & Yentisch 1958, Riley 1937, 1965 and Jassby and Goldman 1974). Despite these studies the principles of phytoplankton sinking and suspension is an area where much still needs to be resolved. The knowledge of this phenomen is vital for a proper understanding of the dynamics of phytoplankton retention in the euphotic zone.
It is important to recognize that continious residence within the euphotic zone is neither necessary, or often practical,for succesful phytoplankton existance. Succesful growth and survival require only that the mean daily residence time within the euphotic zone permits photosynthesis in excess of daily respiratory and organic secretion losses. Thus, the proportion of time spent within the euphotic zone will obviously influence the magnitude of growth (Smayda 1970).

Phytoplankton cells in suspension will be buoyed up by a force equal to the weight of the displaced fluid according to Archimedia's principle (Hutchinson 1967). The resulting force of gravity working on the organism will then be:

$$F = gkd^3(p' - p)$$

where kd^3 is the cell (or colony) volume, g is the acceleration due to gravity, and p' and p are the densities of the organism an the liquid. The term (p'- p) is called excess density. Theoretically an organism can remain suspended in a liquid only if one of the following conditions is met:

1. If the excess density is zero ($p' = p$).

2. If a force is applied to a body it may even when p' is greater then p be moved upward as rapidly as it passively sinks.

3. If by active swimming an organism can exert a force sufficient to balance the force of gravity ($p' < p$).

The cell density p' is effected by the composition and amounts of cell wall cytoplasm as well sap materials. Diatoms with hydrated silicon dioxide cell walls, coccolths with calcium carbonate platelets, and some dinoflagellates with cellulose platelets in the cell walls all have modifications of the cell wall which add a certain amount of ballast. This seems quite paradoxical, since this added density must then be overcome for the organism to remain is suspension. The density of marine organisms varies from 1.03 - 1.10 while that of the sea water varies from 1.021 - 1.028 which is somewhat less than those of phytoplankton cytoplasm and significantly lower than that of cell wall structures (Jacobs 1935). This also holds in freshwater situations where the excess density of diatoms, for example, is between 0.015 - 0.025 (Hutchinson 1967).

From the earliest work on the sinking rates of phytoplankton the hypothesis developed that the situation where p' is greater than p existed. Stokes' law for sphaerical bodies falling through a liquid medium was then applied to phytoplankton. For a concept of the nature of the situation;

$$\nu = \frac{2}{9} g r^2 \frac{p' - p}{N}$$

r is the radius, g is the acceleration due to gravity, N is the viscosity of the liquid. The limitation of Stokes' law is that it applies only to a sphaerical shape which is a shape that occurs infrequently in phytoplankton. The problem thus became one of analyzing the influence of morphological factors on flotation. Ostwald (1902, 1903) proposed that the sinking rate by phytoplankton was directly proportional to excess density and inversely proportional to the vicsosity of water and the organisms form resistance. Mathematically this was expressed as:

$$\nu = \frac{p' - p}{N.R}$$

where R is form resistance.

Ostwald's formula together with these conclusions; that phytoplankton flotation is really a sinking process $(p' < p)$ of variable rate, and that form resistance is extremly variable but excess density is usually constant, had a profound effect on phytoplankton flotation theory. Elaborate discussions of the development of the mathematical theory for the deviation from a sphaerical shape is give in Hutchinson (1967) and Smayda (1970). The morphological characteristics which are usually considered to have an effect on the degree of form resistance include; cell shape and size, colony formation, and protuberances. A partial theroretical evaluation (Munk & Riley 1952) has been done on the sinking behaviour of four main diatom shapes which are often considered to be adaptations to flotation (bladder type, plate or ribbon type, hairlike type, and setose type). They concluded that the effect of shape on the sinking velocity was size dependant but that the rate of the different shapes tends to equalize with increasing size. The sinking speed of a non-sphaerical body can then be given as:

$$\nu_a = \frac{2gr^2}{q} \; \frac{p'- p}{N_{\gamma r}}$$

Where Q_r is the coefficient of form resistance. Hutchinson (1967) discusses the various ways of calculating Q_r given as $Q_r - V_s/V_a$. Where V_s is terminal velocity of an equivalent sphere and V_a the terminal speed of a non-sphaeroid body of simular density and volume. This method has also been used by Eppley, Holmes and Strickland (1967) to calculate the cell density of phytoplankton used in their sinking experiments.

Phytoplankton cells vary in size over four orders of magnitude. In early work (Oltmanns 1923) an increase in size was considered to be an adaptation to flotation. In laboratary experiments, however, an increase in size has been found to accompany an increase in the sinking rate (Boleyn 1974, Titman & Kilham 1978, Smayda & Boleyn 1965, 1966a, 1966b). This is also related to cell age. Titman & Kilham (1976), Boleyn (1974) and Eppley, Holmes and Strickland (1967) all found that cells in the stationary stage sank as much as four times faster cells in the exponetially growing stage. It was also found that the change in sinking rate upon the cessation of growth was striking. Rather than the rate changing gradually and continuously with time the sinking rate was rather constant in the logrithmic phase and then

changed abrupt in a faster but constant rate at the onset of the stationary phase. In general increasing senescense of a population is accompanied by an increase in sinking rate, with larger cells (low area: volume) sinking faster than smaller cells of the same shape.

Due to the method of reproduction in the diatoms the size of the cell and thus silica content of cell wall varies with each generation. In the freshwater diatom Fragilaria crotonensis Einsele & Grim (1938) calculated a density range of 1.1' - 1.45 based on the life stage and silica content. This change in density was thought to account for the variation in sinking rate. Some of the blue-green algae, diatoms and dinoflagellates are capable of forming chain-type colonies. In early phytoplankton wok this was often sighted as a method for the phytoplankton to decrease their rate of sinking. There is, however, theoretical agreement (Oltmanns 1923, Munk & Riley 1952) that chain formation actually favors an increase in sinking rate due to reduction in relative surface area and thus drag resistance.
In laboratory studies (Smayda & Boleyn 9165, 1966a, 1966b) an increase in colony size was accompanied by an increase in sinking rate in setose, gelateneous sheath, overlapping apices, ribbon, and spiral chain-type colonial species. The exception was Skeletonema whose mode of colony formation is the silica rods which interconnect the cells. It has been theorized (Smayda & Boleyn 1966a) that these rods increase frictional drag of the cells and thus decrease their sinking rate. Colony size is not always constant. The number of cells per chain decreases with age no matter what the mode of chain formation (Smayda & Boleyn 1965, 1966a, 1966b). The exact causes of colony breakage (a means of size regulation) are not known. The relative sinking rate usually decreases with a reduction in colony size, however, the reduction in colony size that accompanies senescense is accompanied by an absolute increase in the sinking rate. (Smayda & Boleyn 1965, 1966a, 1966b). The important result is that experimental observations have confirmed that chain formation is usually accompanied by a reduction in sinking rate and therefore can not be thought of as a mechanism to reduce the sinking speed.

Some phytoplankton, especially freshwater species, have a gelatenous sheath around them. These gelatenous sheaths are found in all planktonic blue-green (Except Lingbya & Sphanizomonon), many of the non-flagellate green algae, desmids, as well as some diatoms) as well as developed sheath occurs in Cyclotella, Fragilaria & Stephanodiscus. This sheath does not necessarily

result in a change in the form but does involve an increase in the cell magnitude. It was widely believed (Gessner 1955, Wesenberg-Lund 1908, Ruttner 1940, 1952b) that this was a mechanism related to flotation and the reduction of sinking speed. However, for these secretions to be effective in aiding suspension the density difference between the organism and the sheath (p'org - p'gel) must exceed that between the sheath and the medium (p'gel - p'med.) by two fold (Hutchinson 1967). If the jelly has the same density as the medium (p'gel = p'med) it is possible to reduce the sinking speed to any desired degree by increasing the thickness of the sheath. For values of the density differences between the gel and medium greater than onze and less than two the sheath would be effective as a flotation mechanism. In view of the fact that the density (p') in diatoms may be over 1.1 and as great as 1.45 (Einsele & Grim 1938) it seems likely that the generally accepted idea of the function of the sheath is correct. This is, however, a field in which little actual experimental work has been done.

The many surface extensions on phytoplankton such as; spines, setae, hairs, cells are generally thought to be mechanisms to help the organisms remain suspended. One of the theories of hydrodynamics states that a body moving in a liquid will tend to take the position with greatest area of projection perpendicular to the direction of motion. Thus, it was thought that these cellular projections would provide a potential frictional resistance, aid in orientation, and thus retard the rate of sinking. It was observed by Lund (1959) that Oscillatoria agardhii, single cells Asterionella formosa and filaments of Melosira italica subartica take a vertical position in non-turbulant water and are therefore according to the principles of hydrodynamics not orientated for minimum speed.

Whatever the extent of the envolvement of morphological factors on the sinking rate the following conclusions can be made:

1. Dead cells sink faster than living cells (Fritz 1935, Smayda 1970).
2. Living senescent cells sink faster than viable cells in the laboratory and the sinking rate increases with age (Smayda & Boleyn 1965, 1966a, 1966b),
3. Living natural populations sink with increasing age (Allen 1932, Gillbrecht 1952).
4. Sinking rate decreases with an increase in colony age.
5. Larger cells sink faster than smaller cells.

One can speculate that a physiological means of regulating cell density would be a more effective way for the cell to modify its means of suspension rather than the slow morphological methods. The physiological means which has been investigated include; gas vacuole formation, fat accumulation, and change in ionic composition of the vacuole and cell sap. Gas vacuoles are commonly observed in limnetic plankton (Gessner 1955, Fogg et al 1973, Lund 1959) and thought to have an influence upon suspension. Planktonic species of blue-green algae frequently contain irregular bodies called pseudovacuoles.The purpose of these structures has been studied very little in the past but it is now widely accepted that these vacuoles are filled mainly with nitrogen (Fogg 1952, 1962, 1964, 1975). The destruction of the pseudovacuoles by pressure was found to lead to an increase in the density of algae which generally float when the vacuole is present and sink when it is destroyed (Klebahn 1922). A change in cell density due to loss of gas from the vacuole was also observed by Walsby (1969), and Fogg et al (1973).

Fat formation has also been noted as an adaption to suspension, however, most observations suggest it is unimportant or only partially effective. Oltmanns (1923) and Gessner (1955) pointed out that the presence of fat globules is not an adaption to flotation since even sessile diatoms can be fatty.

Large phytoplankton invariably have large vacuoles. The bulk of a cell can be occupied by the vacuole. Diurnal variation in the hydration state of the cell by selective uptake of certain ions was thought by Eppley, Holmes, & Paasche (1967) to be a possible explanation for diurnal variations in sinking speed in the marine diatom Ditylum brightwelli. This ionic theory of suspension is not applicable to the limnetic phytoplankton due to low quantities of salts in solution in freshwater (Lund 1959).

Light and photoperiod might also influence suspension although to date there is very little information on these topics to make statements of their effect on the sinking rate. Eppley, Holmes & Paasche (1967) found Ditylum brightwelli to exhibit a diurunal variation in sinking rate. A decreased sinking rate in dark was observed by Steele & Yentisch (1960) with Skeletonema costatum.

Physical factors affecting the sinking behaviour are water movements and viscosity. The ratio of the inertial force to the viscous force in the balance influencing plankton sinking is measured by the Reynolds number, R_e;

$$R_e = \frac{dvp}{N}$$

where d is the diameter, v the sinking velocity, p the density of the medium, and n the dynamic viscosity. A Reynolds number less than 0.1 signifies that the viscous forces are significant. The value of increasing frictional drag to aid suspension is evident. The most important factor influencing viscosity is temperature. The sinking rate was found to increase four percent per degree rise in temperature by Smayda (1970) which suggest that tropical and summer populations have an intrinsically more difficult problem of achieving suspension than polar and winter populations.

The liberations of organic substances from plankton cells is also a means of modifying viscosity. Some limnetic phytoplankton liberate soluable high molecular weight polymers which have the property of reducing the fluids friction during turbulent flow. (Hoyt & Soli 1965).

Margalef (1957) presented arguments suporting the existance of "structural viscosity" which is due to electrical properties of components of the outer cell wall. These charges then influence the number of layers of water molecules around the cell, thus,altering the viscosity and sinking speed. However, most of his work was theoretical with little actual experimental evidence. Other studies on the determination of membrane charge of the cell wall have been done by Fritze (1952), Kolin (1955), Ives (1956), but they too provide little evidence to support the views of Margalef. Ives (1956, 1959) determined the surface electrical charges of thirteen limnetic plankton species. All taxa were found to be electro-negative but the charge varied between species and genera. Ives also suggested that the gelatenous sheaths are hydrophilic and that the changes in surface charges would influence the degree to which the gelatenous sheath of the cell wall is hydrophilic or hydrofugic, e.g. differences favoring repulsions of water molecules would increase the degree of slippage and therefore the sinking. A decrease in sedimentation rate of Chlorella sp. was accompanied by the

addition of a few drops of butanol or isopropanal to culture medium. This as observed by Margalef and sited as experimental evidence for structural viscosity. Contrary to the results of Margalef it was found by Smayda (1974) that the sinking rates of diatoms increased when exposed to alcohol. Ives (1956) demonstrated that the addition of various algacides influenced the surface charge although the exact effect on sinking rate was not established.

The fact that water movements are important in the suspension of freshwater plankton has been well established (Utermohl 1925, Gessner 1948, Lund 1959, 1966, Hutchinson 1967). Taking the viewpoint of biological production Riley et al (1949) have demonstrated the quantitative importance of vertical turbulence, together with sinking and growth properties of phytoplankton populations, in the determination of vertical distribution and the depth of the productive layer. In a situation of no turbulence, which is relatively unreal, one can easily predict the sinking behaviour of the phytoplankton. When $p' > p$ the cells will sink downwards, when $p' < p$ the cells will rise to the surface and remain, and when $p' = p$ the cells will remain stationary. The behaviour of phytoplankton in turbulent water is less predictable and in addition to the excess density state will depend upon the velocity and direction of water movement.

The vertical distribution and path followed by the phytoplankton cells in their sinking is complicated by epilimnetic circulation. Langmiur circulation results in circulation patterns that include areas of upwelling and downwelling. An equation model of Langmiur circulation was provided by Stommel (1949). In such a pattern a neutrally buoyant cell will move with the stream line, a sinking cell will always move downward with respect to the surrounding water and thus travel to the thermocline. If the sinking rate is less than a certain critical value the phytoplankton cell will be carried back to the water surface from the thermocline. All other particles will remain in suspension unless turbulence carries them from their trajectory to the region outside this zone of retention.

Titman & Kilham (1976) theorize that changes in sinking rate might well be related to external nutrient condition. The increased sinking rate of nutrient depleted cells (Smayda 1974, Boleyn 1972) should bring them closer to the thermocline. If these cells encounter nutrient rich water their sinking rate

should decrease causing them to accumulate. This decrease in sinking rate near the thermocline could thus result in decreased loss rate of the cells from the euphotic zone.

If sinking were the only means of vertical distribution the phytoplankton could not remain long in the photic zone. A combination of sinking and turbulence would, however, provide a vertical distribution with the following characteristics (Riley et al 1949);

a. A reduced crop in the surface layers
b. Maximum quantity of plankton occuring below the depth of maximum production but above the compensation point of the phytoplankton complex
c. A considerable quantity of plankton below the euphotic zone

Several approaches have been developed to measure phytoplankton sinking rates. These methods fall into three general catagories, a settling chamber technique with or without a microscope, a photometric technique, and a fluorometric technique. The settling chamber technique was independently developed by several investigators (Apstein 1910, Fritz 1935, Bernard & Elkaim 1962, Bernard 1963, Smayda & Boleyn 1965). Inidividual modifications of the settling chamber technique include: measuring time of descent by following the path of the cell with the use of a microscope (Apstein 1910) or the unaided eye (Bernard & Elkaim 1962) in a settling chamber between two marks that are a known distance apart, a second modification is measuring the time taken to fall to the bottom of a settling chamber of a known height that is placed on a inverted microscope (Fritz 1935, Bernard 1963 and Smayda & Boleyn 1965); a third method uses a 1 mm deep Sedgwick Rafter chamber and a compound microscope (Riley 1943). An additional settling chamber method used both in the laboratory (Eppley, Holmes, Paasche 1967) and with natural populations (Riley et al 1943) consists of placing a well mixed suspension of phytoplankton in a graduated cylinder and determining the concentration at various layers for a given time period. The determination of sinking rates by the photometric method involves the change in density of phytoplankton suspension during settlement in a spectrophotometer cuvette (Steele & Yentsche 1960). The restriction here is that only a relative rate is obtained. The fluorometric technique which measures _in vivo_ changes in chlorophyll concentrations has been used by Eppley, Holmes & Strickland (1967), Titman (1975), and Titman & Kilham (1976). Most recently Bienfang, Laws, and Johnson (1977) have critically

reviewed the fluorometric methods discussing the advantage and disadvantage of the method as well as ways to improve the experimental accuracy.

The sinking rates of natural populations have been determined by comparing the changes in population density with depth and the mathematically calculating the rate of descent. Such factors as water movements and grazing losses must than be taken into account. Mathematical considerations of sinking rates have been undertaken by Steeman-Nielson & Jensen (1957) and Riley, Stommel & Bumpus (1949).

The experimental methods all have advantage and disadvantage and these must be kept in mind when calculating or using reported sinking rate values. Some of the things to consider are; the effects of the chamber wall, the hight and diameter of the chamber, and the phytoplankton population densities. The advantage of the settling chamber technique is that the cells can be visually observed and thus, the effects of cell and colony size, age, and shape can be determined. Also, with this very time consuming method the absolute minimum and maximum rates can be determined. The photometric and fluorometric techniques give only relative rates but they are much quicker and with precautions and modifications such as those discussed in Bienfang et al (1977) can be very effective experimental methods.

Ultimately the purpose of the measurements is to apply these sinking rates to a natural environment where the additional influences of light, nutrient concentrations, temperature, and water movement come into play. Thus one must be cautious when applying these laboratory measurements to the natural environment. The laboratory studies have helped, however, to establish the influence of the morphology, age, environmental conditions and physical effects on the actual sinking rates. In Table 7 the sinking rates as found by various investigators for individual species and natural populations are summarized. Information is also given on the condition, growth stage, as well as the method employed to experimentally determine this value.

Tabel 1 : The nitrogen, phosphorus, silicon and chlorophyll content of some phytoplankton species (values in picograms (10^{-12}) per cell)

Species	%N	N content PG/Cell dry wt basis	%P	P content PG/Cell dry wt basis	%Si	Si content PG/Cell dry wt basis	%Chl.	Chlorophyll Cont. PG/Cell dry wt basis	Culture type [1]	Location of field samples	Investigator
GREEN ALGAE:											
Cladophora sp.	2.3		0.1						NP	U	Goldman et al, 1971
" "	2.8								NP	U	Birge & Juday, 1922
Chlamydomonas sp.	5.8	8.58[b]							LB		Milner, 1953
Chlorella ellipsoidea	7.0–9.5						2.4–5.2		LB Lt		Tamiya et al, 1953
" "	5.2–5.7						0.8–1.3		LB dk		Tamiya et al, 1952
Chlorella fusca				.05					LC–O		Soeder, 1970
Chlorella pyrenoidosa	9.3	0.53							LB		Milner, 1953
" "							4–48.0		LB		Aach, 1952
" "	1.4	0.08							LB		Milner, 1953
" "							5.3	.27–.34	BT		Gummert et al, 1953
" "			0.1–3.0	0.03–0.15					NP	U	Goldman et al, 1971
" "			0.9–1.5	0.48–0.77					LB		Scott, 1943, 1945
" "	4.0								LB–op		Shelef et al, 1972
" "			1.3–2.2						LC–ph		Nyholm, 1977
" "				0.10					LB		Al Khloy, 1956
" "	7.7	0.57	2.7	0.15					LB		Ketchum & Redfield, 1949
" "			0.02–0.5						LB		Fitzgerald & Nelson, 1966
" "							0.7–3.0		LC		Galling, 1963
" "	1.2–14.1								LB		Spoer & Milner, 1949
" "			3.0						LC		Azad & Borchard, 1970
" "	7.3								LC		Fitzgerald, 1968
" "	2.6								LC–Ni		Fitzgerald, 1968
" "		0.13–0.22							LB		Aach, 1952
" "				0.05					LB		Rhee, 1973
" "							0.4–4.9		L		Rabinowitch, 1945
Chlorella vulgaris	7.7	0.83	2.6	0.21					LB		Ketchum et al, 1949
" "	1.9–4.3								LB		Fogg & Collyer, 1953
" "	8.0		1.1						BTC		Geoghegan, 1953
" "	8.0								BT–O	R	Baslavskaya & Rusina, 1963
" "							1.8–4.0				Rabinowitch, 1945
Chlorella sp.	9.6								LB–op		Wassink et al, 1953
" "	9.2–10.7								BT–O		Wassink et al, 1953
" "	7.9–10.9								BT–i–op		Wassink et al, 1953
Chlorococcum sp.			0.3						LB		Fitzgerald & Nelson, 1966
Dunaliella tertiolecta	2.0								LC–op–Ni		Caperon & Myer, 1972

Species	%N	N content PG/Cell dry wt basis	%P	P content PG/Cell dry wt basis	%Si	Si content PG/Cell dry wt basis	%Chl.	Chlorophyll Cont. PG/Cell dry wt basis	Culture type	Location of field samples	Investigator
Hydrodictyon sp.	3.9		0.2						NP	U	Goldman et al, 1971
Mougeotia sp.	1.8		0.3						NP	U	Goldman et al, 1971
Oedogonium sp.	2.6		0.08						NP	U	Goldman et al, 1971
Pithophora sp.	2.6		0.3						NP	U	Goldman et al, 1971
Platymonas subcordiformis		11.51–16.74							LC-op-Ni		Wheeler, 1977
Platymonas sp.		3.79–8.70							LB-Ni		North & Stephens, 1971
Rhizoclonium sp.	3.5		0.4						NP	U	Goldman et al, 1971
Scenedesmus bijugatis	4.1–6.1	4.16–6.19	0.5–1.8	0.54–1.83					BT-O	A	Hemans & Stander, 1969
Scenedesmus brasilensis	8.5	1.19	3.1	0.37					LB		Ketchum & Redfield, 1949
Scenedesmus dimorpha			0.02–0.2						LB		Fitzgerald & Nelson, 1966
Scenedesmus obliquus				0.09					LB-op		Golterman et al, 1969
" "	6.1–7.4	2.10–2.53	1.0–1.8	0.04–0.06					LC-op		Krauss & Thomas, 1954
" "	7.5–8.7	1.09–1.42	2.5–3.9	0.36–0.43					LB		Ketchum & Refield, 1949
Scenedesmus quadricauda				0.01					LB		Rhode, 1948
" "		14.0–81.0		0.92–8.70					L-ph		Franzew, 1932
Scenedesmus sp.			3.0	3.05[b]					LC		Azad & Borchardt, 1970
" "		1.1–3.1		0.09–0.41					LC		Rhee, 1976
" "		0.64–1.73		0.34–0.37					LC-Ni		Rhee, 1974
" "				0.53					LC		Rhee, 1973
Selenastrum capricornutum			0.4–0.4						LB-op		Keenan & Auer, 1974
Selenastrum capricornutum				0.10–2.33					LC-ph		Nyholm, 1977
" "			0.1–2.5	0.05–0.68					LC-ph		Brown & Harris, 1978
Spirogyra maxima	1.8								NP	I	Sitaramaiah, 1967
Spirogyra sp.	3.0										Goldman et al, 1971
" "	4.5								NP	U	Wipple & Jackson, 1899
" "	3.5								NP	U	Birge & Juday, 1922
" "	3.8								NP	U	Prescott, 1960
Stigeoclonium stagnitile	6.5		1.9						NP	U	Bogan et al, 1960
Stichococcus bacillaris	3.6–10.0	0.66–1.83[b]							LB		Milner, 1953
" "	6.6	0.42							LB		Ketchum & Redfield, 1948
Volvox sp.	7.6								NP	U	Birge & Juday, 1922
BLUE GREEN ALGAE:											
Anabaena circinalis	9.8	1.35[b]							NP-L	U	Dugdale & Dugdale, 1961
Anabaena cylindrica	1.9	1.09[b]							LB-Ni		Fogg & Collyer, 1953
" "	5.0–7.0	.69–.96[b]							LB		Allen & Aron, 1955
" "	2.5–7.1								LB		Fay, 1969

Table 1. (Continuation)

Species	%N	N content PG/Cell dry wt basis	%P	P content PG/Cell dry wt basis	%Si	Si content PG/Cell dry wt basis	%Chl.	Chlorophyll Cont. PG/Cell dry wt basis	Culture type	Location of field samples	Investigator
Anabaena flos-aquae	7.5	8.32[a]							L		Gorham et al, 1964
" " "	9.4	10.00[a]							L		Pakhomova, 1964
" " "		3.00		0.12					NP-L	G	Grim, 1951
" " "			0.2-1.0						LB		Keenen & Auer, 1974
Anabaena spiroides	7.5	1.04[b]	0.3	0.04[b]					NP-L	A	Prowse & Talling, 1958
" "	7.7	1.06[b]							NP	U	Cameron & Fuller, 1960
Anabaena variablis							3.0-8.0				Healey, 1973b
Anabaena sp.	4.0	0.56[b]	1.2	.17[b]					BT-O	A	Hemens & Stander, 1969
" "	9.4	1.30[b]	0.8	.11[b]					NP	U	Goldman et al, 1971
" "	8.3	1.14[b]	0.5	.07[b]					NP	U	Birge & Juday, 1922
" "	7.3	1.00[b]							LB		Milner, 1953
" "	7.1-9.2	0.97-1.27[b]							L		Venkataraman, 1969
Anabaena + *Microcystis*	7.4-11.0								NP	U	Jackson & Elm, 1897
Anabaena + *Coelosphaerum*	8.4								NP	U	Birge & Juday, 1922
Anacystis nidulans	8.9		1.4						LB-ph		Batteron & Van Baalen, 1965
" "							17.9-19.7		L		Eley, 1971
" "							6.6-23.0		L		Allen & Smith, 1969
Aphanizomenon flos-aquae			0.04-0.4						LB		Fitzgerald & Nelson, 1966
" " "	5.7-13.9	97.00-236.00[c]							LB		Williams & Burris, 1952
" " "	12.2	207.00[c]							NP	R	Pakhomova, 1964
Aphanizomenon sp.	10.5	179.00[c]							NP	U	Prescott, 1960
" "	8.5	149.00[c]	1.2	19.90[c]					NP	U	Goldman et al, 1971
" "	9.3	158.00[c]							NP	U	Birge & Juday, 1922
" "	6.1-9.3	103.00-158.00[c]							LB		Vinogradova, 1953
" "			0.6	10.20[c]					NP	U	Phinney & Peek, 1961
Aphanizomenon + *Anabaena*	9.9								NP	U	Birge & Juday, 1922
Calothrix parietina	3.7								LB		Williams & Burris, 1952
Calothrix sp.	4.4		1.2						BT-O	U	Hemens & Stander, 1969
Coccochloris stagina	7.0								LC-op-Ni		Caperon & Myer, 1972
Gloeotrichia echinulata			0.06-0.4						LB		Fitzgerald & Nelson, 1966
Gomphosphaera sp.	8.3										Guseva, 1952
Lyngbya hemensii	7.5	3.88[a]	1.1	0.55[a]					BT-O	A	Hemens & Stander, 1969
Lyngbya lauterbornii		1.00		0.90					NP	G	Grim, 1951
Lyngbya pseudovacuolata		3.00		0.20					NP	G	Grim, 1951
Lyngbya sp.	0.5	0.30[a]	0.3	0.02[a]					NP	U	Goldman et al, 1971
" "	8.2-9.2	4.00-5.00	0.2	0.07-0.10[a]					NP	U	Birge & Juday, 1922
Microcystis aeruginosa			0.1-0.6						LB		Keenan & Auer, 1974

Table 1: (continuation)

Species	%N	N content PG/Cell dry wt basis	%P	P content PG/Cell dry wt basis	%Si	Si content PG/Cell dry wt basis	%Chl.	Chlorophyll Cont. PG/Cell dry wt basis	Culture type	Location of field samples	Investigator
Microcystis aeruginosa	6.4										Venkataramen, 1961
" "	3.8–9.2		0.3–0.8						LB		Gerloff & Skogg, 1954
" "	6.8		0.7						NP	U	Gerloff & Skogg, 1954
" "	3.9–5.2		0.2–0.4						NP	U	Gerloff & Skogg, 1957
" "	4.0–4.5		.1–2.0						LB		Gerloff & Skogg, 1957
" "	4.1								LB		Williams & Burris, 1952
" "	6.9–8.1		1.0–1.1						NP	I	Khan & Siddiqui, 1971
" "			0.04–0.4						LB		Fitzgerald & Nelson, 1966
Microcystis sp.	8.1		0.7						NP	U	Goldman et al, 1971
" "	8.4								NP	R	Vinogradova, 1961
" "	6.3–9.3		0.5						NP	U	Birge & Juday, 1922
" "	8.5		4.5–7.8						NP	U	Whipple & Jackson, 1899
" "	6.8		0.7						NP	U	Gerloff & Skogg, 1954
Nostoc muscorum	6.1								LB		Williams & Burris, 1952
Oscillatoria agardii		52.00[c]							LC		Van Liere et al, 1975
" "	7.8–8.7	101.00–103.00[c]							NP–L	E	Lund, 1965
" "	6.0	78.00[c]	0.3	.03[c]					LC		Ahlgren, 1977
Oscillatoria isothrix	8.9–10.6	116.00–137.00[c]							L		Lund, 1965
Oscillatoria brevis	7.5	20.16	1.3	3.44					BT–O	A	Hemens & Stander, 1969
Oscillatoria rosea		5.00		0.30					NP	G	Grim, 1950
Oscillatoria rubescens	10.0	26.88[b]							NP–L		Pavoni, 1969
" "	4.7–11.9	18.63–32.00[b]							NP–L		Staub, 1961
Oscillatoria sp.	5.7–7.9	15.18–19.95[b]							LB		Fogg & Collyer, 1953
" "	8.2	22.00[f]									Turner, 1927
" "	7.9–9.0	21.23–24.19[b]							LB		Whipple et al, 1927
" "	9.5	24.90[f]							NP–L	E	Lund, 1950
Spirulina major	6.1–9.2										Venkataraman, 1969
DIATOMS:											
Asterionella formosa				0.06–1.5		0.14			LB		Mackerbeth, 1953
" "				0.23–7.0					NP	E	Mackerbeth, 1953
" "					45–50	97–178			LB		Huges & Lund, 1962
" "		8.0		0.41–0.81		120–140			NP	E	Lund, 1950
" "		7.0		4.40		140.0			LB–ph		Lund, 1950
" "						137.6–525.2			LB–Si		Kilham, 1975
" "						100.0			NP	E	Happey, 1970
" "						175.0			NP–L		Lund, 1949
" "		9.0				65.0			NP	G	Einsele & Grim, 1938

Table 1. (Continuation)

Species	%N	N content PG/Cell dry wt basis	%P	P content PG/Cell dry wt basis	%Si	Si content PG/Cell dry wt basis	%Chl.	Chlorophyll Cont. PG/Cell dry wt basis	Culture type	Location in field samples	Investigator
Asterionella formosa					32-61.0				NP-L		Lund, 1964
" "		5.35-6.41				178.0			NP	U	Whipple & Jackson, 1899
" "						100.0-175.0			LB		Lund, 1950
" "				5.5					NP	S	Rhode, 1948
" "				8.0-9.0		0.8-0.9		125.0-311.0	NP-LB	G	Grim, 1951
Asterionella japonica				15.5					LB		Goldberg et al, 1951
" "								371-1.75	NP	I	Subba Rao, 1961
Asterionella sp.				0.48-2.50					NP	G	Hofmann,1975
" "		9.0		0.69		140.0			NP	E	Mackenzie, 1940
" "						165.0			NP	E	Gardiner, 1953
Bacillaria paradoxa						250.0			LB-Si		Jorgensen, 1953
Coccinodiscus accentericus					30.4-39.8				LC		Pugh, 1975
Coccinodiscus asteromphalus						40.000			L		Kamatani, 1969
Cyclotella bodanica						15.000			NP	G	Einsele & Grim, 1938
" "		1,200-1,250		120-125		3,200-3,500			NP	G	Grim, 1950
Cyclotella comita						750.0			NP	G	Einsele & Grim, 1938
" "		24.0		2.0		861.0			NP	G	Grim, 1950
Cyclotella compta						900.0			NP	G	Einsele & Grim, 1938
Cyclotella cryptica						16.0-25.0			L		Werner, 1966
" "						7.0-11.9			L		Werner & Pierson, 1967
Cyclotella glomerata						100.0			NP	G	Einsele & Grim, 1938
Cyclotella melosiroides						380.0			NP	G	Einsele & Grim, 1938
" "		12.0		1.0		398.0			NP	G	Grim, 1950
Cyclotella nana	5.4								LC-op-Ni		Caperon & Meyer, 1972
Cyclotella pseudostelligera					35.0-55.0	31.0-43.0			NP	Sc	Bailey-Watts, 1976b
" "						35.0			LC		Swale, 1963
Cyclotella socialis						425.0			NP	G	Einsele & Grim, 1938
" "						900.0			NP	G	Einsele & Grim, 1938
" "		55.0-60.6		5.0-6.0		1,233.0-1,500.0			NP	G	Grim, 1950
Cyclotella sp.		9.0-12.0		1.0		400.0-500.0			NP	G	Grim, 1950
Diatoma elongatum						120.0			NP	G	Einsele & Grim, 1938
" "						181.0			NP	Au	Cheng & Tyler, 1972
" "		20.0-60.0		2.0-7.0		250.0-1,104.0			NP	G	Grim, 1950
Ditylum brightwellii		120.0		23.0		190.0		38.0	LB		Darley, 1977
" "						200.0-900.0			LC		Paasche, 1973c
" "		120.0		23.0		730.0			LBT-O		Strickland et al, 1969
Fragilaria crotonensis						70.0-400.0			NP	G	Einsele & Grim, 1938

Table 1: (continuation)

Species	%N	N content PG/Cell dry wt basis	%P	P content PG/Cell dry wt basis	%Si	Si content PG/Cell dry wt basis	%Chl.	Chlorophyll Cont. PG/Cell dry wt basis	Culture type	Location in field samples	Investigator
Fragilaria crotonensis						188.0			NP-L		Lund, 1965
" "		15.0-17.0		2.0		179.0-200.0			NP	G	Grim, 1950
Fragilaria sp.				0.67-0.97					NP	G	Hofmann, 1975
Licmorphoras sp.						80.0-200.0			LC		Paasche, 1973c
Melosira granulata	0.9	2.0[a]	0.16	0.40[a]	25.3	61.0			NP	A	Prowse & Talling, 1958
" "						60.0			NP	G	Einsele & Grim, 1938
" "		7.0-9.0		0.7-0.8		114.0-125.0			NP	G	Grim, 1950
Melosira islandica						220.0-360.0			NP	G	Einsele & Grim, 1938
Melosira italica						120.0-180.0			NP	G	Einsele & Grim, 1938
" "		10.00-160.00		1.0-16.0		133.0-2,857.0			NP	G	Grim, 1950
Melosira italica var. subartica						400.0			NP	Sc	Dickson, 1975
" " "						165.0-274.0			NP-L		Lund, 1965
Navicula pelliculosa						0.80-2.20			LB		Lewin, 1957
" "						2.2-3.8		4.4-5.3	LC-Si		Coombs et al, 1967
Nitzschia actinastades				0.04-0.08					LC-ph		Soeder et al, 1971
" "				0.80					LC- h		Muller, 1971
Nitzschia alba						9.0			LC-Si		Lewin & Chen, 1968
Nitzschia closterium	7.5	1.74		0.179					LB		Ketchum & Redfield, 1948
Nitzschia palea						190.0			LB-Si		Jorgensen, 1953
Phaeodactylum tricornatum		0.42-1.15							LB-op		Shimura & Fujio, 1975
Phaeodactylum sp.		2.15-2.58		0.46-0.56		0.54-1.37			BT-O	A	Ansell et al, 1971
									NP	G	Grim, 1950
Skeletonema costatum								0.5-14.0	NP	Is	Jensen & Sakshaug, 1973
" "						0.56			LC-Si-Ni		Harrison et al, 1976
" "		0.021-0.078		0.019-0.045					LC-Si-Ni		Conway et al, 1976
" "		1.7						5.0	NP-BT-O	U	Eppley et al, 1971
" "		2.2		0.406		3.34		6.7	NP-L	U	Parsons et al 1960
" "		0.14		0.018		0.043			LC-Si		Davis et al, 1973
" "		0.145		0.016		0.059		0.1375	LC-Si-Ni		Harrison et al, 1976
" "						3.8-7.0		0.50	LC-Si		Paasche, 1973A
" "		1.9-5.6						0.16-0.28	LB-Ni-ph		Sakshaug & Holm-Hansen, 1977
" "								0.44-1.0	L		Jorgensen, 1969
" "						1.0-2.0			LC		Paasche, 1973c
" "		13.0-36.0							NP-BL-O		Eppley et al, 1971
Stephanodiscus astraea						4,000.0			NP	G	Einsele & Grim, 1938
" "		400.0-500.0		50.0-56.0		8,333.0-8,611.0			NP	G	Grim, 1950
Stephanodiscus hantzschii						4.0			NP-L		Swale, 1963
" "						100.0			NP-L	G	Kolkwitz, 1914

Table 1: (continuation)

Species	%N	N content PG/Cell dry wt basis	%P	P content PG/Cell dry wt basis	%Si	Si content PG/Cell dry wt basis	%Chl.	Chlorophyll Cont. PG/Cell dry wt basis	Culture type	Location in field samples	Investigator
Stephanodiscus rolata						8,500.0			L		Einsele & Grim, 1938
" "						500.0–730.0			NP	E	Happey, 1970
" "						93.0–126.0			NP	Sc	Happey, 1970
Synedra acus	4.0–8.0	10.84–21.69[b]							NP	G	Einsele & Grim, 1938
" "						321.0			NP	Au	Cheng & Tyler, 1973
Synedra acus var. angustissima						450.0–1,200.0			NP	G	Einsele & Grim, 1935
" " "		60.0–64.0		6.0–8.0		1,093.0–1,300.0			NP	G	Grim, 1950
Synedra acus var. delicatissma		8.0–14–0		0.8–1.0					NP	G	Grim, 1950
Synedra acus var. radians						284.0					Lund, 1965
Synedra ulna						1000.0			NP	G	Einsele & Grim, 1938
" "		20.0–174.0		2.0–20–0		244.0–2,200.0			NP	G	Grim, 1950
Tabellaria fenestrata						170.0–350.0			NP	G	Einsele & Grim, 1938
Tabellaria floculosa						370.0–420.0			NP	G	Einsele & Grim, 1938
" "						250.0–420.0			NP	E	Lund, 1965
" "		23.0		2.0		353.0			NP	G	Grim, 1950
Thalassiosira decipiens						90.0–330.0			LC–Si		Paasche, 1973b
Thalassiosira nitzschioides								1.2	NP–L		Jensen & Sakshaug, 1973
Thalassiosira pseudonana						0.6–1.5			LC–Si		Paasche, 1973c
" "						1.85			LC		Paasche, 1973c
" "		0.66–2.74						0.203–0.485	LC–Ni		Eppley & Renger, 1974
Mixed diatoms	1.56				54.5				LB		Whipple et al, 1927
" "					29–38	100.0–194.0			NP	Sc	Bailey Watts, 1976A
" "					37–54		0.4–1.0		NP–L		Anita et al, 1963
" "						140.0–145.0			NP	U	Wang & Evens, 1969
" "	7.4		1.1						NP	I	Khan & Siddiqui, 1971
" "			0.6						NP	I	Krishnamurthy
DINOFLAGELLATES:											
Cachonina niei		21.5–34.0		5.0–7.0				3.15–4.4	LB		Strickland et al, 1969
Ceratium fucus								0.08–0.130	NP–L		Jensen & Sakshaug, 1973
Ceratium hirundinella		905.0		62.0					NP		Grim, 1950
" "		28.0–1,200		2.0–80.0					NP		Grim, 1950
Cryptomonas erosa		16.0		1.0					NP	G	Grim, 1950
Cryptomonas ovata		11.0–18.0		0.7–1.0					NP	G	Grim, 1950
Cryptomonas sp.		15.0		1.0					NP	G	Grim, 1950
Gymnodinium M.		7.0		0.5					NP	G	Grim, 1950
Peridinium cinctum		50.0–615.0		6.0–38.0							
" "								30.0	NP	Is	Pollingher & Bermar, 1975

Table 1: (continuation)

Species	%N	N content PG/Cell dry wt basis	%P	P content PG/Cell dry wt basis	%Si	Si content PG/Cell dry wt basis	%Chl.	Chlorophyll Cont. PG/Cell dry wt basis	Culture type	Location of field samples	Investigator
Peridinium trochoideum								38.0-64.0	NP-L		Jensen & Sakshaug, 1973
Rhodomonas lacustris		2.0-3.0		0.1-0.2					NP	G	Grim, 1950
Rhodomonas sp.		3.0		0.2					NP	G	Grim, 1950
CHRYSOPHYTES:											
Chara sp.	2.5		0.3						NP	U	Goldman et al, 1971
Coccolithus huxleyi		0.68-1.1							NP-BT-O		Eppley et al, 1971
Dinobryon divergens		25.0		2.0					NP	G	Grim, 1950
" "		26.0-28.0		8.0					NP	G	Grim, 1950
Dinobryon sociale		25.0		2.0					NP	G	Grim, 1950
Dinobryon sp.		8.0-17.0		0.4-2.0					NP	G	Grim, 1950
Mallomonas mirabilis		100.0		7.0		833.0			NP	G	Grim, 1950
" "						400.0			NP	G	Grim & Einsele, 1938
Synura petersoni						0.7-23.3			LB-Si		Klaveness & Guillard, 1975
XANTHOPHYTES:											
Monodus subterraneous	1.4-3.0								LB		Fogg & Collyer, 1953
Nitella sp.	2.8		0.2						NP	U	Goldman et al, 1971
Tribonema aequale	1.7-3								LB		Fogg & Collyer, 1953
EUGLENOPHYTES:											
Euglena sp.	5.1		0.7						NP	U	Goldman et al, 1971

Culture type:
- L = laboratory culture
- NP = natural population
- B = batch culture
- C = continuous culture chemostat
- T = large scale tank culture
- NP-L = natural population isolated and cultured in laboratory
- O = outside (in reference to tank culture)
- i = inside (in reference to tank culture)
- op = optimum conditions 12 hr to continuous high intensity light and constant temperature above 20°C
- ph = experiment involving rates of uptake and/or effect of varying concentrations of phosphores in medium
- Ni = experiment involving rates of uptake and/or effect of varying concentrations of nitrogen in medium
- Si = experiment involving rates of uptake and/or effects of varying concentrations of silica in medium

Location of field samples:
- U = United States
- R = Russia
- I = India
- A = Africa
- G = Germany
- E = England
- S = Sweden
- Au = Australia
- Is = Israel

a = calculated from dry weight value for this species as reported by Grim, 1951

b = calculated from dry weight value for this species as reported by Nalewaijko, 1966

c = calculated from dry weight value for this species as reported by Lund, 1961

Table 2 Rates of mineralization of phosphorus from phytoplankton

Species	Rate of mineralization	Reference
Anabaena variablis	30.97 - 52.65 µgP/mg dry wt/hr.	Healey, 1973B
Anabaena flos-aquae	1.55 - 619.4 µgP/mg dry wt/hr.	Bone, 1971
Cladophora glomerata	0.5% 1 day	Golterman, 1960
	1,6% 2 days	
	15.0% 11 days	
	27% 21 days	
Nitzschia actinastades	2×10^{-7} µgP/cell/hr.	Healey, 1973A
Scenedesmus obliquus	216.8 - 309.7 µg/mg dry wt/hr.	Soeder, 1960
Scenedesmus quadricauda	18% 3.5 hr	Golterman, 1960
	29% 6.0 hr	
	48% 1 day	
	65% 5 days	
	68% 12 days	

Table 3 Rates of mineralization of nitrogen from phytoplankton

Species	Rate of mineralization	Reference
Anabaena cylindrica	8.04 - 12.5 mgN/mg Dry wt/Day	Fogg, 1952
Nostoc muscorum	5% of fixed N is	Stewart, 1963

Table 4 Rates of mineralization of silicon from phytoplankton

Plankton species or community	Extent of dissolution	Laboratory or natural population	Reference
Navicula pelliculosa	0.56 pg/cell/hr.	L	Sullivan, 1976
Nitzschia linearis	pH 5 0.3% pH 8 5.2% in 6 days pH 10 17.2%	L	Jorgensen, 1955
Stephanodiscus nana	0.5% 1 day 1.6% 2 days 15.0% 11 days 27.0% 21 days	L	Golterman, 1960
Thalassiosira nana	pH 4 1.3% pH 8 4.2% in 8 days pH 10 16.4%	L	Jorgensen, 1955
Marine diatoms	0.0020 - 0.0085 pgSi/cell/hr.	N	Nelson et al, 1976
Lake Michigan	0.0016 mg Si/day 10-25% dry wt in 27 days	N	Parker et al, 1977
Lake diatoms	29-36% Si in 38 days	N	Parker et al, 1977
Lake plankton	40% of Si in 55 days	N	Anita et al, 1963
Shallow eutrophic lake	125.4 g Si in 38 days	N	Bailey-Watts, 1976A

Table 5 The percentage of total assimilated carbon excreted by algal cultures under laboratory conditions as determined with the ^{14}C method

Species	Percentage extracellular carbon excreated	Duration of experiment	Reference
BLUE-GREENS			
Anabaena flos-aguae	3.4	7.5 hr	Nalewajko et al,1976
Anabaena flos-aguae	4.0-9.4	3.0 hr	Nalewajko & Lean,1972
GREENS			
Chlorella pyrenoidosa	0.30-1.98	3.0 hr	Nalewajko & Marin,1969
Chlorella pyrenoidosa	8.1	7.0 hr	Nalewajko et al, 1976
Chlorella pyrenoidosa	3.9-9.2	3.0 hr	Nalewajko & Lean, 1972
Dunaliela tertiolecta	16.0	5.0 hr	Hellebust, 1965
Pyramimonas Sp.	20.0	5.0 hr	Hellebust, 1965
DIATOMS			
Asterionella formosa	2.8-7.8	3.0 hr	Nalewajko & Marin, 1969
Asterionella formosa	1.7-2.7	3.0 hr	Nalewajko & Lean, 1972
Chaetoceros simplex	18.0	5.0 hr	Hellebust, 1965
Cyclotella nana	23.0-27.0	5.0 hr	Hellebust, 1965
Melosira binderana	0.6-1.5	3.0 hr	Nalewajko & Marin, 1969
Navicula pelliculosa	1.3-3.0	3.0 hr	Nalewajko & Lean, 1972
Phaeodactylum tricornatum	43.0	5.0 hr	Hellebust, 1965
Rhizosolenia setigeria	85.0	5.0 hr	Hellebust, 1965
Skeletonema costatum	38.0	5.0 hr	Hellebust, 1965
Stephanodiscus tenuis	2.1-5.9	3.0 hr	Nalewajko & Marin, 1969
Thalassiosira fluviatilis	13.0	5.0 hr	Hellebust, 1965
CHRYSOPHYLES			
Coccolithus huxleyi	17.0	5.0 hr	Hellebust, 1965
Olisthodiscus sp.	52.0	5.0 hr	Hellebust, 1965
OTHER PHYTOPLANKLERS			
Exuviella sp.	9.0	5 hr	Hellebust, 1965
Gymnodinium nelsoni	18.0	5 hr	Hellebust, 1965

(All Values determined in three to five hour experiments with ^{14}C method)

Location	water type	month	main algal types	percentage extra-cellular products	reference
Torneträsk	O.F.	Aug.	nannoplankton	11	
Windermere	O.F.	Mar.-Oct.	varied phytoplankton	7-50	Fogg, Nalewajko & Watt, 1965
Blelham Tarn	O.F.	July	mixed phytoplankton	38	Fogg, Nalewajko & Watt, 1965
Lake 5, Signy Island	O.F.	Feb.	Chlorophycean nannoplankton	43	Horne, Fogg & Eagle, 1969
Lake Ontario	O.F.	June	_Stephanodiscus tenuis_ dominant	23-76	Nalewajko & Marin, 1969
Lake 239, ELA, Ontario	O.F.	July	NS	12-30	Nalewajko & Schindler, 1976
Lake Erken	E.F.	Aug.-Sept.	Cyanophyceae	1.5-2.4	Fogg, 1954
Tring Reservoirs	E.F.	Feb.-Oct.	varied	1.5-33	Watt & Fogg, 1966
Gravel Pond, Mass. U.S.A	E.F.	Aug.	NS	7.9	Wright, 1970
Lake 227, ELA-Ontario	E.F.	July	NS	8-43	Nalewajko & Schindler, 1976
Weddell Sea	I	Jan.	Diatoms	<2	Horne, Fogg & Eagle, 1969
Loch Etive	I.B.	Mar.-Oct.	mainly _Skeletonema costatum_	35-46	Ignatiades, 1972
Cochin Backwater	B.Es.	Jan.-Feb.	varied phytoplankton	5-19	Samuels, Shah & Fogg, 1971
Georgia Estuaries	E.Es.	Aug.	NS	<7	Thomas, 1971
SE USA Coastal	C.	Sept.	NS	<21	Thomas, 1971
NE U.S.A. Coastal	C.	Feb.-May	_Thalassiosira leptacylindrus_ & small flagellates	8.1-38	Hellebust, 1965
Sargasso Sea	O.Oc.	Nov.	NS	<44	Thomas, 1971
N.E. Pacific	E.Oc. O.Oc.	July July	NS NS	7 49	Anderson & Zeutschel, 1970
North Sea	S.Se.	June	Diatoms	5.8	Fogg, Nalewajko & Watt, 1965
Indian Ocean	Oc.	June	NS	5-32	Jitts, 1967
Gulf of main	Oc.	April	_Thalassiosira chaetoceros_ dominant	5.2-16	Hellebust, 1965

Water type

O = oligotrophic
E = eutrophic
F = freshwater
I = inshore
B = brackish
Es = estuarine

C = coastal
Oc = oceanic
S = shallow
Se = sea

algal type

Tabel 7 A summary of sinking rates of planktonic algae

Species	Area: Vol. $\mu^2:\mu^3$	Cell condition[1]	Sinking rate m-day^{-1}			Technique[2]	Water[3] type	Experimental[4] or natural conditions	Investigator
			min.	max.	mean				
DIATOMS:									
Asterionella formosa		G	0.09	0.62	0.31	SC-1	F	E	Smayda, 1974
" "		D			0.52	SC-1	F	E	Smayda, 1974
" "		D			0.40	SC-1	F	E	Smayda, 1974
" "		G	0.07	0.84	0.20	SC	F	E	Lund, 1959
" "		G	0.12	0.32		SC	F	N	Lund, 1959
" "		G	0.70	2.90		SC-1	F	E	Fritz, 1935
" "		G	0.17	0.22	0.20	F	F	E	Titman, 1975
" "		G			0.20	F	F	E	Titman & Kilham 1976
" "		S			1.48	F	F	E	Titman & Kilham, 1976
Asterionella japonica		G			0.40	GC	M	N	Margalef, 1961 (calculated from Riley, 1943
" "	0.30	G → S	0.26	0.75		SC-1	M	E	Smayda, 1970
Bacteriastrum hyalinum	0.29-0.33	G → S	0.39	1.27	0.79	SC-1	M	E	Smayda & Boleyn, 1966b
Chaetoceros borealis		D			5.00	SC-2	M	E	Apstein, 1910
" "		D			6.00	SC-2	M	EE	Apstein, 1910
Chaetoceros curvisetus		G	1.00	5.00		Z	M	N	Gillbricht, 1952
Chaetoceros didymus		G			0.53	F	M	E	Eppley, Holmes & Strickland, 1967
" "		D			0.85	F	M	E	Eppley, Holmes & Strickland, 1967
Chaetoceros lauderi		G-S-P	0.46	1.54	0.78	SC-1	M	E	Smayda & Boleyn, 1966b
Chaetoceros sp.					0.25	GC	M	N	Margalef, 1961 (calculated from Riley 1943
" " "					5.00		M	N	Sverdrup, Johnson & Fleming, 1943
" " "					4.00	Z	M	N	Allen, 1932
Coscinodiscus concinnus		D			61.00	SC-2	M	E	Apstein, 1910
" "		D			108.00	SC-2	M	E	Apstein, 1910
" "		D			127.00	SC-2	M	E	Apstein, 1910
Coscinodiscus janischii					21.50	model	M	E	Sakamoto, 1964
Coscinodiscus lineatus		G			1.90	SC-3	M	E	Eppley, Holmes & Paasche, 1967
" "		S			6.80	SC-3	M	E	Eppley, Holmes & Paasche, 1967
Coscinodiscus wailesii	0.05	G → S	7.00	30.20		F	M	E	Eppley, Holmes & Strickland, 1967
Coscinodiscus sp.	0.16	G → S	1.95	6.83		F	M	E	Eppley, Holmes & Strickland, 1967
" "	0.09	E			1.47	F	M	E	Eppley, Holmes & Strickland, 1967
Cyclotella bodanica			1.40	5.30		SC-1	F	E	Fritz, 1935
Cyclotella sp.		G	.45	1.00	.72	SC	F	N	Grim, 1950
Cyclotella comta		G	0.50	0.80			F	N	Grim, 1952
Cyclotella melosiroides		G	0.30	1.50			F	N	Grim, 1952

Tabel 7 (continuation)

Species	Area: Vol $\mu^2:\mu^3$	Cell condition[1]	Sinking rate m-day^{-1} min.	max.	mean	Technique[2]	Water type[3]	Experimental or Natural conditions[4]	Investigator
Cyclotella melosiroides		G	.35	1.10	.74	SC	F	N	Grim, 1950
Cyclotella meneghiniana		G			0.80	F	F	F	Tilman & Kilham, 1976
" "		S			0.24	F	F	E	Tilman & Kilham, 1976
Cyclotella nana	1.20	G → S	0.16	0.76		F	M	E	Eppley, Holmes & Strickland, 1967
Cyclotella sp.		G	2.50	3.50			F	N	Grim, 1939
" "		D	2.50	8.00		SC	F	N	Grim, 1951
Ditylum brightwellii	0.23	G → S	0.60	3.09		F	M	E	Eppley, Holmes & Strickland, 1967
" "	0.16–0.19	G → S	0.13	0.86		SC-1	M	E	Smayda, 1970
" "		G		0.60		SC-5	M	E	Eppley, Holmes & Paasche, 1967
" "		RS	5.80	8.60		CD	M	E	Gross & Zeuthen, 1944
" "		RS	2.70	2.75		CD	M	E	Gross, 1937
" "		S			3.10	SC-1	M	E	Eppley, Holmes, Paasche, 1967
" "		G	0.48	1.83	0.93	SC-1	M	E	Boleyn, 1972
" "		S	1.05	2.75	1.68	SC-1	M	E	Boleyn, 1972
" "		RS	1.21	9.64	3.73	SC-1	M	E	Boleyn, 1972
" "		D	1.03	1.24	1.11	SC-1	M	E	Boleyn, 1972
Ethmodiscus rex		D			465.		M	E	Vinogradova, 1961
" "		D			510.		M	E	Vinogradova, 1961
" "		D			495.		M	E	Vinogradova, 1961
" "		E	28.00	864.00			M	E	Kolbe, 1957
Fragilaria crotonensis		G	1.50	3.00			F	N	Einsele & Grim, 1938
" "		G	1.2	7.00			F	E	Grim, 1952
" "		G	0.50	3.80		SC-1	F	E	Fritz, 1935
Leptocylindrus danicus	0.83–1.00	G → S	0.37	0.46		SC-1	M	E	Smayda, 1970
" "		G	0.80	0.42		GC	M	C	Margalef 1961, (calculated from Riley 194
Melosira italica subartica		G	0.52	2.10	0.95	SC	F	N	Lund, 1959
Melosira agassizii		G			0.67	F	F	E	Tilman & Kilham, 1976
" "		S			1.87	F	F	E	Tilman & Kilham, 1976
Nitzschia closterium		G			0.52	GC	M	N	Margalef 1961, (calculated from Riley 194
" "		G	0.025	0.050		GS	M	E	Riley, 1943
Nitzschia palea		G	21.60	43.20			F	E	Von Denffer, 1949
Nitzschia seriata	1.18–1.65	G → S	0.26	0.50	0.39	SC-1	M	E	Smayda & Boleyn, 1965
" "					4.00	Z	M	N	Allen, 1932
Phaeodactylum tricornutum		G	0.05	0.06		SR	M	E	Riley, 1943

Species	Area: Vol. $\mu^2:\mu^3$	Cell condition[1]	Sinking rate m-day^{-1}			Technique[2]	Water type[3]	Experimental[4] or natural conditions	Investigator
			min.	max.	mean				
Phaeodactylum tricornutum		S	0.02	0.04		SR	M	E	Riley, 1943
Rhizosolenia hebetata		S			0.22	F	M	E	Eppley, Holmes & Strickland, 1967
Rhizosolenia setigera	0.65–0.75	G S	0.11	2.23	0.66	SC-1	M	E	Smayda & Boleyn, 1966A
" "	0.10–0.16	G S	0.10	6.30	2.29	SC-1	M	E	Smayda & Boleyn, 1966A
Rhizosolenia stolterfothii	0.25	G S	1.00	1.96		F	M	E	Eppley, Holmes & Strickland, 1967
Rhizosolenia spp.		G	0.00	0.72		GC	M	N	Margalef 1961, (calculated from Riley 1943)
Skeletonema costatum	0.81–1.01	G S	0.30	1.35	0.53	SC-1	M	E	Smayda & Boleyn, 1966A
Stephanodiscus turrus		G			1.10	F	M	E	Eppley, Holmes & Strickland, 1967
" "		G			2.10	F	M	E	Eppley, Holmes & Strickland, 1967
Synedra acus delicatissima		G	0.40	4.50			F	N	Grim, 1939
Synedra acus delicatissma		G	0.5	5.0		SC	F	N	Grim, 1951
Tabellaria fenestrata		G			1.26	F	F	E	Titman, 1975
Tabellaria flocculosa		G	0.21	0.40	0.39	SC-1	F	E	Smayda, 1974
" "		D			1.50	SC-1	F	E	Smayda, 1974
" "		D			0.95	SC-1	F	E	Smayda, 1974
Thalassionema nitzschoides	0.64–0.92	G S	0.35	0.75		SC-1	M	E	Smayda, 1970
Thalassiosira fluviatilis	0.44	G S	0.60	1.1		F	M	E	Eppley, Holmes & Strickland, 1967
Thalassiosira gravida	0.23–0.30	G S	0.53	0.70		SC-1	M	E	Smayda, 1970
Thalassiosira nana	0.88–1.20	G S	0.10	0.28	0.20	SC-1	M	E	Smayda & Boleyn, 1965
Thalassiosira rotula		S			1.15	F	M	E	Eppley, Holmes & Strickland, 1967
" "	0.23–0.29	G S	0.39	2.10	1.11	SC-1	M	E	Smayda & Boleyn, 1965
Thalassiosira spp.		G	0.10	0.16		GC	M	N	Margalef 1961 (from Riley 1943)
Diatoms–general		G			5.0	Z	M	N	Gillbricht. 1952
" "		G	0.20	1.20			M	N	Lisitsyn et al, 1967
" "		G			0.30		M	E	Bramlette, 1961
" "		D	50	150		G	M	E	Lisitsyn et al, 1967a
" "		G	0.63	0.23			F	N	Grim, 1954
Dinoflagellates:									
Ceratium balticum		D			9.0	SC-2	M	E	Apstein, 1910
" "		D			12.0	SC-2	M	E	Apstein, 1910
Gonyaulax polyedra	0.13	G S	2.80	6.0		F	M	E	Eppley, Holmes & Strickland, 1967
Noctiluca miliaris		D			14.0	SC-2	M	E	Apstein, 1910
" "		D			22.0	SC-2	M	E	Apstein, 1910
Microflagellates:									
Dunaliella tertiolecta	0.87	G			0.39	F	M	E	Eppley, Holmes & Strickland, 1967

(continuation)

Species	Area: Vol. $\mu^2:\mu^3$	Cell condition[1]	Sinking rate m-day^{-1}			Technique[2]	Water type[3]	Experimental or natural conditions[4]	Investigator
			min.	max.	mean				
Monochrysis lutheri	1.20	G			0.18	F	M	E	Eppley, Holmes & Strickland, 1967
COCCOLITHOPHORIDS:									
Coccolithus huxleyi	0.57	G			0.28	F	M	E	Eppley, Holmes & Strickland, 1967
" "	0.46	G			1.30	F	M	E	Eppley, Holmes & Strickland, 1967
Coccolithus sp.					1.50				Bramlette, 1961
Cricospaera carterae	0.35	S			1.70	F	M	E	Eppley, Holmes & Strickland, 1967
Cricospaera elongata	0.40	G			0.25	SC-3	M	E	Bernard, 1963
" "		G			0.25	F	M	E	Eppley, Holmes & Strickland, 1967
Cyclococcolithus fragilis		L			13.2	SC-3	M	E	Bernard, 1963
" "		L			24.7	SC-3	M	E	Bernard, 1963
" "		L			18.2	SC-3	M	E	Bernard, 1963
" "		L			13.6	SC-3	M	E	Bernard, 1963
" "		L			10.3	SC-3	M	E	Bernard, 1963
" "		L		225		SC-4	M	N	Bernard & Elkaim, 1962
" "		L		6150		SC-4	M	N	
GREEN ALGAE:									
Chlorella pyrenoidosa		G	0.018	0.016			F	E	Smith, 1953
Scenedesmus obliquus		G	2	3			F	E	Benesova, 1948 & Margalef, 1961
Scenedesmus quadricauda		G			0.27	F	F	E	Titman & Kilhelm, 1976
" "		S			0.89	F	F	E	Titman, Kilhelm, 1976
" "		G			1.04	F	F	E	Titman, 1975
Staurastrum gracile		G			1.0		F	N	Grim, 1952
BLUE-GREEN ALGAE:									
Anabaena circinalis		G			0.259		F	E	Fogg et al, 1973
Gleotrichi echinulata		G			1.98		F	E	Fogg et al, 1973
Spirulina platensis		G			-0.45	F	F	E	Titman, 1975
Chrysophyta:									
Dinobryon sertularia		G	0.20	0.40			F	N	Grim, 1952
Natural phytoplankton:									
Fladen ground North Sea		G			0.08	GS	M	E	Riley, 1963
North Sea		G			0.10		M	E	Cushing & Vucetic, 1963
Western North Atlantic		G			0.08	GS	M	E	Riley et al, 1949
Vierwaldstatter See		G	0.02	0.04			M	E	Gachter, 1968
Bahia de Kiel		G			5.0		M	E	Gillbrecht, 1953
Sargasso Sea		G	0.025	0.044		GS	M	E	Riley et al, 1949
Georges Bank Atlantic		G	0.020	0.036		GS	M	E	Riley et al, 1949

Table 7 (continuation)

1 - Cell condition

- G = growing
- S = viable but scenescent
- D = dead usually due to heat or preservative
- E = empty frostule
- RS = resting spore
- G S = both growing and scenescent used
- L = living (stationary phase)

2 - Technique

- SC-P settling chamber with inverted microscope as described by Smayda & Boleyn, 1965 Fritz &1935
- SC-2 settling chamber procedure described by Apstein, 1910
- SC-3 settling chamber with inverted microscope column height 1.7-2.6 cm as in Bernard, 1963
- SC-4 settling chamber height 88-110 cm diameter 4-6 cm cells followed with eye Bernard & Elkaim, 1962
- SC-5 well mixed 50 m sample as in Eppley, Holmes & Paasche, 1967
- F fluorometric technique as described by Eppley, Holmes & Strickland, 1967
- GS settling behavior of natural populations when placed into a graduated cylinder as described by Riley, 1943
- Z estimations of sinking rate based on changes in population density with depth and time
- SC settling chamber details not given in article

3 - Water type

- F = fresh water
- M = marine - salt water

4 - Species type

- E = experimental or culture
- N = from natural population

Negative value for sinking rate represents buoyancy

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