Sinking in freshwater phytoplankton: Some ecological implications of cell nutrient status and physical mixing processes[1]

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Abstract

Sinking rates of *Asterionella formosa, Melosira agassizii, Cyclotella meneghiniana,* and *Scenedesmus quadricauda* in stationary and exponential phases of growth are reported. Stationary phase populations sink 4× more rapidly, on the average, than exponentially growing populations. Time series of sinking rates during change from one growth phase to another demonstrate the viability of rapidly sinking cells. A consideration of sinking in Langmuir circulations indicates that the frequently used algebraic relationship between sinking rate and rate of loss of cells from the mixed layer may greatly overestimate loss rates. A theoretical net potential growth curve, that combines both loss from sinking and growth from sinking-dependent nutrient uptake, demonstrates that nutrient depleted cells may have optimal growth rates (highest fitness) at high sinking rates.

Smayda (1970, 1974), Smayda and Boleyn (1965, 1966), Boleyn (1972), and Eppley et al. (1967) reported that sinking rate of phytoplankton is not a species specific constant. They found that nutrient depleted cells sink 2× to 4× more rapidly than nutrient replete cells. Eppley et al. (1967) hypothesized that cells of a given species may exist in up to three distinct physiological states with respect to buoyancy, with rapid transition from state to state: neutral buoyancy, a moderate sinking rate state, and a high sinking rate state, with transition to higher sinking rate states occurring with declining physiological activity. Such apparent control of sinking rate may imply that there are times when movement relative to the immediately surrounding parcel of water is valuable and times when it is not, and could be explained in part by considerations of movement-dependent nutrient uptake (Munk and Riley 1952; Hulburt 1970; Pasciak and Gavis 1974, 1975). Movement relative to the surrounding water can bring a cell into regions from which it has not depleted nutrients, thus at least partially overcoming molecular diffusion limitation of nutrient uptake. Control of sinking could also impart some ability to regulate position in a body of water, perhaps increasing the time which nutrient depleted cells may spend in a patch of relatively nutrient-rich water.

Here we report the ranges of sinking rate exhibited by four species of freshwater phytoplankton in exponential and stationary phases of growth and also time series of sinking rate changes as cultures go from nutrient limited to nutrient unlimited states, and vice versa. We hypothesize that sinking rate may be controlled so as to maximize potential growth from nutrient uptake, within the constraints of increased loss rates caused by increased sinking rates.

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Methods

All cultures were grown in a culture box at 20°C on a light–dark cycle of 14–10 h under "cool-white" fluorescent bulbs at ca. 55 μEinstein cm^{-2} s^{-1} (ca. 4,000 lux). This should be sufficient illumination for photosaturation under our culture conditions (Benndorf 1973). The algal medium used was "WC" (Guillard and Lorenzen 1972), an inorganic salts medium with vitamins and trace metals but no buffer. All media were autoclaved before use. Populations were estimated by counts using a Sedgwick-

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Table 1. A comparison of mean sinking rates (S.R.) for exponential phase and stationary phase cultures of four species of freshwater phytoplankton. Population means are shown with their 0.95 confidence limits. The ratio given is mean sinking rate of stationary phase cultures to that of exponential phase cultures for each species.

Species	Radius (μm)	S. R. (exponential) (m day^{-1})	S. R. (stationary) (m day^{-1})	Ratio (stat./exp.)	Means Sig. Dif. (0.95 level)
C. meneghiniana	1.0	0.08 ± 0.10 (n=4)	0.24 ± 0.31 (n=4)	3.0	NO
S. quadricauda	4.2	0.27 ± 0.04 (n=8)	0.89 ± 0.06 (n=14)	3.3	YES
A. formosa	12.5	0.20 ± 0.06 (n=6)	1.48 ± 1.05 (n=7)	7.4	YES
M. agassizii	27.4	0.67 ± 0.48 (n=3)	1.87 ± 0.38 (n=15)	2.8	YES

Rafter chamber (Guillard 1973) or with a calibrated Celloscope (an automatic counting and sizing device). Cell sizes were determined by measurement with a calibrated ocular micrometer (*Asterionella formosa, Melosira agassizii,* and *Cyclotella meneghiniana*) and a calibrated Celloscope (*A. formosa, C. meneghiniana,* and *Scenedesmus quadricauda*); the two methods agreed when size was expressed as the radius of a sphere of equivalent volume.

Generally, ca. 250 ml of sterile medium in a 500-ml Erlenmeyer flask was inoculated with 1 ml of algal suspension from stock cultures. As cultures grew, sinking rates and often population size and phosphate levels (for phosphate limited cultures) were monitored. Sinking rate determinations from exponential and stationary phase cultures grown in complete medium were made for 3–15 replicate cultures of each species. Phosphate limited cultures were started in WC with ca. 2.5 μM phosphate, instead of 50 μM and used in phosphate enrichment experiments after they reached stationary phase.

Reactive phosphate was measured by a modified molybdate-ascorbic acid method (Strickland and Parsons 1965). The extinction of filtered 10-ml samples with 1.0 ml of mixed reagent added was measured on a Spectronic 100 (Bausch & Lomb). A fixed position, 10-mm flowthrough cell was used that permitted measurement of phosphate from 0.04–10.0 μM.

Sinking rate was determined by a sensitive fluorometric technique (Titman 1975) modified from methods used by Steele and Yentsch (1960) and Eppley et al. (1967). The technique allows rapid determination of sinking rate, requiring from 15 min to about 2 h, within the range of sinking rates measurable with the technique (20 to about 0.1 m d^{-1}).

Asterionella formosa Hass. (clone L262, isolated from Windemere) was provided by J. W. G. Lund. The clone is unialgal but not axenic. *Melosira agassizii* (clone Fat Mel) was isolated by S. S. Kilham from L. Kioga, Uganda, into unialgal but not axenic culture. *Cyclotella meneghiniana* (clone CyOcF2) was isolated by S. S. Kilham from L. Ohrid, Yugoslavia, and obtained in axenic condition by V. McAlister. *Scenedesmus quadricauda* (clone ICC 76) was provided by the Indiana Culture Collection in axenic condition.

Results

A comparison of sinking rates of different species in the same physiological condition indicates that in general larger species tend to sink more rapidly than smaller species (Table 1). Except for *C. meneghiniana,* mean sinking rates of stationary phase cultures of each species are significantly higher than the sinking rates of exponentially growing cultures (0.95 level). At the midrange of sizes studied (10-μm radius), the ratio of sinking rates of stationary phase to exponential phase cultures is 4.0, as cal-

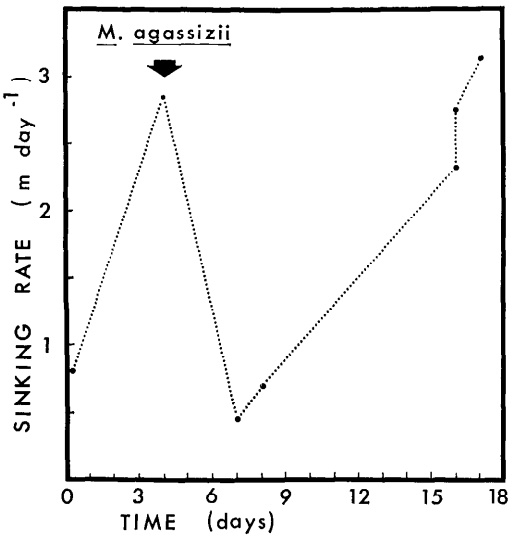

Fig. 1. Sinking rate change in a culture of *Melosira agassizii* following nutrient enrichment when the culture reached stationary phase (arrow).

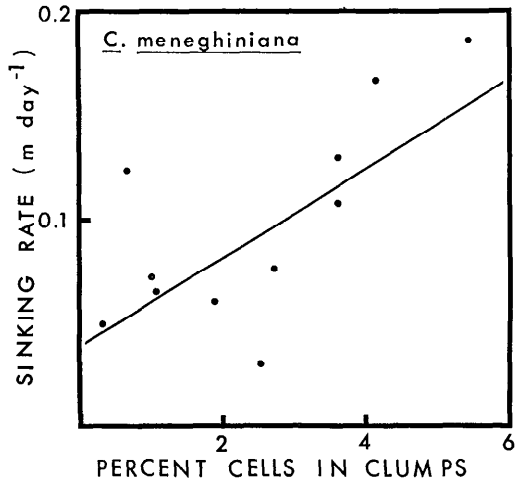

Fig. 2. Effect of multicell aggregates on mean population sinking rate of *Cyclotella meneghiniana*. Data points are lumped from four cultures, two enriched and two unenriched.

culated by least squares linear regressions of log-log transformed data..

A phosphate limited culture of *M. agassizii* was chosen for the first study of the time course of sinking rate change in response to nutrient enrichment. On day 0 (Fig. 1) the culture was approaching stationary phase. On day 4 the culture had a sinking rate of 2.8 m d^{-1}. It was enriched with complete WC at the time indicated by the arrow. The sinking rate of this enriched culture was measured immediately and periodically for the next 12 days. By day 7 the sinking rate had fallen to 16% of that at enrichment; by day 16 sinking rates had again increased to the level before enrichment.

Two phosphate enriched batch cultures of *C. meneghiniana* and two unenriched controls were started by dividing a phosphate limited chemostat culture (5.0 μM phosphate in the influent medium, at 0.5 d^{-1}, with extracellular levels <0.04 μM) into four aliquots of ca. 250 ml. Sinking rate changes in these cultures were monitored for 9 days. Each determination required from 2 to 8 h. Sinking rates were often at or below the reasonable limit of detection of the fluorometric technique used. No replicate determinations were possible. No significant divergence of sinking rate between the enriched and the unenriched cultures had occurred by day 9. All four cultures exhibited a peak in sinking rate in the middle of this period. In all cultures, *C. meneghiniana* secreted a mucus-like substance (probably a polysaccharide, cf. Guillard and Wangersky 1958). Aggregates of up to 20 cells then formed, averaging 5–7 cells per aggregate. Both control cultures formed aggregates on the third day after removal from the chemostat. The enriched cultures formed aggregates 2 and 4 days after their extracellular phosphate levels fell below 0.04 μM. In all cultures, the aggregates dispersed within 3 days of their formation. Sinking rates increased with aggregate formation. Data, pooled from all four cultures in which percent cells in aggregates was determined, are graphed with the concomitant mean sinking rate in Fig. 2. The least squares linear regression line has a slope significantly greater than zero ($p \geq 0.95$), indicating that aggregate formation has a positive effect on sinking rate.

Figure 3 shows the changes in the sinking rate of a phosphate limited population of

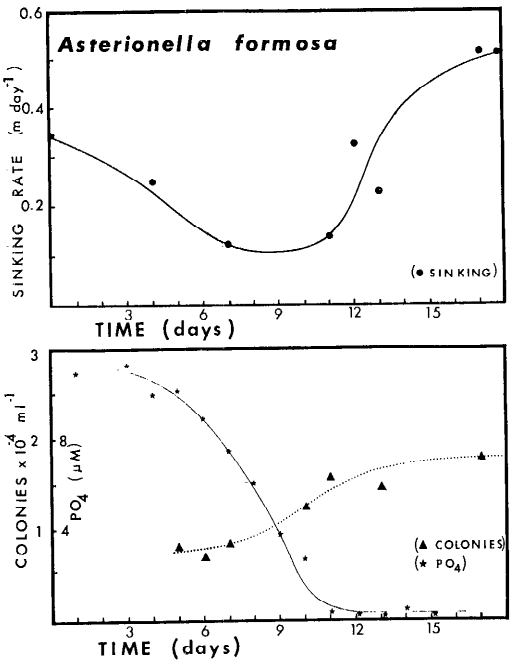

Fig. 3. Change in sinking rate, extracellular reactive phosphate, and population size for a stationary phase population of *Asterionella formosa* enriched on day 0.

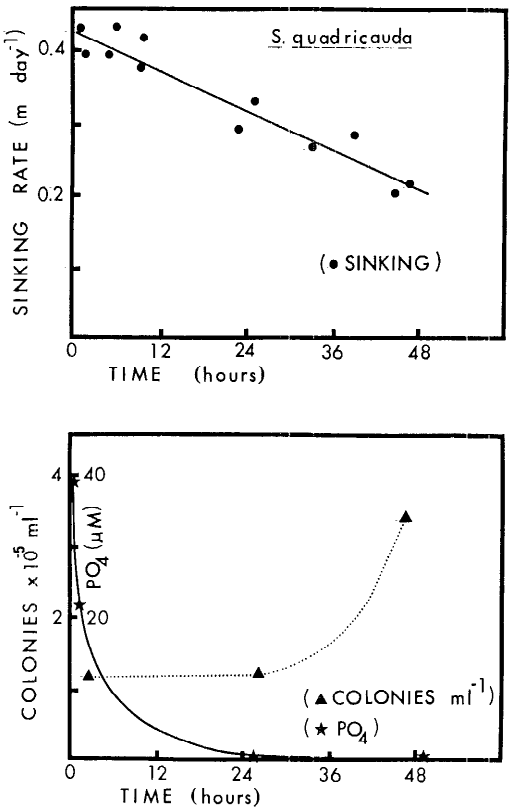

Fig. 4. Change in sinking rate, extracellular phosphate, and population size in a culture of *Scenedesmus quadricauda* enriched at hour 0.

A. formosa which, on day 0, was approaching stationary phase. The culture was enriched on day 0. Following enrichment, sinking rate decreased until day 9. As phosphate fell to undetectable levels (day 12), sinking rate began increasing.

A shorter term experiment was performed for *S. quadricauda*. At hour 0 (Fig. 4) a phosphate limited culture of *S. quadricauda* was divided into two aliquots, one of which was enriched and one of which was not. Through the next 48 h the sinking rate of the unenriched culture increased slightly, but insignificantly (0.95 level). Sinking rate of the enriched culture decreased to 50% of the starting level during this same time period. Within 24 h phosphate had fallen to 0.10 μM. Population numbers tripled within 48 h.

Discussion

Smayda (1970) reported that sinking rates of stationary phase populations of marine phytoplankton are higher than those of rapidly growing cultures. Our results for freshwater species agree with that trend. The generally higher sinking rate of larger species in the same physiological state is also consistent with the results summarized by Smayda (1970).

The time series of sinking rate change for *M. agassizii* and *A. formosa* indicates that the higher sinking rate of stationary phase cells was an apparent response to external nutrient conditions, not an indication of lack of viability (*see* Eppley et al. 1967). Because changes in sinking rate are shifts in the mean sinking rate of an entire population, the sinking rate changes of individual cells or colonies can be interpreted in two ways: the decrease could be a result of a gradual lowering of the sinking rates

of all individuals in the population, or could be caused by a rapid decrease in the sinking rate of some individuals that responded more rapidly than others to increased nutrients. If the second interpretation is correct, the actual time needed for a significant proportion of the *S. quadricauda* population to respond to changed nutrient conditions would be much less than the 48 h needed for the sinking rate of the entire population to decrease by 50%.

The observed changes in sinking rate as related to external nutrient conditions may be important in determining the vertical distribution of a species in the water column. Generally considered, the increased sinking rate of nutrient depleted cells should bring them closer to the thermocline. If these cells encounter nutrient-rich water, their sinking rate should decrease, causing cells to accumulate near the region of the nutrient gradient (*see* Steele and Yentsch 1960). The decrease in sinking rate near the thermocline could result in a decreased loss rate of cells from the euphotic zone.

The vertical distribution and path followed by individual cells is complicated by the patterning of epilimnetic circulation. Langmuir circulation, the major process by which heat is distributed in a body of water (Myer 1969; Faller 1971; Scott et al. 1969), results in a circulation pattern that includes regions of upwelling and downwelling water. Stommel (1949) provided a descriptive differential equation model of Langmuir circulation which we have modified to include the observation that the maximal rate of upwelling is generally half the maximal rate of downwelling (Fig. 5A). In such a circulation pattern, a neutrally buoyant cell will move with the streamlines shown. A sinking cell will always move downward with respect to the immediately surrounding parcel of water, traveling closer, on average, to the thermocline. If the sinking rate of a particle is less than a critical value, it will be carried back to the surface water from the thermocline (Fig. 5B). The trajectories shown are for particles with a sinking rate of 85 m d^{-1} (chosen for ease of graphical illustration) in a circulation system with a maximal rate of downwelling of 1.0 cm s^{-1} and an epilimnetic depth of 10 m. Particles initially outside the outer closed curve (broken line) will sink out of the mixed layer. All other particles will stay in suspension unless turbulence carries them from their trajectory to the region outside the zone of retention.

It is interesting to speculate on how such a circulation pattern may affect loss rates of phytoplankton from the mixed layer. A simple algebraic relationship is used by most modelers to describe the relationship between loss rate and sinking rate (Bannister 1974; Kozerski 1974; Uhlmann 1971; Lehman et al. 1975). The relationship, loss rate = (sinking rate)/(depth), is shown for a mixed layer 10 m deep (Fig. 6, curve A). A rough estimate of loss from a Langmuir circulation pattern can be made by calculating the area (volume) outside the zone of retention for particles of a given sinking rate compared to the total area (volume) of the mixed layer. Loss rate should equal this multiplied by the rate at which turbulent effects bring particles out of the zone of retention. For the purpose of calculation, this was taken to be 2.0 d^{-1} (i.e. a complete remixing of the epilimnion twice each day). The existence of small-scale patches (Richerson et al. 1970) argues against turbulent mixing much greater than this. For the circulation system of Fig. 5, loss rates for particles of various sinking rates are shown (Fig. 6, curve B). The discrepancy between the two curves of Fig. 6 illustrates the lack of information concerning the relationship between sinking rate and the loss rate of cells from the mixed layer. Because of the critical importance of loss rates in understanding the ecology and productivity of lakes and oceans, much more work, experimental and theoretical, needs be done.

When the nutrient-dependent changes in sinking rate observed in the laboratory occur within a Langmuir circulation pattern, the resultant paths followed by cells can be viewed as a type of "vertical migration." As nutrient depleted cells increase in sinking rate, they enter trajectories which take them closer to the bottom of the circulation

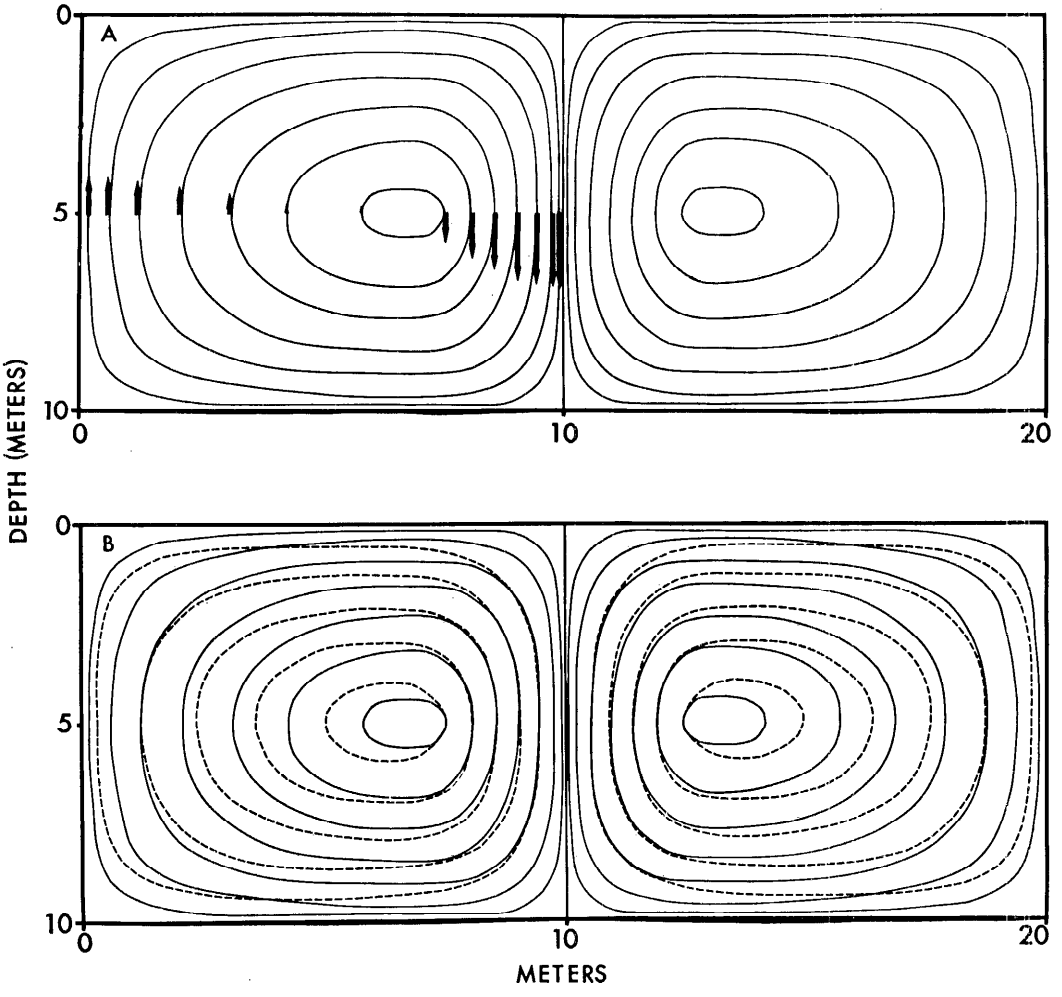

Fig. 5. A—vertical cross-sectional view of Langmuir circulation as produced by a model modified from Stommel (1949). Tangential vectors are velocity vectors. The solid closed curves are streamlines, paths followed by small parcels of water. The vertical scale is depth below the surface; horizontal scale is horizontal distance. B—streamlines of graph A on which are superimposed the trajectories followed by particles with a sinking rate of 85 m d^{-1} (broken line curves). The region within the outermost trajectory is the region of retention for particles of this sinking rate.

system. These cells have an increased probability of encountering water of higher nutrient content. When they do, their sinking rate will decrease, bringing them into trajectories which take them closer to the surface. In the same body of water, a "sinking species" may thus encounter a different average nutrient concentration than a "nonsinking species."

Munk and Riley (1952), Hulburt (1970), and Pasciak and Gavis (1974) have hypothesized that the movement of a cell relative to the surrounding parcel of water may be important in overcoming diffusion limitation of nutrient uptake. Pasciak and Gavis (1975) demonstrated that the diffusion limitation of nutrient uptake is greatest at low nutrient concentrations. Increased sinking rates of nutrient depleted cells could be important in overcoming diffusion

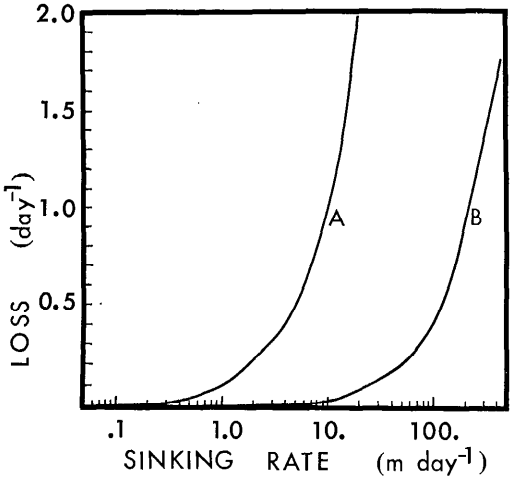

Fig. 6. Loss rates for particles of various sinking rates as predicted by the algebraic relationship (loss = S.R./depth; curve A) and for particles in the circulation system of Fig. 5 (curve B).

limitation. The formulation of Pasciak and Gavis (1974) allows calculation of uptake rates at various sinking rates. A measure of the extent of diffusion limitation comes from P (for motionless cells) and P' (for moving cells) defined as

$$P = 14.4\pi RDK/V_{max},$$

and

$$P' = 14.4\pi RDK(1 + 0.5Ru/D)/V_{max},$$

where V_{max} is the maximal rate of nutrient uptake for a spherical cell, K is the half-saturation constant, R is the radius of a spherical cell, D is the diffusivity of the nutrient, and u is the rate of movement of the cell relative to the surrounding water.

Pasciak and Gavis assumed, for the purpose of discussion, that diffusion limitation is important when P or P' is less than 2.0. The higher the value of P' compared to P, the greater the effect of motility (sinking, swimming, positive buoyancy) in overcoming diffusion limitation of nutrient uptake. In their survey of diffusion limitation of marine phytoplankton, they indicated that few species might be diffusion limited. For the species they considered motile (flagellated forms), they demonstrated that motility was sufficient to overcome diffusion limitation. Pasciak and Gavis did not consider sinking as a possible form of motility. If sinking rates available for similar sized congeners are included in the analysis, one of the two species they considered diffu-

Table 2. The influence of sinking on diffusion limitation of nutrient uptake. P is calculated assuming no motility. P' includes the effect of sinking. A value of 2.0 or greater for P or P' indicates little diffusion limitation of nutrient uptake. Average sinking rates listed are for exponentially growing (G) and stationary phase (S) populations.

Species	Nutrient	Vmax (μM cell^{-1} h^{-1})	K (μM)	Radius (μm)	P	P'	S.R. (m day^{-1})
Rhizosolenia robusta	NO_3*	2.27×10^{-5}	9.3	42	1.17	1.38 2.06	1.1 (G)† 4.7 (S)†
Coscinodiscus lineatus	NO_3*	9.0×10^{-6}	2.8	25	0.53	0.63 0.88	1.9 (G)‡ 6.8 (S)‡
Ditylum brightwelli	NO_3*	1.25×10^{-6}	0.6	75	2.44	2.86 4.63	0.6 (G)‡ 3.1 (S)‡
Asterionella formosa	PO_4§	9.14×10^{-8}	0.6	12.5	3.71	4.11	1.5 (S)||
Cyclotella meneghiniana	PO_4§	5.5×10^{-9}	0.75	1.0	6.16	6.17	0.24 (S)||

* from Pasciak and Gavis (1974).
† from Smayda and Boleyn (1966) for *R. setigera*.
‡ from Eppley at al. (1967) for *Coscinodiscus* sp. clone AD or for *D. brightwelli*.
§ unpublished results.
|| from this work.

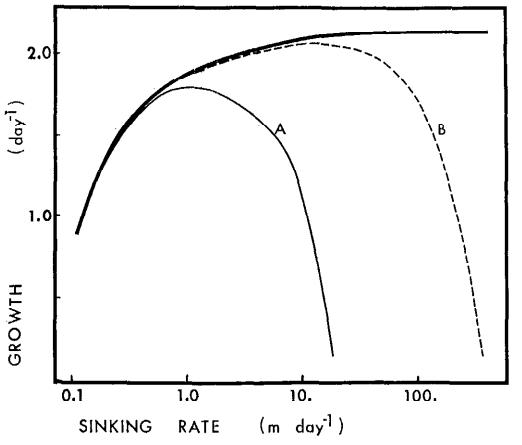

Fig. 7. Theoretical relationship between potential growth and sinking rate for *Asterionella formosa*. The upper, thick curve is calculated uptake at various sinking rates divided by minimal internal stores and is a measure of potential growth. The difference between the potential growth curve and the loss curves of Fig. 6 yields the two net potential growth curves, with optima at 1.0 and 10.0 m d^{-1}.

sion limited may not be and the extent of limitation is reduced for the other species (Table 2). The increase in P' over P for stationary phase populations (S) of *Rhizosolenia robusta* and *Ditylum brightwelli* indicates the potential importance of sinking in overcoming diffusion limitation of nutrient uptake. Stationary phase cultures of *Coscinodiscus lineatus* are still diffusion limited by their definition of $P = 2.0$. However, the sinking rate we used for the purpose of calculation was for *Coscinodiscus* sp. (clone AD), which is significantly smaller than *C. lineatus*. This may underestimate the importance of sinking in overcoming diffusion limitation for this species.

Under low nutrient conditions, increased sinking rates may be important in at least partially overcoming diffusion limitation. Because diffusion limitation decreases with increasing sinking rate, it might seem best for nutrient depleted cells to have very high sinking rates. But high sinking rates lead to increased loss rates. The "optimal" sinking rate for a species at a given nutrient concentration would be the result of the quantitative tradeoff between increased growth from sinking-dependent nutrient uptake and increased losses from sinking. This is shown for *A. formosa* in Fig. 7. The upper, solid curve shows the calculated potential growth rate (nutrient uptake divided by minimal internal stores) at various sinking rates. When loss from sinking is subtracted from the potential growth curve, net potential growth curves are obtained. Curve A (Fig. 7) results from subtraction of loss curve A (Fig. 6); curve B (Fig. 7) results from subtraction of loss curve B (Fig. 6). Depending on which loss curve is used, the optimal sinking rate for a cell of *A. formosa* in an environment with 0.20 μM phosphate is between 1.0 and 10.0 m d^{-1}. Although this is too broad a range to have much quantitative meaning, it illustrates a possible evolutionary basis of selection for high sinking rate of nutrient depleted cells. The observed mean sinking rate of nutrient depleted cultures of *A. formosa* is 1.5 m d^{-1}. The highest observed value is 5.0 m d^{-1}. These values fall within the theoretically predicted range.

In conclusion, the observed changes in sinking rate of freshwater phytoplankton may have two effects of major ecological importance. First, the high sinking rate of nutrient depleted cells may allow these cells to at least partially overcome nutrient limitation by reducing the extent of diffusion limitation of nutrient uptake. Second, the variability of sinking rate with nutrient status of a cell will affect the loss rate of phytoplankton from the mixed layer of a lake. Although the extent of the effect will depend on the patterning, magnitude, and probability of various types of circulation, indications are that loss rates may be much lower than those predicted by the currently used algebraic relationship. If sinking is to be included in models of phytoplankton population dynamics, both the effects on nutrient uptake and on loss rate should be considered, as well as complications introduced by circulation patterns.

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