Journal of Plankton Research Vol.18 no.9 pp.1727–1734, 1996

Sedimentation loss of phytoplankton cells from the mixed layer: effects of turbulence levels

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Abstract. In this paper, we describe a study of the role of turbulence in the loss by sedimentation of phytoplankton cells from the mixed layer. The approach presented allows the quantification of the sedimentation rate of phytoplankton in the whole range of turbulence levels of this layer. Two types of phytoplankter can be distinguished according to the effect that turbulence can exert on their sedimentation rate. The rate of those cells whose settling velocity is lower than ~1 m day^{-1} will not be modified by turbulence. The sedimentation rate of cells with higher settling velocities can, however, be modified by the level of turbulence. A set of dimensionless numbers is given to delimit several processes that are important in the dynamics of phytoplankton sedimentation in a turbulent regime. The use of these dimensionless numbers suggests that an increase in the turbulence level in the mixed layer does not always imply a decrease in the sedimentation rate of phytoplankton cells.

Introduction

Turbulence is considered to be one of the main environmental variables affecting phytoplankton dynamics because of its potential capability to decrease the rate at which these populations sink from the upper ocean (Walsby and Reynolds, 1980; Harris, 1986). Owing to turbulence, the sinking of a phytoplankton cell from the upper ocean can be considered as the combination of two movements: a deterministic one due to the sedimentation of the cell and a random one imposed by the turbulent flow. This is usually formulated in studies of marine phytoplankton through the model of Riley *et al.* (1949), which makes use of the advection–diffusion equation. On an intuitive basis, pelagic ecologists have usually assumed that turbulence increases the residence time of phytoplankton cells in the upper-ocean layers. This assumption has been accepted to such an extent that it can be considered as a paradigm of pelagic ecology. Nevertheless, we want to call attention to the fact that it is an idea which might not be based on solid grounds. Thus, it could be argued that turbulent flow will sometimes displace the individual cell downwards as well as upwards. These vertical movements due to turbulence would cancel each other on average and hence they should not affect the residence time expected for the cell.

A more rigorous analysis of the problem should help to select between this logical objection and the intuitive assumption. An example of this can be found in the work by Lande and Wood (1987) which, on the basis of stochastic theory, demonstrated that turbulence can increase the residence time of particles near the surface of the ocean. Nevertheless, this effect is only apparent under the uncertain assumption of a substantial reduction of phytoplankton sinking velocity in the thermocline.

Another possibility by which turbulence might decrease the settling of phytoplankton from the mixed layer is the trapping of cells in the divergence zone of flow structures such as Langmuir cells (Smayda, 1970; Fung, 1993). Nevertheless, the flow at the surface of the ocean is not always arranged in organized structures. These other cases have been considered by Smith (1982) (see also Reynolds, 1984), analysing the sedimentation of phytoplankton under two extreme conditions of turbulence levels, i.e. the absence of turbulence and a turbulence level that allows a high and constant mixing of particles. The approach of Smith then allows the delimitation of the range of residence times expected for phytoplankton populations in the mixed layer.

In this paper, we extend the results of Smith by also considering intermediate levels of turbulence. This has been done after applying to phytoplankton the approach proposed by Ruiz (1996) for marine snow. This approach allows quantification of the sedimentation rate of particles in the whole range of turbulence levels in the mixed layer, and separates two types of phytoplankton cells according to the effect that turbulence can exert on their sedimentation rate. The sedimentation rate of the cells whose settling velocity is lower than ~1 m day^{-1} will not be affected by turbulence. On the other hand, those cells that sink at higher velocities have sedimentation rates that are affected by turbulence. Moreover, if these cells have some ability to modify their sinking velocities (e.g. by physiological changes), they will require smaller differences between maximum and minimum velocities to modify greatly their sedimentation rates.

The sedimentation of phytoplankton in a turbulent environment

The control accomplished by turbulence on the sedimentation rate of phytoplankton in the mixed layer is carried out by modifying the sedimentation flux. This downwards flux is equal to $wC(h, t)$, where w is the sinking velocity of the phytoplankton cell in still water and $C(h, t)$ is the concentration at the bottom of a mixed layer of height h at time t. The possibility that turbulence alters the velocity at which particles sink has recently been the subject of very detailed analysis by fluid dynamicists (Fung, 1993; Wang and Maxey, 1993). These studies predict that the average sinking velocity of a particle is not modified by turbulence if the inertia of the particles is small. The inertia of a particle immersed in a turbulent flow is measured as the Stokes number of the particle. This number is the ratio between the time scale of the particle and that of the flow (Wang and Stock, 1993). In the case of turbulent flow, the time scale to be used is related to the time scale of the largest eddies and can be obtained under dimensional grounds (Ozmidov, 1992). The time scale of the particle represents the time necessary for the velocity of a particle injected into a quiescent fluid to reach 1/e of its initial value if the drag on the particle is in the Stokes range (Wang and Stock, 1993). Phytoplankton cells have very low Stokes numbers in the mixed layer (see Figure 1), which indicates that they tend to follow the turbulent movements of the flow. In the cases in which the Stokes number of a particle is very low, turbulence does not have the capacity to alter its average sinking velocity (Fung, 1993; Wang and Maxey, 1993) which, therefore, remains equal to w. A consequence of this is that if, in spite of this, turbulence still has an effect on the sedimentation flux of phytoplankton from the mixed layer, it must be attributed to the control exerted on the other term of the sedimentation flux, $C(h, t)$, and, hence, on the vertical distribution of plankton in

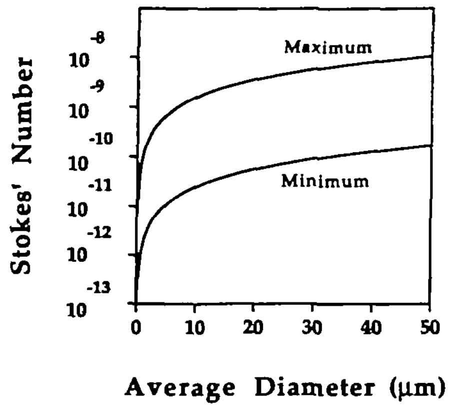

Fig. 1. Range of variation of the Stokes number for phytoplankton cells of different sizes. The range of variation was calculated with a maximum and a minimum time scale for the flow as obtained from simple dimensional grounds (Ozmidov, 1992) from data of Brainerd and Gregg (1993). The time scale of the phytoplankton cell is ($\Delta\rho\, s^2/18\mu$), where $\Delta\rho$ is the difference in density between the cell and the seawater, s is the diameter of the cell and μ is the dynamic viscosity of seawater (McCave, 1984). The characteristics of the phytoplankton cells used to find their time scales were obtained from the formula fitted by Jackson and Lochmann (1992) to data of Smayda (1970) ($\Delta\rho = (9\, \nu\rho\zeta/g)r^{-0.83}$, where ρ and ν are the density and kinematic viscosity of seawater, $\zeta = 1.24$ cm$^{-0.17}$ s^{-1}, g is gravitational acceleration and r is cell radius).

the mixed layer. As explained below, this distribution is the result of the balance between sinking and turbulent mixing of phytoplankton cells in the mixed layer.

The vertical distribution of sinking particles immersed in a turbulent flow has often been modelled through the advection–diffusion equation (Riley *et al.*, 1949; Pasquill, 1962; Csanady, 1963; Graf, 1971; Pruppacher and Klett, 1978; Okubo, 1980; Lau, 1989). This equation has also been implemented for studying the role of buoyancy in the formation of cyanophyte blooms (Humphries and Lyne, 1988) or in the accumulation of these algae at the downwind end of lakes (Webster, 1990; Hutchinson and Webster, 1994; Webster and Hutchinson, 1994). The sinking (or flotation) velocity implemented in this equation is that of a particle in still fluid (w). On the other hand, the coefficient of vertical eddy diffusivity (K) usually included in this formulation is the coefficient of the fluid flow, although the coefficient of the particle should be used. Nevertheless, we can consider that the differences between the value of K for the fluid and for the particle are not significant in the case of individual phytoplankton cells sinking in the mixed layer. These differences arise when either the Stokes number of the particle is high or when w is similar to (or higher than) the turbulent velocities that characterize the movement of the largest eddies in the mixed layer. Individual phytoplankton cells do not fall within these cases as they have small Stokes numbers and their sinking velocity is much lower than the turbulent velocities of large eddies (with values of ten to hundreds of metres per day). However, when phytoplankton cells form aggregates or colonies, they can reach velocities of the order of ten to hundreds of metres per day. Then, the value of K that should be used is that of the particle, which can be obtained through the parameterization of Csanady (1963) or Wang and Stock (1993).

The different terms that constitute the advection–diffusion equation (sinking and diffusion) compete to distribute the phytoplankton cells within the mixed layer in different ways. Thus, sinking tends to cause accumulation of cells at the bottom of the layer, whereas diffusion tends to make the distribution uniform. The distribution of particles in the mixed layer will be the result of the balance between the two tendencies. The balance can be expressed by D, the dimensionless diffusivity of the particle ($D = K/wh$), which arises from the non-dimensionalization of the advection–diffusion equation (Humphries and Lyne, 1988; Lau, 1989; Webster, 1990). As a result of this balance between diffusion and sinking, when $D > 1$, the turbulence levels are high enough to make uniform the distribution of phytoplankton in the mixed layer, whereas for $D < 1$ the cells will accumulate at the lower part of the mixed layer. As the sedimentation flux is $wC(h, t)$, the sedimentation rate of phytoplankton will be higher under a low-turbulence regime than under a high-turbulence one. This is due to the distribution of particles, which tend to accumulate in the lower part in an environment of low turbulence and are more uniformly distributed in the case of high turbulence.

As mentioned above, Smith (1982) calculated the minimum (absence of turbulence) and maximum (high and constant turbulence) time required for sedimentation to eliminate a phytoplankton assemblage from the mixed layer. When extended to intermediate levels of turbulence (Ruiz, 1996), a factor (F) appears that depends on the balance between sinking and diffusion:

$$d\bar{C}/dt = Fw\,\bar{C}/h \qquad (1)$$

where $\bar{C}$ is the average concentration of particles in the mixed layer, F is the ratio of phytoplankton concentration at the bottom of the mixed layer to the average concentration in the whole layer; its mathematical derivation can be found in Ruiz (1996). Equation (1) shows how we can expect higher sedimentation rates at higher values of F.

The factor F is very sensitive to values of D when $D < 1$. We can then say that an increase in K would imply an increase in D and, consequently, a decrease in the value of F. This is the way in which the turbulence affects the sedimentation rate of phytoplankton. On the other hand, F is not sensitive to values of D when $D > 1$, in these cases F is one, or very close to one, independently of the value of D. When considering this argument and the usual levels of turbulence found in the ocean, the effect of turbulence on the sedimentation rate of phytoplankton is not always so apparent, as F could always be one for many phytoplankters.

In fact, substantial changes in the sedimentation of phytoplankton cells that are due to turbulence only take place for cells with high sinking velocity (w). This is clear in Table I, which shows the range of variation of D for different phytoplankton groups calculated from their sinking velocity and two extreme conditions of turbulence (h = 40 m, K = 10 000 m^2 day^{-1} and h = 100 m, K = 100 m^2 day^{-1}). In this table, we can see how numerous phytoplankton species have values of D that are always higher than one. This means that changes in turbulence levels will not imply big changes in the sedimentation flux of these phytoplankters, since F will always remain close to one, as their vertical distribution will always be

Table I. This table shows the range of variation of D (dimensionless diffusivity) and F (correction factor for sedimentation under intermediate levels of turbulence) for different phytoplankton species. For each species, the maximum (w_{max}) and minimum (w_{min}) settling velocities (m d^{-1}) were taken from Smayda (1970). The values of D were calculated as explained in the text and the value of F as explained in Ruiz (1996). The column with the value of F_{min} is not represented as for all the phytoplankters F_{min} is equal to one. The original genus names of Smayda (1970) have been kept

Species	w_{max}	w_{min}	D_{max}	D_{min}	F_{max}
Diatomophyceae					
Asterionella japonica	0.75	0.26	962	1.333	1.1
Bacteriastrum hyalinum	1.27	0.39	641	0.787	1.2
Chaetoceros didymus		0.53	472	1.887	1.1
Coscinodiscus wailesii	30.2	7	36	0.033	7.4
Coscinodiscus sp.	6.83	1.95	128	0.146	2.3
Cyclotella nana	0.76	0.16	1563	1.316	1.1
Ditylum brightwelli	3.09	0.13	1923	0.324	1.6
Leptocylindrus danicus	0.46	0.37	676	2.174	1.1
Nitzschia seriata	0.5	0.35	714	2.000	1.1
Phaeodactylum tricornutum	0.06	0.02	12500	16.667	1.0
Rhizosolenia hebetata		0.22	1136	4.545	1.0
Rhizosolenia setigera	6.3	0.1	2500	0.159	2.2
Rhizosolenia stolterfothii	1.9	1	250	0.526	1.3
Skeletonema costatum	1.35	0.3	833	0.741	1.2
Stephanopyxis turris	2.1	1.1	227	0.476	1.4
Thalassionema nitzschioides	0.78	0.35	714	1.282	1.1
Thalassiosira fluviatilis	1.1	0.6	417	0.909	1.2
Thalassiosira cf. *gravida*	0.7	0.53	472	1.429	1.1
Thalassiosira cf. *nana*	0.28	0.1	2500	3.571	1.0
Thalassiosira rotula	2.1	0.39	641	0.476	1.4
Dinophyceae					
Ceratium balticum	12	9	28	0.083	3.4
Gonyaulax polyedra	6	2.8	89	0.167	2.1
Noctiluca miliaris	22	14	18	0.045	5.7
Prymnesiophyceae					
Coccolithus huxleyi	1.3	0.28	893	0.769	1.2
Cricosphaera carterae		1.7	147	0.588	1.3
Cricosphaera elongata		0.25	1000	4.000	1.0
Cyclococcolithus fragilis		13.2	19	0.076	3.7
Chlorophyceae					
Dunaliella tertiolecta		0.18	1389	5.556	1.0

uniform independently of the observed levels of turbulence in the upper ocean. Nevertheless, some species are within a range of D where their sedimentation flux is very sensitive to turbulence, as is apparent from the range of variation of their factor F (Table I). As an example, the sedimentation flux of *Coscinodiscus wailesii* can differ by a factor of 7.4 depending on the levels of turbulence, that in this case clearly affects the vertical distribution of cells.

Changes in turbulence levels will only have some influence in the sedimentation of phytoplankters that settle at velocities >1 m day^{-1}, since this is the lowest sinking velocity for which values of D smaller than one can be achieved (Table I). These are the phytoplankters for which the buoyancy changes, noted by several authors (Smayda, 1970; Bienfang *et al.*, 1983), will be more advantageous. The reason for this can be derived from the formulation of phytoplankton sedimentation rate [equation (1)]. Thus, for those phytoplankters that have a value of D which is always higher than one, a physiological change that decreases the settling velocity will only modify w in equation (1). However, for those cells having a D which is lower than one, a decrease in the settling velocity has an additional effect on the sedimentation rate through a change of F.

The importance of this feature for the global phytoplankton sedimentation rate is very apparent if we consider that ~50% of both individual and colony-forming phytoplankters (Smayda, 1970) exhibit sinking velocities that are <1 m day^{-1} when they are actively growing but become >1 m day^{-1} when the cells are senescent. This actually implies that the physiological condition of the cells could switch from a turbulence-insensitive to a turbulence-sensitive state in about half of the sea phytoplankters.

Limitations of the approach

The precise determination of the sedimentation rate through an equation with a correction factor has an important limitation. This is a consequence of other terms such as phytoplankton growth rate in the advection–diffusion equation, that can affect the value of F. However, the growth rate of phytoplankton must be both high and depth dependent in the mixed layer to affect the F value. Given these conditions, the vertical distribution of phytoplankton could be more dependent on the place of the mixed layer where growth is higher than on turbulence and sinking. Fortunately, the cases in which this happens can be detected by the examination of two dimensionless numbers. The first one, rh/w (where r is the growth rate), detects whether the magnitude of the growth rate is high enough to affect the value of F. The second one detects whether the depth dependence of growth rate is high enough to affect it. This new term was not contemplated in the original model of Ruiz (1996) since the growth rate is not as important when studying marine snow. This new number must contain the rate of change with depth of the growth rate and hence it is $(\partial r/\partial z)h^2/w$ (note that this number is also the derivative of the dimensionless growth with respect to dimensionless depth). Therefore, for the growth rate to affect the value of the factor F, both ratios rh/w and $(\partial r/\partial z)h^2/w$ must be higher than one. On the other hand, if one of these two terms is lower than one, no matter how high the value of the other is, F is not affected by growth rate.

Another point that must be taken into account is the fact that the balance between the sinking and diffusion of particles in the mixed layer is not achieved instantaneously, but it takes a time approximately equal to $2h/w$ (Ruiz, 1996). This implies a time of the order of days to months for phytoplankton. Thus, the actual distribution of cells in the mixed layer is the result of averaging the turbulence levels that have been present during a certain time in the layer. This necessarily includes the effect of the daily changes in sinking velocity of some phytoplankton cells, as observed by Smayda (1970). Owing to the long transient time necessary to reach a stable vertical distribution for a given turbulence level, daily changes of sinking velocity will not necessarily imply big changes of sedimentation rates between day and night. This feature can be also explored by means of a dimensionless number. In this case, the number is the dimensionless frequency of oscillation (Ω). This is obtained from the dimensional frequency of oscillation of the sinking velocities (i.e. 1 day^{-1}), w and h ($\Omega = 1\ \mathrm{day}^{-1}\ h/w$). The amplitude of the daily oscillations in sedimentation rate resulting from changes in the sinking velocity is strongly reduced for values of Ω higher than 0.5 (Ruiz, 1996). For instance, daily changes of w have been described for *Ditylum brightwelli* and for *Skeletonema costatum* (Smayda, 1970). Owing to these changes in w, both species might require the use of a different F in equation (1) for day and night. Nevertheless, the lowest possible value of Ω for these species is 13 and 30, respectively. Therefore, due to the high value of Ω, daily changes of w will not imply oscillations of F.

Turbulence and the motility of flagellate phytoplankters

The approach followed for the sinking of phytoplankton can also be applied to study the capacity of some planktonic flagellates to control their vertical position in the mixed layer. The key parameter that will determine whether a flagellate can control its position in the mixed layer is also the dimensionless diffusivity D. Now, the diffusivity includes swimming instead of sinking velocity of the flagellate, i.e. K/vh (where v is the swimming velocity of the flagellate). For values of $D > 1$, the flagellate population cannot control its position in the mixed layer. The examination of the range of variation of D in a size-spectrum fashion shows that large flagellates are able to control their position in the mixed layer better than small ones (Figure 2). Therefore, when accumulations of small flagellates ($D > 1$) are found in the mixed layer, this must be assigned to other mechanism like growth, rather than to their motility.

Taken in total, this paper presents a simple approach which is helpful for a better understanding of the role that turbulent phenomena have in the ecology of phytoplankton. We analyse the sedimentation of phytoplankton not only in

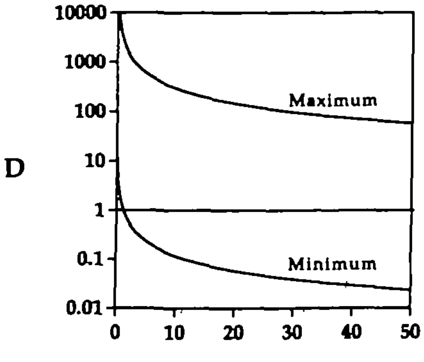

Fig. 2. Range of variation of the dimensionless diffusivity, D, of phytoplankton motility versus cell size. The range of variation was calculated, as in Table I, using the swimming velocity of the phytoplankton cell and assuming two extreme conditions of turbulence ($h = 40$ m, $K = 10\,000\ \mathrm{m}^2\ \mathrm{day}^{-1}$ and $h = 100$, $K = 100\ \mathrm{m}^2\ \mathrm{day}^{-1}$). The swimming velocity of the flagellates was assumed to be between 1 and 10 times their diameter per second (Purcell, 1977, 1978).

extreme cases, but also under intermediate levels of turbulence. This is accomplished by means of dimensionless numbers whose use suggests that an increase in the level of turbulence does not always imply, as one might intuitively assume, a decrease in phytoplankton sedimentation rate.

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Received on December 5, 1995; accepted on April 16, 1996