

Plankton sinking and turbulence

Lecture given on 1 July 2010 by A. Provenzale

1 Introduction

In still fluid, heavy particles tend to fall and reach, after some time, a terminal velocity determined by the balance between the pull of gravity and the viscosity of the fluid. Often, plankton cells are slightly heavier than sea water, and as a consequence they tend to sink in the water column. This sinking could then take them below the euphotic layer, arresting photosynthesis.

To overcome sinking, plankton have devised various types of strategies. One is swimming, that is, an active, energy-consuming self-propulsion that can oppose gravitational sinking. Other phytoplankters can modify their buoyancy, becoming, at least for some time, positively buoyant. Others can exploit the turbulence in the mixed layer, using it to stay suspended for longer times. This latter option was discussed at length by Margalef [5], who associated the level of turbulence in the surface layer with the type of organisms that are environmentally favoured. The terminal velocity of spherical impurities with the same density grows with the squared radius of the falling impurity. Thus, larger plankton cells tend to sink faster than smaller ones, provided they can be approximated by a somewhat spherical shape. When the turbulence in the euphotic layer is low, Margalef argued, smaller, possibly swimming phytoplankters such as flagellates are favoured as the larger species sink more rapidly out of the euphotic zone. On the other hand, when the level of turbulence is high, larger plankton can benefit from turbulent suspension and become favoured with respect to the small ones (which feel diffusion limitation of nutrients more severely).

One potential problem with this view is that it is not clear whether turbulence really favours a prolonged suspension of heavy impurities. For example, the results of an experiment by Ruiz et al [8] apparently indicate that turbulence make heavy particles sink faster than in still fluid. However, other experiments considering different flow configurations gave the opposite result, see for example [1]. A careful study of this issue is thus required.

2 Suspension of heavy impurities

The non-dimensional equation of motion for a heavy impurity under the influence of gravity is written as

$$\frac{d\mathbf{V}}{dt} = \delta \frac{D\mathbf{u}}{Dt} - \frac{1}{St} (\mathbf{V} - \mathbf{u} + \hat{\mathbf{z}}W) \quad (1)$$

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where \mathbf{V} is the velocity of the impurity, \mathbf{u} is the fluid velocity, W is the terminal velocity of the impurity in still fluid, z points vertically upwards and St is the Stokes number defined as

$$\text{St} = \frac{2}{9\delta} \left(\frac{a}{L}\right)^2 \text{Re}$$

where $\delta = \rho_f/\rho_p$ is the ratio between the density of the fluid and the density of the impurity, L is a typical lengthscale of the flow, U is a characteristic flow velocity and Re the Reynolds number. The terminal velocity W is found by equating the gravitational force to the Stokes drag, and its non-dimensional version is given by

$$W = \frac{2}{9} \frac{gL}{U^2} \left(\frac{a}{L}\right)^2 \frac{1-\delta}{\delta} \text{Re}. \quad (2)$$

2.1 Permanent suspension in a cellular flow field

Stommel [10] studied the vertical settling of small heavy impurities in a simple flow configuration composed by a network of vortices with horizontal axis; all the dynamics takes place in the vertical plane (x, z) and the vortices are infinitely long in the y direction. Stommel neglected the pressure term $\delta D\mathbf{u}/Dt$ (which we shall also do in the rest of this section) and neglected also the inertia of the impurities, imposing $d\mathbf{V}/dt = 0$ in equation (1), which gives

$$\vec{V} = \vec{u} - \hat{z}W. \quad (3)$$

Defining the two-dimensional stationary streamfunction

$$\Psi = 2(\cos x + \cos z). \quad (4)$$

The flow field is given by

$$\vec{u} = (u, w) = \left(-\frac{\partial\Psi}{\partial z}, \frac{\partial\Psi}{\partial x}\right)$$

and the velocity of the impurity is

$$\vec{V} = (u, w - W) = \left(-\frac{\partial\Psi}{\partial z}, \frac{\partial\Psi}{\partial x} - W\right) = \left(-\frac{\partial\tilde{\Psi}}{\partial z}, \frac{\partial\tilde{\Psi}}{\partial x}\right)$$

where $\tilde{\Psi} = \Psi - Wx$. The solution is sketched in Figure 1. The flow is characterized by regions with closed streamlines of $\tilde{\Psi}$, surrounded by jet-like channels with essentially downward velocities, owing to the effects of gravity. The impurities which end up in the downward jets fall faster than in still fluid, but some impurities get trapped in the cells with closed streamlines and remain suspended forever. Stommel [10] thus argued that permanent suspension is possible also for heavy particles and that turbulence (or cellular flow fields) can keep heavy impurities afloat. An extension of this approach to the case of a time-varying stream function was discussed in [9].

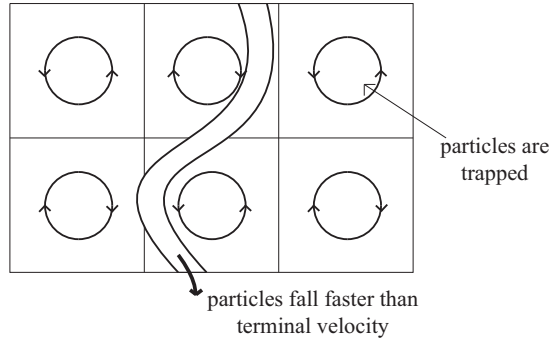
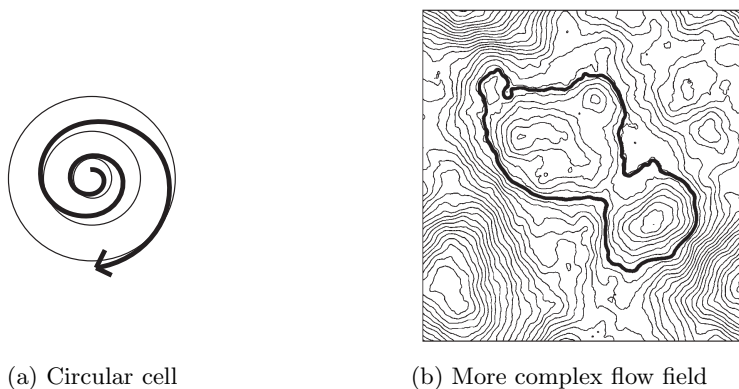


Figure 1: The motion of passively advected heavy impurities in the cellular flow field considered by Stommel [10].



(a) Circular cell

(b) More complex flow field

Figure 2: (a) Heavy impurities in an array of circular flow cells drift away from the center owing to inertial effects. (b) Impurities in a (frozen) flow field with more complex streamlines can stay suspended forever (from [7]).

2.2 The role of inertia

According to Maxey and Corrsin [6] permanent suspension is actually not possible when particle inertia is not neglected. Owing to the centrifugal force acting on a particle, in their motion in the circulation cells the impurities will spiral out, away from the cell center, as illustrated in Figure 2a. This has later become known as the sling effect: heavy particles tend to be ejected from high vorticity regions and concentrate in high strain regions between the flow cells; closed orbits no longer exist and heavy particles eventually end up in the downdrafts between the cells, causing an increase of the mean settling rate compared to what happens in still fluid, in keeping with the results of the experiment mentioned above [8].

However, consideration of flows with a more complex streamline pattern, such as that depicted in figure 2b, can change the picture. The work of [7] considered a spatially random, two-dimensional, incompressible stationary flow with energy spectrum $E(k) \propto k^{-5/3}$. In this flow, impurities are now pushed by their own inertia outwards as well as inwards, depending on the streamline curvature. In turn, this can lead to the emergence of closed

trajectories, which corresponds to a limit cycle in the four-dimensional impurity phase space (X, Y, V_x, V_y) .

Thus, the study of the motion of small, heavy, spherical particles in a random, stationary two-dimensional flow shows that permanent particle suspension is possible when the randomness suitably alters the curvature of the streamlines around an eddy. A stationary random two-dimensional flow will have two distinct groups of impurities, as shown in figure 3a. The particles in one group will stay very close to where they started (that is, they stay suspended), moving on limit cycles with closed trajectories. The impurities in the other group move away from where they started, reach the downdrafts and sink with an average settling speed which is larger than their terminal velocity in still fluid.

Owing to inertial effects, identical particles can thus have significantly different behavior when moving in a random steady flow. Some particles are swept into the downdrafts between the eddies and settle at rates that are larger than in still fluid. Other particles remain suspended, moving on closed trajectories, so that their vertical motions are oscillatory. These two different types of behavior result in a bimodal distribution of vertical displacements. As a result, the mean settling velocity can be either larger or smaller than the terminal velocity in still fluid depending on the fraction of suspended particles.

For a time-varying random two-dimensional flow, the distinction between the population of suspended impurities and that of rapidly falling ones does not remain so strict as particles can move from one group to the other. In this case, permanent suspension is no longer possible, but suspension can still last for a long time. Overall, these results confirm the view of Stommel and Margalef, who claimed that turbulence could indeed help heavy impurities to stay suspended for longer times than in still fluid.

3 Phytoplankton competition in turbulent waters

As turbulence affects the sinking rate of phytoplankton, one may go back to the old Margalef question and ask how populations of phytoplankton species with different size respond to a turbulent environment. Larger plankton species seem to be favoured in conditions of strong turbulent suspension while smaller phytoplankton can thrive in quieter conditions.

To explore this issue, we follow [3] and consider two phytoplankton species with radius a_1 and a_2 that compete for the same nutrient, N . The population dynamics is described by the following (non-dimensional) NP system:

$$\begin{aligned} \frac{DN}{Dt} &= I - \beta(a_1) \frac{NP_1}{k+N} Q(a_1) - \beta(a_2) \frac{NP_2}{k+N} Q(a_2) + \mu_N m [P_1 Q(a_1) + P_2 Q(a_2)] \\ \frac{DP_1}{Dt} &= \beta(a_1) \frac{NP_1}{k+N} - [m + s(a_1)] P_1 \\ \frac{DP_2}{Dt} &= \beta(a_2) \frac{NP_2}{k+N} - [m + s(a_2)] P_2. \end{aligned} \tag{5}$$

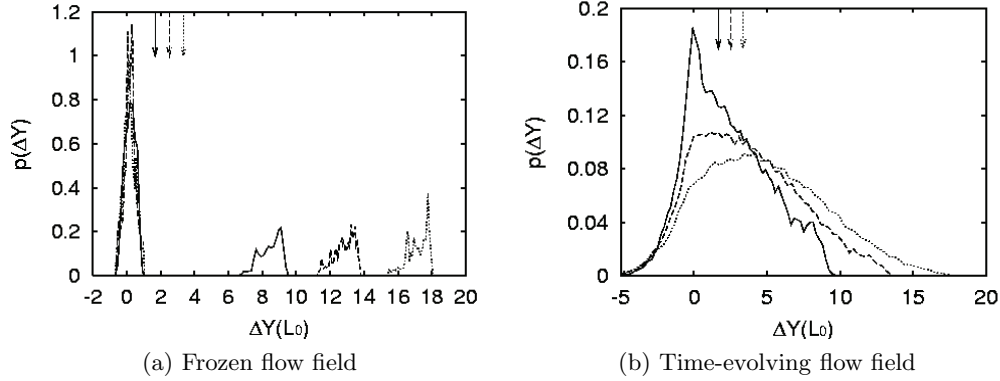


Figure 3: (a) In a frozen turbulent flow some impurities can stay suspended forever, while others move away from their initial position and fall faster than in still fluid. As a result, the distribution of particle displacements is bimodal. The three curves show the probability distributions of the vertical displacement of falling impurities at different times and the arrows indicate the displacement that the impurities would have had if they moved at the Stokes settling velocity W . On the left of the plot, there are particles which stay suspended forever and their displacement from the initial position does not grow with time. (b) In a time-evolving random field there is no strict separation between suspended and falling particles and permanent suspension is not possible, but a large fraction of the impurities can fall more slowly than in still fluid. From [7].

where P_1 and P_2 are the concentrations of the two species of phytoplankton, β is a growth rate, k is a limiting term for phytoplankton growth, m is a size-independent natural phytoplankton mortality rate, s is the size-dependent sinking rate, and Q is the nutrient quota of phytoplankton, used to transform biomass into nutrient amount.

The terms in the nutrient equation of system (5) describe two sources of nutrients: a constant external nutrient source, I , and the nutrients regenerated from dead phytoplankton, as described by the recycling term $\mu_N m [P_1 Q(a_1) + P_2 Q(a_2)]$ with $\mu_N < 1$. Nutrients are consumed by phytoplankton at a rate β , describing the phytoplankton efficiency to uptake nutrient which is assumed to be a function of phytoplankton size.

In their study, Jiang et al [3] recalled that there is a complex relationship between the efficiency/growth rate β and the size of phytoplankton species. Observations show that the growth rate of relatively large phytoplankton species decreases with increasing size while the opposite tends to be true for small phytoplankton species. This suggests that there should be an optimal phytoplankton size at which the growth rate is maximized. A simple analytic form of the phytoplankton growth rate that has these characteristics is

$$\beta(a) = \frac{a}{\alpha_1 a^2 + \alpha_2 a + \alpha_3} \quad (6)$$

where α_1 , α_2 , and α_3 are positive constants. The form of the growth rate described in (6) is only meant to capture the qualitative structure of observed phytoplankton growth rates

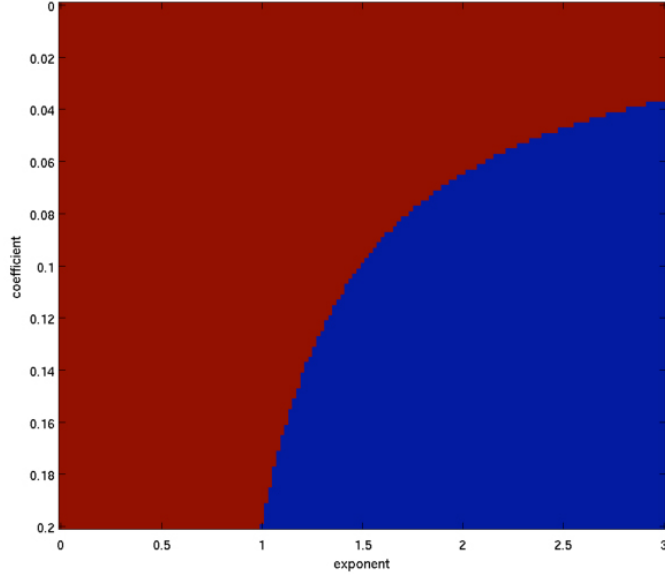


Figure 4: Outcome of species competition in a turbulent environment, parameterized by the values of the exponent σ and the coefficient s_0 . Red (in the upper left area) indicates dominance of the larger species with $a = 1.4$, blue indicates dominance of the smaller species with $a = 0.7$. Cell radii are in non-dimensional units.

and is not necessarily universal.

The growth of phytoplankton populations, thanks to nutrient consumption, is balanced by plankton mortality, m , and plankton sinking, $s(a)$. In the phytoplankton competition model (5), the mortality rate m is assumed to be independent of phytoplankton size, unlike the sinking term. In the absence of turbulence and assuming spherical particles, the settling velocity of an individual phytoplankter can be derived from Stokes law obtaining $s(a) = s_0 a^2$; this form was assumed in [3] with $s_0 = 2$. With this choice, it was found that the most favoured species is always the smaller one, and that there should be a natural tendency towards dominance of smaller phytoplankton species. In this view, the higher efficiency in nutrient uptake of the larger species is not enough to balance their faster sinking rate, leading to a dominance of the smaller organisms.

In reality, the sinking rate depends on the level of turbulence, which can alter the above result. In a subsequent study, Demonte et al [2] kept all parameter values as in [3] but assumed the sinking rate to be proportional to a power of the phytoplankton cell radius, a , through a simple relationship

$$s(a) = s_0 a^\sigma \quad (7)$$

where s_0 is the coefficient and σ is the exponent. The motivation of this choice is that turbulence can alter the simple dependence of sinking velocity on radius observed in still fluid. What is found in this case is that the outcome of species competition depends on the properties of turbulence, that is, on the assumed values of s_0 and σ . Figure 4

shows the outcome of competition for two species with (non-dimensional) radius 0.7 and 1.4, respectively. For the parameter values chosen in [3], the smaller species is favoured. However, by varying the values of σ and/or s_0 , one can get the opposite result. Even by keeping $\sigma = 2$ but varying the coefficient s_0 , one can obtain dominance of the larger species. This is consistent with the view that the outcome of competition of phytoplankton species with different size depends on the properties of the turbulent environment, and it seems to further confirm Margalef's view.

4 Vertical velocities in mesoscale flows

In the previous sections we have seen that turbulent suspension can be an important mechanism in plankton dynamics. We can ask whether these effects are visible also on scales larger than those of homogeneous and isotropic turbulence: for example, whether they can play a role at the ocean mesoscales where fronts, vortices and waves dominate the flow, as discussed in the first lecture.

Although a final answer is still missing, an important point concerns the structure and intensity of the vertical velocity field at the mesoscales. If there are strong and organized vertical velocities, then these can also induce suspension (in upwelling regions) and rapid sinking (in downwelling areas), thus affecting plankton dynamics, besides their role in determining the nutrient input to the euphotic layer.

In proximity of fronts, vertical velocities can be very intense, creating a complex pattern of upwelling and downwelling. However, other mesoscale structures can also play a role: coherent vortices, in particular, have been shown to be associated with a complicated pattern of strong vertical velocities [4]. In their study, Koszalka et al. have considered a primitive equation model, using the ROMS ocean model, with doubly periodic boundary conditions and idealized surface forcing. The simulations show the emergence of coherent vortices, similarly to what happens in two-dimensional or quasi-geostrophic (QG) turbulence. The horizontal dynamics and transport properties of this flow are not too dissimilar from what happens in QG turbulence, suggesting that approaches based on simple QG models capture a relevant portion of the horizontal dynamics. However, the vertical velocities associated with the vortices in the primitive equation setting can be very strong, at variance with the situation found for QG vortices.

Figure 5a shows a slice of the vorticity field in one of the primitive equation simulations discussed in [4], and figure 5b shows the vertical velocity field associated with one of the vortices. The vertical velocities in proximity of the vortex are very intense, and can lead to various consequences for the marine ecosystem, ranging from enhanced nutrient input to the suspension of phytoplankters in the upwelling areas and their rapid sinking in the downwelling regions.

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