Sinking phytoplankton in a turbulent flow

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Received __________________; accepted __________________
Most phytoplankton species are heavier than water, thus they sink. As numerous earlier work did, we focus on the question of how and when these sinking species manage to persist. It is known that the main factors which determine the dynamics of phytoplankton species are the self-shading of phytoplankton individuals and the redistribution of phytoplankton caused by the turbulent flow. While turbulent structures and the finite size of plankton individuals are neglected in earlier models, we have taken both these effects into account. Since the dynamical problem is extremely complex, we modelled the turbulent flow by point vortices, and solved it by individual based simulation of the plankton components. We made a series of simulations with a set of biologically relevant parameters. In accordance with experimental observations and earlier models we found stable population density distributions with a peak near the water surface, however the population density fluctuations are markedly higher than in earlier models in this state due to the hydrodynamical fluctuation. If the population is located in the upper layers initially, then we find that both weak and very intense turbulent diffusion can favor a phytoplankton bloom in deep waters. If, however, the population is below a critical level initially, we find that an intermediate level of turbulence can support the persistence of phytoplankton in deep waters.

Subject headings: light limitation, population dynamics, phytoplankton bloom, sedimentation, turbulence
1. Introduction

Phytoplankton as photosynthetic organisms require light to survive. What is more, light is often the limiting factor for phytoplankton production (Mitchell et al. 1991; Colijn & Cadée 2003). It is thus surprising that the bulk of phytoplankton species have a higher density than water: they sink (Hutchinson 1967; Smayda 1970; Reynolds 1984). Consequently, the following questions arise naturally: How do these species ensure their persistence? What kind of mechanisms help the sinking phytoplankton to remain near the well lit water surface? What kind of physical circumstances favor for the phytoplankton bloom?

Since the flow is typically turbulent in the upper mixed layers of lakes and oceans, its role is crucial on the sedimentation velocity, or more generally on the population dynamics. Consequently, the problem of sinking phytoplankton, which has been investigated for decades (Riley et al. 1949; Sverdup 1953; Shigeshada & Okubo 1981; Huisman et al. 1999; Huisman et al. 2002), emphasizes the role of hydrodynamical mixing in the population dynamics of sinking phytoplankton. The classical papers neglect numerous important parts of the dynamics, such as the light dependence of phytoplankton growth (Riley et al. 1949), and the non-uniform phytoplankton profile that varies with depth as a result of turbulent diffusion and sinking (Sverdup 1953). A more recent work by Huisman et al. 2002 take self-shading of phytoplankton, turbulent mixing and sinking into consideration in a comprehensive two dimensional model which leads to an ordinary differential equation for the steady state phytoplankton density. They assume phytoplankton individuals to be infinitesimally small particles, and turbulence is only taken into account through an enhanced diffusion characterized by a single parameter, the vertical turbulent diffusivity. However, turbulent flows have characteristic vortex structures, and phytoplankton individuals have a finite size, thus they interact with the
flow in the sense that they do not acquire the fluid velocity instantaneously. We might think that these details can be neglected, but both theoretical and numerical studies (Maxey 1987b; Wang & Maxey 1993; Wereley & Lueptow 1999) show enhanced sinking of finite size particles in turbulent flows. A recent experiment by Ruiz et al. (Ruiz et al. 2004) measures the sinking velocity of different plankton species at various levels of turbulence, and finds that the settling velocity increases with turbulence. They conclude that turbulence does not enhance the presence of phytoplankton in the well-illuminated water surface, thus they challenge the view of the positive role of turbulence in preventing phytoplankton from sinking. They emphasize that upwellings have a crucial role in balancing the sinking of heavier cells (Ruiz et al. 2004; Rodriguez et al. 2001). This experiment only reinforces what is known from theoretical and numerical studies (Wereley & Lueptow 1999): the vortex structure of turbulence and the finite size of sinking particles make particles move downwards more than upwards. Thus, the phenomenological description used by earlier studies neglects essential characteristics of the phenomenon.

It is natural to describe the advection of finite size particles on an individual basis. The equation of motion for small finite size particles heavier or lighter than the ambient fluid has been known since the work of Maxey and Riley (Maxey & Riley 1983) (see also (Auton et al. 1988)). Their approach has lead to a series of experimental and theoretical investigation of finite size particle motion under different conditions (for reviews see (Michaelides 1997; Magnaudet & Eames 2000), for a few recent examples, see (Mordant & Pinton 2000; Falkovich et al. 2005) and (Bec et al. 2005), respectively). For the advection of plankton individuals we are going to use this equation. The difficulty with inertial particles is that they tend to strongly accumulate in certain regions of the flow (Bec et al. 2005; Falkovich et al. 2005), and thus a continuum description (based on the density of the particles) does not exist in general, or if it exists in a certain limit, the equations of motions are rather involved. This is why we follow and individual based
model, which, of course, has its own numerical limits since the number of particles cannot be chosen to be realistically high.

Our aim in this paper is to study the dynamics of light-limited sinking phytoplankton by a two-dimensional flow model where the vortex structure of turbulence and the irregular sinking of the individual particles are taken into account. We point out that the fluctuation in the plankton density is pronounced in our hydrodynamics-based model in contrast to the mean field model of Huisman et al. (Huisman et al. 2002) where fluctuations are suppressed. We faithfully describe the enhanced sinking of plankton and show that in spite of this, a dynamical steady state can evolve. Individual particles all sink on average and die, but on the level of the population an equilibrium can set in, due to the enhanced birth in the well-lit upper layers. The possibility of long term persistence of phytoplankton is studied as a function of the initial position of the population, the water depth and the turbulence level. Since long term persistence of phytoplankton in the upper layers is necessary for bloom (a rapid temporal increase in population density), we study the necessary conditions for bloom of sinking phytoplankton (Huisman et al. 2002).

In the next Section we formulate the model on three different levels. Then, in Section 3 we present a realistic choice for the parameters. The numerical results are presented in Section 4, where the deep-water distribution, the dependence on the turbulence level and on the fluid depth is displayed, along with the condition for survival in the two-dimensional parameter space. The last section contains our conclusions. In the appendix we present the Maxey-Riley equations and show that they reduce to the form used in the bulk of the paper. These equations are valid when the particle size is very much smaller than the characteristic length of the flow.
2. The model

Our model contains three levels: (i) a particular hydrodynamical representation of the chaotically time dependent irregular fluid flow in the vertical plane in terms of point vortices, (ii) the individual modelling of the advection of particles in this fluid flow, and (iii) the individual modelling of a single phytoplankton species whose growth rate is determined by the light intensity and the shielding effect of the plankton individual above the given depth, in the spirit of the formulation by Huisman and coworkers (Huisman et al. 1999; Huisman et al. 2002; Huisman et al. 2006)

2.1. The flow

The flow field $u(x, z, t)$ generated by $N$ point vortices moving in the vertical plane has the velocity components

\[
\begin{align*}
    u_x &= -\sum_{j=1}^{N} \frac{K_i(z - z_j(t))}{r_j^2}, \\
    u_z &= \sum_{j=1}^{N} \frac{K_i(x - x_j(t))}{r_j^2},
\end{align*}
\]

(1)

where $(x_j(t), z_j(t))$ is the instantaneous location of vortex $j$ of strength $K_j$, given by the solution of an ordinary differential equation (Newton 2001; Kundu 1990), and $r_j(t) = \sqrt{(x - x_j)^2 + (z - z_j)^2}$ represents the distance between point $(x, z)$ and the vortex.

For simplicity we consider $N = 5$ point vortices of the same strength $K_i \equiv K$ to move in a square of size $L$. The flow field is extended periodically in both directions. Since the dynamics of $N > 2$ vortices is already chaotic (Newton 2001), the velocity field of 5 vortices is in general irregularly time-dependent over arbitrarily long time intervals, and is in this respect a good model of turbulence. Since a chaotic time-dependence is known to lead to a diffusive spreading over long times (Ott 1993), $K$ can be considered to be the analog of the vertical turbulent diffusivity. $K$ is thus the basic fluid dynamical parameter of our model, the 'strength of turbulence'.
To use dimensionless quantities, we choose a time unit \( T \), and measure distance in units of \( L \). The dimensionless equations are of the same form as (1), but with the vortex strengths replaced by the dimensionless parameter

\[
\kappa = \frac{KT}{L^2}.
\]

(2)

This is a dimensionless measure of the strength of turbulence. Since the order of magnitude of the velocity is

\[
U = \frac{K}{L} = \frac{\kappa L}{T},
\]

(3)

the velocity field is measured in these units from here on.

2.2. Advection dynamics in the limit of very small particles

The equation of motion of a small rigid spherical particle of radius \( a \) in a homogeneous fluid is given by the Maxey–Riley equation (Maxey & Riley 1983; Auton et al. 1988) (for details see Appendix). For very small particles with a density different from the density \( \varrho_f \) of the fluid, the dimensionless Maxey–Riley equation simplifies to

\[
\dot{\mathbf{r}} = \mathbf{u}(\mathbf{r}, t) - W\mathbf{n},
\]

(4)

where \( \mathbf{r} \) is the location of the particle, \( \mathbf{u}(\mathbf{r}, t) \) is the undisturbed velocity field of the fluid in the absence of the particle, and \( \mathbf{n} \) is a unit vector pointing upwards. The quantity

\[
W = \frac{w}{U} = \frac{2 a^2 g L \Delta \varrho}{9 \nu K \varrho_f}
\]

(5)

represents a dimensionless sinking velocity (in a fluid at rest) where \( w \) is the Stokesian (dimensional) sinking velocity. Here \( g \) is the gravitational acceleration, \( \nu \) is the kinematic viscosity of the fluid, and \( \Delta \varrho > 0 \) represents the density difference between the particle and the fluid. The Stokesian sinking velocity is the velocity \( w \) for which the Stokes drag
6\pi a v f w \text{ compensates the buoyancy-reduced weight: } 4a^3\pi \Delta \rho g/3. \text{ Equation (4) expresses the fact that the horizontal advection dynamics is close to that of an ideal, point particle, augmented by sinking.}

After estimating the typical parameters in section 3, and comparing the behaviour of Eq. (4) and that of the original Maxey–Riley equation (Eq. (11)) in the Appendix, we conclude that Eq. (4) is a faithful model for phytoplankton.

This equation (and the vortex dynamics equations) were solved by means of a fourth order Runge-Kutta method of fixed time step (Press et al. 1992). Depending on the strength of turbulence, the time step was selected in the interval \( dt \in (4 \cdot 10^{-5}, 2 \cdot 10^{-4}); \) smaller values of \( dt \) correspond to larger values of \( \kappa. \)

The advection dynamics is periodic in the horizontal direction. This expresses that the flow is assumed to be translationally invariant in the \( x \)-direction on average. In the vertical direction we consider \( M \) cells of unit size. Both along the upper edge of the uppermost cell \((i = 1)\) and along the lower edge of the lowermost \((i = M)\) cell the following boundary condition is applied: if a particle does cross the boundary, it is shifted back to the boundary with the same \( x \) coordinate and horizontal velocity component as it would take on outside the boundary. We thus do not apply an elastic reflection at the boundary, which would be unrealistic, instead we just take away the particle’s vertical momentum and let it move along the boundary. The local flow will advect it anyhow upwards from the bottom or downwards from the top of the water after some time.

\section*{2.3. The biological dynamics}

The main factors which determine the reproduction success of an individual is the local light intensity which depends on the height of the water-column above the individual and
the self-shielding effect of phytoplankton individuals. This is taken into account by writing
the light intensity at height $z < 0$ within cell $i$ as

$$I(z, t) = I_0 \exp\left(- \sum_{j=i-1}^{i} k N_j(t) + k_{bg} z\right),$$

where $I_0$ represents the incident dimensionless light intensity, $z < 0$ is the dimensionless vertical coordinate. Within cell $i$ variable $z$ fulfills $i - 1 < -z < i$. $N_j(t)$ is the number of plankton individuals in cell $j$ at time $t$, $k$ and $k_{bg}$ are the light absorption coefficients of the phytoplankton solution and of the water, respectively. The number $N_j(t)$ is determined numerically after each reproduction cycle. The birth of plankton individual takes place at integer multiples of a biological time unit $\tau$ with probability

$$P_b(z, t) = \frac{I(z, t)}{I(z, t) + H},$$

where $H$ is a half-saturation constant, as in (Huisman et al. 2002; Huisman et al. 2006).

The death rate, denoted by $P_d$, is constant. The newly born individuals are placed randomly with uniform probability within a small square of edge size $\varepsilon = 2 \cdot 10^{-3}$ around the mother individual, (with the velocity of the mother).

As a first insight in how the model works, we show in Fig 1 the spreading and increase of a population of $N_0 = 10000$ individuals, initially distributed uniformly within cells $i = 2-4$. The final number of living organisms at time $t = 34$ is $N(t) = 2714$.

3. Parameters

A fluid layer of $4 - 100$ m is considered, corresponding to the mixing layer in the ocean, or the full depth of a lake. Consequently, the size of the cells is taken between $L = 1$ and $L = 5$ meters. The number of cells will be chosen as $M \in (4, 100)$. The time unit is taken to be $T = 4 \cdot 10^4$ s, which is about 11 hours.
Fig. 1.— Time evolution of a sinking plankton population. The snapshots are taken in panels a) to f) at dimensionless time instants $t = 0, t = 5, t = 10, t = 15, t = 20, t = 25$. Parameters are $M = 100$, $W = 0.2$, $\kappa = 2$ and the other parameters as in Table 1.

The range of relevant vertical turbulent diffusivities is between $10^{-5}$ and $10^{-2}$ m$^2$/s (King & Devol 1979; Law et al. 2001). The dimensionless turbulence strength (2) is then obtained with $L = 2 - 5$ m in the range $\kappa = 0.01 - 100$. The average Stokesian sinking velocity of phytoplankton is on the order of 1 m per day (Huisman et al. 2002), i.e., $w \approx 10^{-5}$ m/s. The dimensionless sinking velocity (5) is $W = wT/(\kappa L) = 4 \cdot 10^{-1}/\kappa$ for $L = 1$ m. We therefore vary $W$ between 4 and 0.001.

The biological time unit is $\tau = 0.1$, corresponding to about 1 hour. The light absorption parameters are taken as $k_{bg} = 2.5 \cdot 10^{-2}$ and $k = 10^{-5}$. The latter implies that $10^5$ particles generate an additional factor $1/e$ to light absorption. This factor was chosen because the realistic maximal number of plankton individuals is on the order of
in our numerical simulations. Thus the effect of light absorption and phytoplankton self-shading is on the same order, which corresponds to the assumption of Huismann at el 2002 (Huisman et al. 2002). The incident intensity is chosen to be $I_0 = 0.08$, the half-saturation constant in (7) is taken as $H = 0.9$. Thus the maximal birth probability is $0.08/(0.08 + 0.9) = 0.0816$. We choose $P_d$ to be 0.0813 to keep the maximal population size on a computationally tolerable level.

Table 1 summaries the parameter ranges investigated. It also contains an estimate of the parameters $R$ and $A$ characterizing the full Maxey-Riley equations presented in the Appendix. The density of plankton is a few percent higher than that of the water, therefore the density ratio (10) is practically $R = 2/3$. The inertia parameter $A$ (12) depends quadratically on the size of the particles, and covers therefore a very broad range. Since the phytoplankton radius is roughly between 10 $\mu$m and 100 $\mu$m, we obtain that the corresponding inertia parameter $A$ lies between $10^3$ and $10^9$.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>values</th>
</tr>
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<tbody>
<tr>
<td>Flow: $\kappa$</td>
<td>$0.01 - 100$</td>
</tr>
<tr>
<td>$M$</td>
<td>$4 - 100$</td>
</tr>
<tr>
<td>Advection: $R$</td>
<td>$2/3$</td>
</tr>
<tr>
<td>$A$</td>
<td>$10^3 - 10^9$</td>
</tr>
<tr>
<td>$W$</td>
<td>$4 - 10^{-3}$</td>
</tr>
<tr>
<td>Biology: $I_0$</td>
<td>$0.08$</td>
</tr>
<tr>
<td>$k$</td>
<td>$10^{-5}$</td>
</tr>
<tr>
<td>$k_{bg}$</td>
<td>$0.025$</td>
</tr>
<tr>
<td>$H$</td>
<td>$0.9$</td>
</tr>
<tr>
<td>$P_d$</td>
<td>$0.0813$</td>
</tr>
</tbody>
</table>

Table 1: The range of dimensionless parameters investigated in the model
4. Results

4.1. Populations in deep waters

Eq. (4) has been solved with the biological activity as described in Section 2.3 for a wide range of parameters in a time interval corresponding to several months. Since practically no light penetrates in deep waters, a depth $M \geq 80$ corresponds to an infinitely deep water layer. We start reviewing the results with populations initiated at different depths.

With the chosen light intensity $I_0$, the population does not die out in weakly turbulent flows if the initial population starts in the uppermost cells. The instantaneous number $N(t)$ of the population oscillates around the mean with quite large fluctuations. These fluctuations are due to the hydrodynamical flow which is chaotic in time. Consequently, the flow changes all the time, and only long-time averages can be defined. Note that this steady state is in a kind of dynamical equilibrium: plankton individuals continuously sink in deeper water layers but this loss is compensated by the birth of new individuals due to light. With other initial population sizes the same steady state has been found to set in, in the sense that the long-time averages are identical (see Fig. 2b). A characteristic feature of these profiles is the existence of a pronounced local maximum, a few cells below the water surface. Fig. 2 also shows that without any illumination (thus without the chance of reproduction) individuals would simply sink to any depth.

Local upwellings can push individuals to the upper layers (Ruiz et al. 2004), from which they spread horizontally by the horizontal advections and mixing. The choice that individuals are initiated in the upper layers is based on this scenario. Since upwellings transport not only the phytoplankton individuals but the dissolved nutrients too (nitrogen, phosphorus, silicate), light limited phytoplankton density is typically correlated with
upwellings. Thus we mainly focus on this initial condition in the following. Absence of upwellings in the vicinity of the observation area implies that individuals are in the deeper layers initially. Such initial conditions will also be investigated. We only mention here that if the population is below a threshold depth initially, then population dies out in weakly and strongly turbulent flows, but it can survive if turbulence is of an intermediate level. This observation is demonstrated later in subsection 4.3, where the effect of turbulence is studied at finite water depths.

Fig. 2.— Steady population in deep waters. a.) Location of plankton individuals (black dots) and non-living particles (grey dots) vs. time (in the range $0 < t < 200$ dimensionless time units, $\kappa = 0.2$). b.) Normalised profile $n(z, t) = N_j(t)/N(t)$, $z = j/2$ at time $t = 20$ and $t = 100$. c.) Particle number $N(t)$ vs. time (continuous and dashed line for various initial conditions $N_0 = 13500, 15000, 16500$ and 20000, respectively. Parameters are $\kappa = 0.2$, $W = 0.002$, $M = 100$ and the others as in Table 1.

4.2. The effect of turbulence strength in deep waters

The increase of the turbulence level enhances sedimentation as mentioned earlier. Consequently the average location of the 'centre of mass' of the population sinks upon taking larger values of $\kappa$. For sufficiently strong turbulence, the population survives over
a finite (occasionally long) period, but eventually it dies out (Fig. 3). It is remarkable, however, that the normalised profile remains practically the same over a long period of time.

Fig. 3.— Decaying population in deep waters. a.) Location of particles (black dots) vs. time (in the range $0 < t < 200$ dimensionless time units). Particle number $N(t)$ vs. time (continuous line), initial condition $N_0 = 15000$ (dashed line). b.) Normalised profile $n(z, t) = N_j(t)/N(t)$, $z = j/2$ at time instants $t = 10, 25, 100$. Parameters are $\kappa = 2$, $M = 100$, $W = 0.002$ and those of Table 1.

4.3. The effect of turbulence strength at finite water depth

For a fixed strength of the turbulence the plankton population might die out, but the same population becomes steady in a shallower layer of fluid where the lower boundary has a stirring up effect and helps to maintain efficient mixing throughout the layer. Fig. 4 (a–c.) illustrates that at a fixed finite depth, a weak increase of the turbulence level might lead to a decaying population, which however, becomes stationary by a further increase
of the turbulence level. Simultaneously, the profile loses its local maximum and becomes practically homogeneous at stronger turbulence levels (Fig. 4 c., f.).

The situation is qualitatively the opposite if the population is initially in deeper layers. A continuously decaying population leads to extinction at low (Fig. 4 d.) and at high (Fig. 4 f.) turbulence, while an intermediate level of turbulence can maintain a stable population for a long time (Fig. 4 e.). Then the maximum of the population density can be found typically at a lower water level than in the cases when population is present initially at upper layers and turbulence is weak (Fig. 4 a.).

Since only an intermediate level of turbulence is able to mix individuals up to the well-lit region, the qualitatively different options are the same both in finite (Fig. 4. (d.–f.)) and in infinitely deep waters (subsection 4.1.) if the initial population is below a threshold level. At high turbulence, individuals are mixed homogeneously within a few time steps, thus population dynamics is qualitatively independent of the initial position.

**4.4. Condition for steady populations in the parameter space**

We have seen in the previous subsection that the initial position of the population can have a crucial effect on the long term steady state. Similarly we have shown that the water depth and the level of turbulence are both crucial factors in determining phytoplankton persistence. In this section we summarise our findings concerning the effect of these physical factors. For populations that are initially in the upper layers, we find the chart of Fig. 5 which indicates the condition for survival. To obtain a more detailed picture, we also determined the average lifetime for decaying populations, and the average population number for surviving populations indicated by shading in Fig. 5.

According to Fig. 5, for shallow waters with $M > 8$ phytoplankton persists typically at
Fig. 4.— Populations in waters of finite depth at the different strength of turbulence and for initial conditions in upper and lower layers. The quantities shown are: Location of plankton particles (black dots) vs. time (in the range $0 < t < 200$ and 300 dimensionless time units), particle number $N(t)$ vs. time (continuous line) and averaged, normalised profiles $n(z, t) = N_j(t)/N(t)$, $z = j/2$ over a time range marked with gray bars on the time axis. Left column: Population is initially in the upper region ($j = 2, 3, 4$). Turbulence increases from top to bottom ($\kappa = 0.1, 2.0, 20$ for a.), b.) and c.), respectively). Right column: Population is initially in deeper layers ($j = 5, 6, 7$) at $\kappa = 0.02, 0.2, 2.0$ respectively, for d.), e.) and f.).

$M = 8$, $W = 0.002$, while other parameters are as in Table 1.

Low and high levels of turbulence, thus the results shown in Fig. 4. are not the consequence of fine tuning of parameters. The case of very low turbulence ($\kappa < 0.1$) needs some
Fig. 5.— Properties of populations initiated in the upper layers summarized in the \((M \kappa)\) parameter space. The bold line divides the regions of steady and of decaying (and eventually extinct) populations obtained in simulations of \(t = 200\) units. White (black) frame around the boxes mark persistence (no persistence). The shading indicates the average population number (average lifetime), with darker colour implying higher population numbers (average lifetime). Parameters \(W = 0.002\). The other parameters of each simulation as in Table 1.

In this case, while the population’s centre of gravity and the population density decrease continuously but slowly, living plankton individuals remain present for 200 or 300 units of time. Since the time unit is about 11 hours, populations are practically persistent over months. Naturally, the asymptotic state is population extinction, but it would take years to reach this equilibrium.

5. Discussion and Conclusion

Earlier studies have determined four characteristic points separating persistence and no-persistence regions when this phenomenon is investigated as a function of water depth and turbulent diffusivity in the continuum model (cf. the schematic diagram of Fig. 6). The explanation of the concepts of compensation depth, critical depth and ‘maximal’ and
Fig. 6.— Schematic plot of the persistence and no persistence regions vs water depth and turbulent diffusivity, according to Huisman et al. 2002.

‘minimal’ turbulence, used by Huisman et al. (Huisman et al. 1999; Huisman et al. 2002) is as follows:

- Compensation depth: The depth where death and birth rates are equal assuming that there is no self-shading (e.g. there is only one individual at this depth).

- Critical depth: The depth where the depth-integrated birth and death rates are equal when diffusion mixes the population uniformly throughout the water column.

- ‘Maximal turbulence’: A threshold value of turbulence below which the population growth overbalances the turbulent diffusivity, that is enough individuals remain in the upper well-lit region of the water. Above this point turbulence disperses individuals in the deeper part of the water, and hence prohibits phytoplankton persistence.

- ‘Minimal turbulence’: The minimal level of turbulence which is enough to prevent sinking of the phytoplankton population. According to this view, turbulent diffusion disperses individuals randomly, thus part of them moves upwards, consequently
a minimal level of turbulent diffusion is needed to maintain persistence in deep waters. (If ‘minimal turbulence’ is not smaller than ‘maximal turbulence’ because of faster sinking of individuals, a single ‘no persistence’ region appears in Fig. 6. Then persistence depends only on water depth (Huisman et al. 2002).)

Comparing our results (Fig. 5) with that of Huisman et al. (Fig. 6), it is clear that our model behaves in a qualitatively different manner. Besides that the shape of the no persistence region is not a rectangle, compensation depth and minimal turbulence are not observed. The absence of minimal turbulence is the following: If turbulence is weak, then convergence to the steady state is slow. Below $\kappa = 0.1$, where the minimal turbulence might be expected to be, we find that population extinction (the convergence to a ”no persistence state”) would take years. Consequently, for $\kappa$ below 0.1 the population remains in the persistent state for months. Because the sinking is so slow in this region, the difference of birth and death events cause a net growth and a long transient state which is observed as persistence on the ecological time scale. The ecological importance of long transients has been emphasized in other context in Hastings (2004). Since phytoplankton persistence is present for every water depth the compensation depth is missing as well. Since earlier works focused only on the steady states of the models e.g. (Huisman et al. 1999; Huisman et al. 2002), they found no persistence regions both above the compensation depth and below the minimal turbulence. We note here that the time scale of biomass duplication is longer in our model than in real biological situations, so this long transient cannot be an artefact because of too fast replication in the model.

If individuals are initially positioned in deep water columns, below a threshold, then birth events cannot overbalance death events for weak turbulence, and consequently extinction is fast (Fig 4 d.). Using this type of initial condition, we really can observe an intermediate level of turbulence where phytoplankton population is persistent (see
discussion at the end of Section 5.3). This threshold below which populations become extinct rapidly for weak turbulence plays the role of the compensation depth. With the parameters used in our model and knowing that by definition \( P_d = P_b \) at the compensation depth, we obtain that the theoretical compensation depth would be between one and two dimensionless length units (cell sizes).

According to the Huisman et al. (2002) model, above the maximal turbulence, the critical depth is independent of the turbulence level (Fig. 6). This is not the case in our system. If population is initiated in the upper layers turbulence increases the maximum value of the critical depth (Fig. 5). The intuitive explanation is that a weaker turbulence is sufficient to move individuals to the well-lit region in less deep waters. If a population persists at a relatively low turbulence level, it has an even better chance to persist at a lower turbulence level.

In waters shallower than the compensation depth, phytoplankton persists independently of the level of turbulence both in the mean field and in our individual based models. Turbulence can only enhance the probability of birth by mixing the individuals up. In deeper waters, the mean field model forecasts that a medium level of turbulence favors the emergence of phytoplankton persistence (Fig. 6). In summary, the situation is more complex in our system: As mentioned earlier, regional upwellings (Rodriguez et al. 2001) can push populations to the upper well-lit region of the water. Then populations are positioned above the compensation depth initially, and a week turbulence is sufficient for the persistence. If water is not too deep, then not only weak but also strong turbulence can facilitate persistence (see Fig. 5 e.g. at \( M = 10 \)). If the population is below the compensation depth initially (because of weak or missing upwelling), then again a medium level of turbulence is favorable for maintaining populations for a long time.
Phytoplankton blooms are a seasonally recurrent transient events controlled by environmental forcing. We have explored conditions under which the long term (much longer than a month) presence of sinking phytoplankton in the upper layers (euphotic layer) is possible. We consider that this prolonged presence of phytoplankton in the upper layers is a necessary condition for bloom. However, we do not investigate how an additional rapid temporal population increase occurs. This process has been studied in other models which emphasize the periodically forced nutrient-phytoplankton interaction in generating blooms (Huppert et al 2002; Huppert et al. 2005), while phytoplankton-zooplankton interaction seems to be important in other cases (Stone & Berman 1993; Franke et al. 1999).

Incident light intensity ($I_0$), which was set up to be constant in our model varies periodically in most phytoplankton ecosystems. Furthermore, diffusion is not constant along the vertical direction, water is often stratified: there is an upper mixed layer and a deeper unmixed layer separated by a thermocline. Similarly to the periodicity in light intensity, many aquatic systems endure recurrent stratification events from year to year (Burshe et al. 1997; Holliday et al. 2006; Jöhnk et al 2008). These effects can easily be built into our model, and will be studied in the near future.

As we have shown, the hydrodynamical flow results in an increased sinking velocity as turbulence becomes stronger. Consequently, our model predicts a role for turbulence in maintaining phytoplankton populations different from that of Huisman et al’s mean field model (Huisman et al. 2002). One can, however, build this effect into the mean field model by assuming that the sinking velocity $v_{sink}$ depends on the strength of turbulence, characterized by the turbulent diffusion coefficient $D$. According to our numerical simulations (Fig. 7) (and the experiments by Ruiz et al (Ruiz et al. 2004)) $v_{sink}$ decreases monotonically with $D$. We found that $v_{sink}$ can be considered as a linear function of $\ln D$, for weak turbulence levels at least.
Our work suggests that the initial position of individuals (that is the presence or absence of upwellings in the vicinity of the studied area) basically determines the role of turbulence in maintaining phytoplankton blooms if the population growth is light limited. If the population is initially in the upper well-lit region then a weak or a strong turbulence promotes the emergence of a bloom. If the population is below this threshold initially, the situation is the opposite: only a medium level of turbulence can maintain sinking populations for a long time.

6. Acknowledgments

This work was supported by the Hungarian Science Foundation (OTKA) under grants T72037. We thank William McKiver for the careful reading of the manuscript.
7. Appendix

In an infinite homogeneous fluid of density $\rho_f$, the equation of motion for the location $\mathbf{r}(t)$ of a small rigid spherical particle of radius $a$ and mass $m_p$, starting from rest at $t = 0$, is given by the Maxey–Riley equation (Maxey & Riley 1983; Auton et al. 1988):

$$m_p \ddot{\mathbf{r}} = m_f \frac{D\mathbf{u}}{Dt}(\mathbf{r}, t) + \frac{1}{2} m_f \left( \frac{D\mathbf{u}}{Dt}(\mathbf{r}, t) - \ddot{\mathbf{r}} \right) + (m_p - m_f) \mathbf{g} - 6\pi \nu \rho_f (\dot{\mathbf{r}} - \mathbf{u}(\mathbf{r}, t)), \quad (8)$$

where $\mathbf{u}(\mathbf{r}, t)$ is the undisturbed velocity field of the fluid in the absence of the particle, $D\mathbf{u}/Dt = \partial \mathbf{u}/\partial t + (\mathbf{u} \cdot \nabla)\mathbf{u}$ is the usual hydrodynamical time derivative of the velocity following a fluid element, $m_f$ is the mass of the fluid displaced by the sphere, and $\nu$ is the kinematic viscosity. The force terms on the right hand side represent the hydrodynamical force, the added mass contribution, the buoyancy corrected weight, and the Stokes drag. The equation is valid for small relative velocities: $\dot{\mathbf{r}} - \mathbf{u}$. The fact that the vorticity diffuses away from the particle is taken into account by the appearance of a history term, which we assume to be negligible (Michaelides 1997).

Using that for spherical particles $m_{p(f)} = 4a^3\pi \rho_{p(f)}/3$, we find

$$\ddot{\mathbf{r}} = \frac{3}{2} R \frac{D\mathbf{u}}{Dt}(\mathbf{r}, t) - \frac{9}{2} R \frac{\nu}{a^2} (\dot{\mathbf{r}} - \mathbf{u}(\mathbf{r}, t)) + \frac{\rho_p - \rho_f}{\rho_p + \rho_f/2} \mathbf{g}, \quad (9)$$

where $\mathbf{g}$ is the vector of the gravitational acceleration, $\rho_{p(f)}$ represents the particle (fluid) density and

$$R = \frac{2\rho_f}{\rho_f + 2\rho_p} \quad (10)$$

is a density ratio.

Measuring length and velocity in units of $L$ and $U$ (see (3)), respectively, a dimensionless advection equation is obtained as

$$\ddot{\mathbf{r}} = \frac{3}{2} R \frac{D\mathbf{u}}{Dt}(\mathbf{r}, t) - A (\dot{\mathbf{r}} - \mathbf{u}(\mathbf{r}, t)) - AW \mathbf{n}. \quad (11)$$
Here \( \mathbf{n} \) is a unit vector pointing upwards,

\[
A = R \frac{9}{2} \left( \frac{L}{a} \right)^2 \frac{\nu}{K} = R \frac{9}{2} \frac{\nu T}{\kappa},
\]

(12)

is the inertia parameter and \( W \) has been given by (5).

As \( A \to \infty \), we expect a convergence of the phytoplankton dynamics based on (11) towards that based on (4). This is illustrated by Fig. 8 which shows the number of plankton individuals as a function of time for an increasing sequence of the inertia parameters \( A \), and the corresponding plankton profiles. One can easily check that for large \( A \) the correction to Eq. (4) is on the order of \((3R/2 - 1)/A\). Since the density of phytoplankton is higher only with a few percents than the density of water, \((3R/2 - 1) \approx 1/100\), and the correction is about \(1/(100A)\) which is less than \(10^{-5}\) in our case. Thus, both numerical and theoretical evidences indicate that Eq. (4) is a faithful model of the advection of phytoplankton, on length scales larger than 1 meter.

![Fig. 8.— Time evolution of plankton populations for increasing inertia parameters. a.): particle number \( N(t) \) vs \( t \), b.): normalised profile \( n(z, t) = N_j(t)/N(t), z = j/2 \) at time \( t = 6 \). The inertia parameters are \( A = 200, 600, 1400, 2200 \) (gray lines), \( A = \infty \) (black line). Results for finite \( A \) are solutions of (11), while that for \( A = \infty \) are obtained from (4). Other parameters are \( M = 100, W = 0.2, \kappa = 1.0, P_d = 0.08 \) and those of Table 1.](image)
REFERENCES


