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Residence time and exposure time of sinking phytoplankton in the euphotic layer

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ABSTRACT

The residence time of a sinking particle in the euphotic layer is usually defined as the time taken by this particle to reach for the first time the bottom of the euphotic layer. According to this definition, the concept of residence time does not take into account the fact that many cells leaving the euphotic layer at some time can re-enter the euphotic layer at a later time. Therefore, the exposure time in the surface layer, i.e. the total time spent by the particles in the euphotic layer irrespective of their possible excursions outside the surface layer, is a more relevant concept to diagnose the effect of diffusion on the survival of phytoplankton cells sinking through the water column.

While increasing the diffusion coefficient can induce both a decrease or an increase of the residence time, the exposure time in the euphotic layer increases monotonically with the diffusion coefficient, at least when the settling velocity does not increase with depth. Turbulence is therefore shown to increase the total time spent by phytoplankton cells in the euphotic layer.

The generalization of the concept of exposure time to take into account the variations of the light intensity with depth or the functional response of phytoplankton cells to irradiance leads to the definition of the concepts of light exposure and effective light exposure. The former provides a measure of the total light energy received by the cells during their cycling through the water column while the latter diagnose the potential growth rate.

The exposure time, the light exposure and the effective light exposure can all be computed as the solution of a differential problem that generalizes the adjoint approach introduced by Delhez et al. (2004) for the residence time. A general analytical solution of the 1D steady-state version of this equation is derived from which the properties of the different diagnostic tools can be obtained.

1. Introduction

The identification of the characteristic timescales of biological systems is central for the description and understanding of many aspects of their dynamics. Significant interactions can indeed only take place between processes sharing similar timescales. In particular, biological processes interact with the hydrodynamic processes with similar characteristic timescales which, in turn, imprint their characteristic length scales on the biological structures, a process sometimes called ecohydrodynamic adjustment (e.g. Nihoul and Djenidi, 1991; Delhez, 1998; Ennet et al., 2000; Lessin and Raudsepp, 2007).

Many environmental phenomena strongly depend on hydrodynamic timescales. The occurrence of eutrophication problems can be related to the increased residence time in coastal waters (e.g. Wang et al., 2004; Lillebo et al., 2005; Painting et al., 2007). The ratio of the characteristic timescales of horizontal diffusion and the growth rate of phytoplankton cells is often regarded as an important factor for phytoplankton patchiness (e.g. Malchow, 1996; Martin, 2003). According to many authors, the occurrence and magnitude of deep chlorophyll maxima depend not only on the light level at and below the pycnocline but also on the rate of nutrient replenishment from the deeper layers, the specific growth rate of the phytoplankton cells or the sinking rate of organic matter (e.g. Varela et al., 1994; Ediger and Yilmaz, 1996; Hodges and Rudnick, 2004).

The intensity of the vertical mixing plays a crucial role in the dynamics of primary production. According to the basic Sverdrup theory (Sverdrup, 1953; Lande and Yentsch, 1988; Huisman et al., 1999; Mann and Lazier, 2006), phytoplankton can thrive in the surface layer if the surface mixed layer is shallower than the so-called critical depth. This classical argument can be rephrased in terms of characteristic timescales with the blooming of phytoplankton depending on the ratio of the timescale of vertical mixing vs the net growth rate. If the mixed layer is too deep,

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phytoplankton cells will spent too much time in the darkness and the bloom will not start. On the contrary, cells will be able to develop if they receive enough light energy on average during their mixing through the surface layer. All together, it is important to understand how the hydrodynamics of the surface layer influence the level of irradiance received by photosynthetically active cells during their vertical mixing.

The issue is particularly complex for large phytoplankton species that can sink through the water column. In this case, not only the depth of the mixed layer is important but also the strength and vertical structure of turbulence, the sedimentation rate and the rate of light attenuation with depth also seem critical for the net growth of the phytoplankton cells (e.g. Huisman and Sommeijer, 2002; Huisman et al., 2002).

It is generally believed that turbulence increases the residence time in the surface layer of settling particles and can therefore helps sinking phytoplankton cells to remain for a longer time in the euphotic layer. This statement is, however, seldom supported by analytical proofs or numerical demonstrations. In previous studies, apparently conflicting conclusions were even presented by various authors (e.g. Lande and Wood, 1987; Maxey, 1987; Fung, 1993; Wang and Maxey, 1993; Ruiz, 1996; Franks, 2001; Deleersnijder et al., 2006a; Ross, 2006).

In this context, the aim of this manuscript is to use the concept of exposure time (e.g. Monsen et al., 2002; Delhez, 2006; Wolanski, 2007) to shed new light on the issue of the influence of turbulence on the time spent by sinking phytoplankton cells in the euphotic layer. In the last section, the concept of exposure time is also generalized to take into account the amount of light energy received by phytoplankton cells during their vertical mixing and provide therefore a better diagnosis of the influence of turbulence and sedimentation rate on the fate of phytoplankton cells in the euphotic layer.

2. Residence time in the euphotic layer

The residence time of a water parcel, of a particle or of a phytoplankton cell in the euphotic layer can be roughly defined as the 'the time taken by this water parcel, particle or phytoplankton cell to leave the euphotic layer' (e.g. Bolin and Rhode, 1973; Takeoka, 1984; Delhez et al., 2004). This concept provides therefore and apparently obvious way to tackle the issue of whether turbulence allows negatively buoyant particles to remain for a longer time in the euphotic layer.

Strictly speaking, each particle has its own residence time. The residence time is of course a function of the depth at which the particle is released and starts its journey. In a turbulent flow, different particles will also follow different paths even if they are released in exactly the same conditions. Therefore, one should speak about the (statistical) distribution of the residence time, reflecting the individual histories of the particles (e.g. Bolin and Rhode, 1973; Takeoka, 1984; Delhez et al., 2004). Alternatively, the mean or any other relevant statistics of this distribution can be used. In the following, as in most previous studies, the focus will be on the mean value of the distribution.

The mean residence time of sinking particles has been evaluated by many authors. While some authors argue that turbulence increases the residence time in the surface layer (e.g. Fung, 1993; Ruiz, 1996; Deleersnijder et al., 2006a), others give the opposite conclusion (e.g. Maxey, 1987; Wang and Maxey, 1993; Franks, 2001). Using a random walk model, Ross (2006) computed the residence time in the surface mixed layer of a 1D vertical model of the water column. His numerical results suggest that turbulence increases the residence time. The opposite effect is, however, observed when a highly simplified representation of the vertical structure is used. Both behaviors are also obtained by Spivakovskaya et al. (2007) using the forward and backward versions of an Îto random walk model (LaBolle et al., 2000).

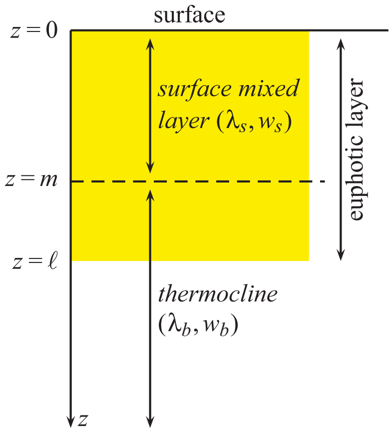

Fig. 1. Schematic description of the two-layer model of the water column with piecewise constant profiles of the diffusivity coefficient and settling velocity.

Lande and Wood (1987) provide a detailed analytical solution of the problem in the context of a two-layer model of the upper ocean. They consider a surface mixed layer of depth m on top of the thermocline and compute the residence time in an euphotic layer that is assumed to be deeper than the surface mixed layer, i.e. $\ell > m$ where ℓ denotes the depth of the euphotic layer (Fig. 1). Although Lande and Wood (1987) also address a more general model of the water column, the most detailed results are given for a simplified two layer model in which the sinking rate and the turbulent diffusivity coefficient take the constant values (w_s, λ_s) and (w_b, λ_b), respectively, in the surface mixed layer and in the thermocline. Since vertical mixing is reduced by stratification, one has in general $\lambda_b \ll \lambda_s$. The different settling velocities w_s and w_b account for the dependency of the vertical settling velocity on the density difference between the sedimenting particle and the surrounding water.

According to Lande and Wood (1987), the expected time for a particle to reach the thermocline starting from a depth $z_0 \le m$ in the mixed layer, i.e. the residence time in the mixed layer, is

$$\theta_m(z_0) = \frac{m - z_0}{w_s} - \frac{\lambda_s}{w_s^2}\left(e^{-z_0 w_s/\lambda_s} - e^{-m w_s/\lambda_s}\right) \tag{1}$$

(the vertical coordinate z is positive downward from the surface). The expected time for a particle to leave the euphotic layer starting at a depth $z_0 \in [m, \ell]$ in the thermocline is

$$\theta_\ell(z_0) = \frac{\ell - z_0}{w_b} + \frac{\lambda_b}{w_b^2}\left(e^{-(z_0-m)w_b/\lambda_b} - e^{-(\ell-m)w_b/\lambda_b}\right) \times \left[\frac{\lambda_s w_b}{\lambda_b w_s}\left(1 - e^{-m w_s/\lambda_s}\right) - 1\right] \tag{2}$$

Finally, the residence time in the euphotic layer for a particle initially located at depth $z_0 \le m$ in the surface mixed layer is the sum of the time needed to reach the bottom of the surface mixed layer and the time to leave the euphotic layer from that depth, i.e.

$$\theta_\ell(z_0) = \theta_m(z_0) + \theta_\ell(m) \tag{3}$$

According to (1), the residence time in the surface layer θ_m is a decreasing function of the diffusivity coefficient λ_s in that layer. Because of diffusion, the particles hit the bottom of the mixed layer earlier than if they were simply advected vertically at the velocity w_s.