



A Lagrangian model for phototaxis-induced thin layer formation

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ABSTRACT

We have developed a Lagrangian model to investigate a potential mechanism based on phototaxis behavior of phytoplankton cells for the formation of thin layers. We assume that all cells follow a time-regulated diurnal vertical migration during which they experience photo-acclimation based on the Denman and Marra (1986) model. When a cell experiences stress due to strong light that exceeds a threshold level, the cell swims downward, away from the light. We applied the Lagrangian model to a one dimensional second order turbulence closure model that generates a realistic surface mixing condition for a given set of physical parameters, such as wind and optical water type. For the chosen swimming velocities and prescribed behavior, we found that, in coastal water type and Jerlov III type, thin layer formation takes place up to 5 m s^{-1} winds, while 10 m s^{-1} winds cause sufficiently strong mixing to prevent the formation of thin layer. We have also investigated the effects of changing the irradiance threshold for the onset of the photoinhibition, the initial density profile and random walk swimming. In conclusion, thin layer formation due to photoinhibition may be possible for a low value of photoinhibition threshold that may occur either due to upwelling or strong light exposure.

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1. Introduction

Phytoplankton thin layers are ubiquitous phenomena in coastal areas around the world. Thin layer thickness typically ranges from a few tens of centimeters to a few meters, in which the phytoplankton concentration is significantly higher than the background concentration (GEOHAB, 2008). The structure is also horizontally extensive. Dekshenieks et al. (2001) mentioned that thin layers may extend horizontally for a few kilometers and persist for several days. Moline et al. (2010) observed that the bioluminescence decorrelation length scale for thin layers in Monterey Bay was about 3 km. During the 2005 Layered Organization in the Coastal Ocean (LOCO) field program, extensive field surveys were conducted in Monterey Bay to study the dynamics of thin layers (Sullivan et al., 2010; Rines et al., 2010; Cheriton et al., 2010; Ryan et al., 2010). Thin layers are important from an ecological point of view. They often occur in stratified water columns and can have special importance related to the dynamics of Harmful Algal Blooms (HABs). The layer structure also plays a role in phytoplankton growth dynamics, sexual reproduction and prey–predator interactions.

In this study we used the following operational definition of a thin layer (GEOHAB, 2008):

- 1) It must have a minimum spatial coherency horizontally.
- 2) The feature must be less than three meters thick measured at half maximum intensity.
- 3) The magnitude of the property must be significantly higher (five times) than background.

This operational definition is slightly different from the original definition suggested by Dekshenieks et al. (2001). In this paper we only deal with a one dimensional model, so condition (1) does not apply here.

Both physical and biological mechanisms contribute to thin layer formation. A shear induced straining mechanism has been proposed as one physically driven process (Franks, 1995; Birch et al., 2008). Buoyancy control is another such mechanism (Alldredge et al., 2002). Dinoflagellate swimming behavior (Kamykowski, 1995) also provides a biological vector that can interact with physical processes. Durham et al. (2009) proposed a combined mechanism between biological and physical processes where cells with gyrotaxis migrate in a sheared layer. Vertical migration of dinoflagellates formed a layer and the formation took place within few hours (Sullivan et al., 2010), demonstrating that migration alone can cause thin layers to form. Stacey et al.

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(2007) discuss the formation and maintenance of thin layers in the presence of turbulent diffusion. Since turbulence broadens layers, convergence mechanisms must exist either physically or biologically. They considered shear, buoyancy and swimming as a potential mechanism. Steinbuck et al. (2009) found that directed swimming could be balanced against turbulent diffusion to maintain a thin layer. The time scale for formation was a few days, and layer breakdown due to turbulent mixing required around 10–100 h. Sullivan et al. (2010) observed a persistent phytoplankton thin layer in Monterey Bay under various biological and physical conditions. Some layers were dominated by non-motile diatoms; on the other hand, some layers were dominated by highly motile dinoflagellate species. Internal waves may accumulate phytoplankton cells at an interface according to an Eulerian model study (Lennert-Cody and Franks, 1999, 2002), but the maximum concentration does not exceed twice the background concentration. Thus this mechanism is unlikely to create a thin layer that requires at least five times higher than the background concentration. An excellent review on thin layer formation mechanisms can be found in Durham and Stoker (2012).

A clear diel vertical migration was observed in an estuary using a fluorescence probe with signals dominated by dinoflagellates (Huon Estuary Study Team, 2000). Both field and laboratory data show that dinoflagellates may change their migration pattern depending on the intensity of light (Kamykowski et al., 1998, 1999). In this case, a cell experiences stress as photoinhibition when it is exposed to too much light. Marshall et al. (2000) reviewed mechanisms and models of photoinhibition. Ault (2000) observed that the marine dinoflagellate *Prorocentrum triestinum* migrated toward the surface during daylight hours until an adequate light level was reached, followed by a shift toward the mid-water column. Clegg et al. (2007) demonstrated that daylight was prominent among several environmental cues that influenced the vertical distribution of phytoplankton, such as dinoflagellates, especially in stratified water columns.

When individual cell movements are important, a Lagrangian model that traces individual cell trajectories is useful for studying the biological–physical coupling problems. Flynn and Fasham (2002) studied the behavior of migratory cells using a numerical model and found that cells remained at a subsurface location by migration, avoiding photoinhibition and behaviorally responded to changes in internal nutrient storage. Ralston et al. (2007) and Ji and Franks (2007) modeled swimming behavior as a function of the internal nutrient storage.

Visser and Thygesen (2003) and O'Brien et al. (2003) provided scale arguments for formation of aggregate due to swimming under the influence of mixing, applying highly idealized mixing conditions. Ross and Sharples (2007, 2008) developed a sophisticated Lagrangian model to study phytoplankton motility in a stratified environment taking both light and nutrient factors into account. They focused on tidally generated turbulence in the bottom boundary layer, but no forcing mechanisms at the surface, e.g. wind stress and convective processes, are integrated in the model. They also fixed the temperature profile by fixing stratification, so that the consequences of mixing are not considered.

In this study, we examine a simple, new potential scenario that may lead to the formation of thin layers driven by vertical migration under the influence of photoinhibition alone using realistic mixing conditions in the upper ocean. Although important previously proposed thin layer formation mechanisms include both light and nutrients (GEOHAB, 2008), the present model isolates a mechanism that focuses on the attenuation of solar radiation and dinoflagellate behavioral responses. This type of behavior represents a subset of thin layers that might occur in oligotrophic water columns. One example would be *Karenia brevis* in the Gulf of Mexico. The formation of biomass maxima

often appear to be related to physical convergence mechanisms (Janowitz and Kamykowski, 2006; Janowitz et al., 2008; Hetland and Campbell, 2007), not in situ growth. Nutrients are, therefore, not the major cause of the biomass accumulation. Under proper photoacclimation circumstances, the biomass peak can react to high incident radiation by migrating away from the surface.

2. Method

We have combined the biological behavior model described by Kamykowski and Yamazaki (1997) and Nagai et al. (2003) with a state-of-the-art one-dimensional water column mixed layer model (General Ocean Turbulence Model, GOTM) described by Umlauf and Burchard (2005) in order to simulate realistic mixing conditions in the upper ocean. We briefly describe the physical model first, and then the adapted biological behavior model is introduced.

2.1. Physical model

With the Boussinesq approximation, the Navier–Stokes equations are simplified into two one-dimensional equations for vertical distribution of momentum when horizontal homogeneity of the hydrographic background is assumed.

$$\frac{\partial U}{\partial t} - fV = \frac{\partial}{\partial z} \left(A_v \frac{\partial U}{\partial z} \right) \quad (1)$$

$$\frac{\partial V}{\partial t} + fU = \frac{\partial}{\partial z} \left(A_v \frac{\partial V}{\partial z} \right) \quad (2)$$

$$A_v = c_\mu k^{1/2} l \quad (3)$$

where the vertical coordinate is taken upward, U is east-west mean velocity component (positive east), V is north-south mean velocity component (positive north), and f is the Coriolis parameter. The eddy viscosity A_v is obtained from the kinetic energy of turbulence k , the integral length scale l and the stability parameter c_μ , calculated by means of the turbulent closure of Canuto et al. (2001) as integrated into a two-equation turbulence closure model described by Burchard and Bolding (2001).

Under the same assumptions, the temperature equation is expressed as

$$\frac{\partial T}{\partial t} = \frac{\partial}{\partial z} \left(K_v \frac{\partial T}{\partial z} \right) + \frac{1}{c_p \rho_o} \frac{\partial I}{\partial z} \quad (4)$$

$$K_v = c'_\mu k^{1/2} l \quad (5)$$

where T is the local mean temperature, I is solar radiation, c_p is the heat capacity, and ρ_o the mean density of water. The vertical eddy diffusivity for heat/tracers K_v is expressed in terms of k , l and stability parameter c'_μ . The solar radiation consists of an infrared part (> 780 nm) and visible part (400 nm $<$ wavelength $<$ 700 nm)

$$I(z) = I_0 \left\{ \text{Rexp} \left(\frac{z}{\lambda_1} \right) + (1-R) \exp \left(\frac{z}{\lambda_2} \right) \right\} \quad (6)$$

where I_0 is the surface value of solar radiation, the absorption length scale for infrared light is λ_1 , for visible light is λ_2 , and R is a weighting factor which was empirically obtained from field data for the contribution of infrared light to solar radiation (Paulson and Simpson, 1977; Zaneveld et al., 1980). Table 1 provides the values we used.

Phytoplankton cells make use of the visible light component, also called photosynthetically active radiation (PAR), to perform

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