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# Effect of mixed layer depth on phytoplankton removal by coagulation and on the critical depth concept

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## ABSTRACT

Coagulation theory predicts that there is a maximum particle concentration that is sustainable in an algal bloom; the critical depth theory of Sverdrup [Sverdrup, H.U., 1953. On conditions for the vernal blooming of phytoplankton. *Journal du Conseil/Conseil International pour l'Exploration de la Mer* 18, 287–295.] predicts a different maximum particle concentration based on light-limitation of phytoplankton growth. This paper uses a model incorporating both coagulation and light-limited algal growth to predict the effect of mixed layer depth and wind velocity on maximum phytoplankton populations. As part of this process, the critical concentration parameter is compared to the results of full coagulation simulations. Including phytoplankton aggregation decreases the maximum phytoplankton concentration but increases the rate of particle export through sedimentation. The results help explain field observations made in the Antarctic Ocean. They also suggest that the accuracy of the critical concentration parameter depends on the average shear rate.

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## 1. Introduction

When Sverdrup (1953) analyzed the role of the ocean's surface mixed layer in the initiation of phytoplankton blooms, he provided a crucial insight into how physical processes can control plant growth. Because light irradiance decreases with depth, increasing the mixed layer thickness can decrease the average photosynthetic rate of each algal cell, but not its respiration rate. Phytoplankton populations increase as long as the total gross primary production over the whole mixed layer is larger than the summed respiration. Deepening the mixed layer can add phytoplankton respiration faster than it adds gross production. The critical depth is the surface mixed layer thickness for which integrated gross production equals integrated respiration; it depends on phytoplankton concentration. Any additional deepening of the mixed

layer makes net production negative and prevents the phytoplankton population from increasing. For a spring bloom to occur, the mixed layer depth must be shallower than the critical depth.

The critical layer concept has achieved such an important role in the consciousness of biological oceanographers that it has been the subject of cautionary notes (e.g., Smetacek and Passow, 1990) as well as vigorous defenses (e.g., Platt et al., 1991). While usually interpreted in terms of predicting a minimum mixed layer depth that allows an algal bloom, it can also be interpreted to predict the maximum phytoplankton concentration possible for a given mixed layer thickness (e.g., Mitchell et al., 1991). More recently, mixed layer limitation has also been invoked to describe the limitation of biomass concentration placed on the bloom resulting from an iron fertilization experiment (de Baar et al., 2005; Boyd et al., 2007).

Coagulation has emerged as another physical process which theory (e.g., Jackson, 1990, 2005) and observations (e.g., Boyd et al., 2002, 2005; Kiørboe et al., 1994; Jackson

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and Kiørboe, 2008) show can limit phytoplankton population size in natural situations as well as in iron fertilization experiments. In this mechanism, collisions of algal cells with each other cause the formation and growth of aggregates, which accelerate algal removal by sedimentation from the surface mixed layer. At high algal concentrations, the kinetics of coagulation makes this rapid enough to remove algal cells produced by continued algal division and thereby to limit algal population despite continued growth. This limitation has been described in terms of the *critical number concentration*  $C_{cr}$ , the maximum algal concentration attainable for a given growth rate value, at which production by algal division equals removal by coagulation (e.g., Jackson and Kiørboe, 2008). The critical concentration is calculated from a simple formula without solving elaborate coagulation models.

The effects of light and coagulation limitations are not independent. The critical concentration depends on the average specific growth rate of the phytoplankton over the surface mixed layer; the critical depth depends on the effect of algal concentration on light attenuation. As the mixed layer deepens and approaches the critical depth, the average algal specific growth rate  $\mu$  decreases, thereby decreasing the critical concentration. Mixed layer deepening also has an effect on algal collision rates by changing the average contact rate driven by turbulent shear. Wind energy is dissipated over the mixed layer; a deeper mixed layer spreads that energy dissipation over a larger region, decreasing the average energy dissipation rate and, therefore, the average turbulent shear rate (e.g., Mackenzie and Leggett, 1993). The ultimate limitation of phytoplankton populations in the surface mixed layer is the result of the interaction of light and coagulation limitations.

The goal of this paper is to combine a photosynthetic model capturing the critical depth concept with a coagulation model to understand how the two interact to modify the critical concentration. The results from using a coagulation simulation are compared against the predictions from the simple critical concentration formula. In addition, model results are compared to observations from the Antarctic Ocean.

There are three related but distinct issues associated with coagulation theory that are relevant here: the maximum particle concentration allowed in a given system; the sedimentation flux and its properties, especially average sinking velocity; and the particle size distribution. The maximum particle concentration can be estimated simply; the particle distribution and average sinking velocity require numerical solution of the relevant differential equations.

## 2. Methods

### 2.1. Photosynthesis model

The model and parameterizations used here are those used by Mitchell et al. (1991), which were derived from the formulation of Platt and Jassby (1976). The instantaneous

photosynthetic rate is

$$P_G = BP_m \left( 1 - \exp\left(\frac{-\alpha I}{P_m}\right) \right), \quad (1)$$

where  $B$  is the plant concentration,  $I$  is the irradiance,  $P_G$  is the gross photosynthetic rate,  $P_m$  is the maximum specific rate of gross photosynthesis, and  $\alpha$  is the biomass-specific initial photosynthesis slope.

For a uniformly mixed water column, light irradiance is approximated using a Beer's law formulation:

$$I = I_0 \exp(-kz), \quad (2)$$

where  $I_0$  is the daily surface irradiance,  $k = (k_0 + Bk_1)$  is the diffuse attenuation coefficient, and  $z$  is the depth (Fasham et al., 1990).

The vertically averaged gross photosynthetic rate for the surface mixed layer of thickness  $Z$ , as determined by integration of Eq. (1), is

$$\bar{\mu}_g = \frac{P_m B}{kZ} (kZ + E_1(I_0 \alpha P_m^{-1})) - E_1(I_0 \alpha P_m^{-1} e^{-kZ}), \quad (3)$$

where  $\bar{\mu}_g$  is depth averaged specific photosynthetic rate, uncorrected for respiration, and  $E_1(x)$  is an exponential integral ( $= \int_x^\infty (e^{-t}/t) dt$ ; Eq. (5.1.1), Abramowitz and Stegun, 1965).

Mitchell et al. (1991) lumped all of their loss terms (respiration, sinking, and grazing) into one parameter that they estimated from their field observations. Coagulation models provide separate rates for the sinking loss. In order to compare the no-coagulation case to the coagulation cases, these calculations use an assumed specific respiration rate,  $R = 0.1P_m$  (Frost, 1987).

The rate of algal growth, expressed as the specific growth rate is

$$\mu = \bar{\mu}_g - R. \quad (4)$$

### 2.2. The coagulation model

The coagulation equations for an algal population growing exponentially at a rate  $\mu$ , either fixed or determined using the photosynthesis model, and a shear rate  $\gamma$  were solved numerically for steady state conditions (e.g., Jackson and Lochmann, 1992; Jackson et al., 2005). Standard parameter values are given in Table 1. Appendix A has a brief display of the structure of the coagulation model.

The model formulation places particles into size regions (sections) whose upper size limits have twice the mass of the lower limits. Particles are created by growth in the smallest section, where all the growing algae are assumed to lie. While the models can allow algal growth within aggregates, the simulations presented here do not. Particle mass moves from one section to another as the result of collisions. There are two collision mechanisms considered, shear and differential sedimentation. Particle mass is lost from the mixed layer by sedimentation out the bottom. Because larger particles settle faster, sedimentation rates are enhanced by the formation of larger aggregates. Measures of the extent of coagulation include the ratio of total (summed mass over all sizes) to

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