A vertically resolved model for phytoplankton aggregation

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This work presents models of the vertical distribution and flux of phytoplankton aggregates, including changes with time in the distribution of aggregate sizes and sinking speeds. The distribution of sizes is described by two parameters, the mass and number of aggregates, which greatly reduces the computational cost of the models. Simple experiments demonstrate the effects of aggregation on the timing and depth distribution of primary production and export. A more detailed ecological model is applied to sites in the Arabian Sea; it demonstrates that aggregation can be important for deep sedimentation even when its effect on surface concentrations is small, and it presents the difference in timing between settlement of aggregates and fecal pellets.

1. Introduction

The Arabian Sea exhibits large seasonal differences in the sedimentation of particulate organic matter (Haake \(et\ al\) 1993; Nair \(et\ al\) 1989). Especially in the western parts, deep flux is strongly coupled to the increase in wind speed during the Southwest Monsoon (SWM). This increase in deep sedimentation is accompanied by an increase in the proportion of biogenic silica, indicating a major contribution of diatoms to sedimentation. It has been proposed, that diatoms sink to these depths either via large (copepod) fecal pellets (Smith \(et\ al\) 1998), or in large, fast-settling aggregates, which are often observed during and after phytoplankton blooms in nearshore environments (Alldredge and Silver 1988; Alldredge and Gotschalk 1989) and in the open ocean, e.g. the North Atlantic (Lampitt 1985). Aggregates of \textit{Pseudonitzschia} and \textit{Nitzschia closterium} have also been observed in the the Arabian Sea (Garrison \(et\ al\) 1998).

Sedimentation of particulate organic matter (POM) is the product of mass and sinking speed of POM in the above layers. High concentrations of POM can be found, for example, as phytoplankton during blooms. The sinking speed of particles depends on various factors, such as the origin and size of particles. The sinking speed of phytoplankton may be enhanced when phytoplankton form large aggregates. Some large aggregates are formed by organisms, such as discarded mucus feeding webs, tunicate houses etc. (Alldredge and Silver 1988); others by the aggregation of smaller particles by purely physical processes. In the second type of aggregation, physical factors as turbulent shear or differences in the settling velocity of particles control the rate at which particles get into close proximity to each other. If the particles are sticky, they stay attached after contact, and form a larger particle.

Aggregation is a density dependent process, rapid during times of high phytoplankton abundance (Riebesell and Wolf-Gladrow 1992; Jackson 1990). It is therefore of interest to investigate the influence of (physical) phytoplankton aggregation and sedimentation together with the vertical transport of organic matter by fecal pellets in a biogeochemical model. Jackson (1990) and Riebesell and Wolf-Gladrow (1992) have created models of how the mechanisms of aggregation lead to changes in the size distribution of particles. These models describe the size distribution in great detail (hundreds of size classes) and are therefore too computationally demanding to be employed in large biogeochemical models with detailed spatial resolution.

Kriest (1999) and Kriest and Evans (1999; hereafter referred to as KE99) described a numerically efficient way to model the size distribution of particles and how it changes over time. We presented results for a

\textbf{Keywords.} Model; phytoplankton; aggregation; Arabian Sea.
well-mixed surface layer. In the present paper we shall study also the coupling between surface events and what reaches the deep ocean – for example what is recorded in sediment traps almost a kilometre below the production events that create the original small particles. In this paper we study the representation of KE99 in a model in which the water column is resolved into many numerical layers. We consider first the range of behaviour possible in even the simplest biogeochemical model that represents the necessary processes of particle formation and aggregation. We then describe a more ecological model including zooplankton, and their fecal pellets as another type of sinking particle, and compare its results with data collected in the Arabian Sea.

2. The nutrient-phytoplankton model

2.1 Simulations with constant physical forcing

Mass balances. We model nutrient and phytoplankton concentrations in a water column in which all components undergo vertical mixing, and phytoplankton sink. Phytoplankton growth is limited by the product of nutrient and light terms. The equations for nitrate (NO₃) and phytoplankton mass (PHY) and numbers (PHYNOS) are:

\[
\frac{\partial \text{NO}_3}{\partial t} = -\frac{\text{NO}_3}{k_{\text{NO}_3} + \text{NO}_3} J(z,t) \text{PHY} + \frac{\partial}{\partial z} K(z) \frac{\partial \text{NO}_3}{\partial z},
\]

\[
\frac{\partial \text{PHY}}{\partial t} = \frac{\text{NO}_3}{k_{\text{NO}_3} + \text{NO}_3} J(z,t) \text{PHY} + \frac{\partial}{\partial z} K(z) \frac{\partial \text{PHY}}{\partial z} - \frac{\partial \Psi}{\partial z},
\]

\[
\frac{\partial \text{PHYNOS}}{\partial t} = \frac{\text{NO}_3}{k_{\text{NO}_3} + \text{NO}_3} J(z,t) \text{PHYNOS} + \frac{\partial}{\partial z} K(z) \frac{\partial \text{PHYNOS}}{\partial z} - \frac{\partial \Phi}{\partial z} - \xi
\]

where \(J(z,t)\) describes light limitation, \(\Psi\) is the vertical flux of phytoplankton mass, \(\Phi\) the flux of numbers of particles, and \(\xi\) the rate of aggregation of particles. Cell growth and division is assumed to produce more aggregates, not larger aggregates: cells separate after they divide. We now describe the flux and aggregation terms in detail.

Representation of phytoplankton aggregates. As in KE99 we assume that the distribution of aggregates as a function of diameter can be described by a two-parameter function \(p(\theta) = A \theta^{-\epsilon}\) over a size range from \(m\), the diameter of a (typical) single cell, to \(\infty\). The total number of phytoplankton aggregates PHYNOS is thus

\[
\text{PHYNOS} = A \int_{m}^{\infty} \theta^{-\epsilon} d\theta = A \frac{m^{1-\epsilon}}{\epsilon - 1}
\]

provided \(\epsilon > 1\).

If the mass, \(C\), of an aggregate is related to its diameter, \(\theta\), by \(C(\theta) = C \theta^{\zeta}\), and \(C_{m} = C m^{\zeta}\) is the mass of a single cell, then the total mass of phytoplankton aggregates is

\[
\text{PHY} = A C \int_{m}^{\infty} \theta^{-\epsilon} d\theta = A C_{m} \frac{m^{1+\zeta-\epsilon}}{\epsilon - 1 - \zeta}
\]

provided \(\epsilon > \zeta + 1\).

Equations (4) and (5) can be solved for \(A\) and \(\epsilon\) in terms of PHY and PHYNOS; so, the shape of the size distribution is a dynamical variable.

Sinking. The sinking flux of numbers and mass of phytoplankton aggregates are given by

\[
\Phi(z) = \int_{m}^{\infty} p(z,\theta) w(\theta) d\theta \quad \text{and} \quad \Psi(z) = C \int_{m}^{\infty} p(z,\theta) \theta^{\zeta} w(\theta) d\theta
\]

where \(w(\theta)\) is the sinking speed of a particle of size \(\theta\). Because the size distribution exponent varies with depth and time, average sinking speeds also vary with depth and time. KE99 assumed \(w = B \theta^{\eta}\). All the indefinite integrals (from \(m\) to \(\infty\)) must converge. In the model for a single well-mixed layer, the largest particles sink out. Thus, provided the initial model conditions are set up so that the integrals converge, no subsequent divergences can evolve. In a vertically resolved model there is an extra complication: the largest particles that sink out of one layer sink into the layer below and shift its size distribution towards larger cells. This effect cannot trigger a divergent integral of mass, of course; but it can trigger a divergence of average sinking speed. To sidestep this problem, we arbitrarily decide that the increase of sinking speed with particle mass has an upper limit at mass \(M: w = B \min (\theta, M)\). The effect of this upper limit is negligible in practice: it is the difference between sinking at 1900 m/day, which is fast enough to leave no influence on the water column, and infinitely fast.

Aggregation. The probability of collision of particles is a function of particle size, concentration, the rate of turbulent shear and the difference of the settling velocities of two different particles. The equations for collisions due to shear and differential settlement as presented by Jackson (1990) have been converted to a size-continuous form and solved. To bound the aggregation integrals from getting out of the range of