Effect of coagulation on a model planktonic food web.

George A. Jackson  
Department of Oceanography  
Texas A&M University  
College Station, TX 77843  
Phone: 409-845-0405  
FAX: 409-845-8219  
Email: gjackson@tamu.edu

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ABSTRACT

Observations have shown that aggregates (“marine snow”) are an important fraction of the vertical flux of organic matter in the ocean. There has been separation between coagulation models, which have focused on phytoplankton blooms in which particle concentrations are high and grazing is low and negligible, and plankton models which have focused on food web interactions but that have ignored coagulation dynamics. This separation has partly resulted from the difficulty in describing the interactions among the multiple particle sources using a coagulation model for a food web. New approaches for describing particle dynamics now make it possible to do so. The present study examines the effect of combining the food web model of Fasham et al. (1990) with a particle dynamics model and applying the combined model to describe the annual cycle of an oligotrophic plankton system. Results show that coagulation can have an important effect on particle flux even in such a low particle concentration environment by increasing average particle settling speed and by increasing the ratio of maximum to minimum daily vertical flux over the course of a yearly cycle. In addition, coagulation forms large, rapidly sinking particles. Grazing and the accompanying formation of fecal pellets can compete for particles, but the fecal pellets can also participate in the formation of large aggregates. Among the variables that can influence export rates are phytoplankton size and concentration as well as depth of the surface mixed layer. The results provide evidence for the importance of coagulation processes in enhancing particle export even in central ocean regions.

KEYWORDS

Aggregation, coagulation, food webs, plankton, model, vertical flux
INTRODUCTION

The settling of particles is a crucial pathway for the redistribution of such biologically-active materials as carbon in the sea; particle size is an important property determining particle sinking velocity. Understanding the processes controlling particle formation is important for understanding the fate of organisms as well as the vertical movement of matter. Coagulation, the formation of larger particles from the collision and joining of smaller particles, has emerged as a significant process in controlling particle size, thereby determining particle fate.

There is extensive evidence that aggregates represent the dominant agents of organic matter sedimentation. Sediment trap data and in situ camera observations indicate that marine particles do indeed settle as aggregates (Asper, 1987; Silver and Gowing, 1991; Lampitt et al., 1993). Large aggregates have been observed in the water column and their concentrations correlated with material collection rates in sediment traps (Walsh and Gardner, 1992). The composition of the settling material provides further information on its sources. Examination of the contents of sediment traps has shown that aggregates dominate the flux, with identifiable fecal pellets constituting a relatively small fraction (10-30%) of the C flux (e.g., Miquel et al., 1994; Marty et al., 1994). What, then, regulates the formation of aggregates?

Experimental (Alldredge and Jackson, 1995), observational (Kiorboe et al., 1994; Kiorboe et al., 1996) and theoretical studies (Jackson, 1990; Hill, 1992; Jackson and Lochmann, 1992) of the role of coagulation in plankton systems have focused on phytoplankton blooms because these are situations with high particle concentrations and little competition between coagulation processes and zooplankton grazing to remove particles. The development of models to explain bloom systems has been helped by this simplicity of algal blooms. The combination of observations, experiments, and theoretical developments has led to a surprising level of understanding that has included the field verification of predictions of the maximum particle concentrations (Jackson, 1990; Kiorboe et al., 1994).

Extending models to other marine regions where zooplankton grazing competes with coagulation as a phytoplankton loss and where fecal pellet production and organic colloid excretion provide additional particle sources is more difficult. The multiple sources of particles make it difficult
to predict the length of a new particle formed when two smaller particles unite. With a single particle source, fractal scaling relates aggregate mass and aggregate length (e.g., Sutherland, 1967). However, there is no unique relationship between the two particle attributes when multiple particle sources exist. For example, if the algae are 10 μm in radius and the only source of new particles, then a 100 μm particle must be an algal aggregate; if there are fecal pellets also around, then a 100 μm particle may have the mass characteristic of an algal aggregate or that of a fecal pellet. Without a means to predict the two particle properties, mass and length, it is difficult to construct a model of a planktonic food web which includes aggregation.

Two-dimensional particle size spectra combined with rules to predict the diameter and mass of a new particle formed by the collision of two smaller ones provide the means to describe the interactions between particles produced by the varied sources in a planktonic food web (Jackson, 1998). In particular, Jackson (1998) has argued that if fractal scaling is a geometric property, then a quantity that is the length to the fractal dimension \( \lambda = r^{d_l} \) should be conserved in collisions in the same way that mass is.

This paper describes the joining of a coagulation model to the Fasham et al. (1990) model of a plankton system, which was developed to describe the dynamics of the plankton, particularly the export of new production, off Bermuda in the relatively oligotrophic waters of the Atlantic Ocean. The goal of this work is to understand how the a model of particle dynamics affects the planktonic system. An understanding of the interaction between the two different types of particle descriptions can influence our interpretation of ocean observations.

MODEL

**Particle collision/coagulation rates**

Particle dynamics describes the fate of particles as they collide to form new particles and ultimately settle out of their system. Classical coagulation models emphasize three mechanisms for particle-particle contact: Brownian diffusion, laminar and turbulent shear, and differential sedimentation. For each of these, the rate \( R_{ij} \) of forming new particles of mass \( (m_i + m_j) \) from the collision of two smaller particles of masses \( m_i, m_j \) and radii \( r_i, r_j \) is given in terms of the number concentrations of the two colliding particles \( c_i = c(m_i, r_i) \) and \( c_j = c(m_j, r_j) \) and a rate constant
called the coagulation kernel $\beta_{ij}$:

$$R_{ij} = c_i c_j \beta_{ij}$$

(1)

(Note: some authors separate the $\beta$ terms into two factors, one to represent the collision rate for simple fluid model and a second to incorporate higher order corrections. The two factors are consolidated into this $\beta$.)

The three different mechanisms for particle-particle contact are usually assumed to operate independently, allowing the total rate of formation of new particles to be expressed as the sum of the individual rates. Using the subscripts $Br$, $sh$, and $ds$ to denote the different mechanisms, this leads to

$$R_{ij} = c_i c_j (\beta_{Br,ij} + \beta_{sh,ij} + \beta_{ds,ij})$$

(2)

The coagulation kernel for differential sedimentation and shear have been calculated using varying levels of detail. The rectilinear formulations embed the interacting particles in the flow, with no effort to account for the effect of the particles on the fluid flow. The curvilinear formulations can include the effect of the larger particle on the flow field but embed the smaller particle in it, with the smaller particle usually having no effect on the flow. Further refinements include calculating the flow field as it is affected by both particles and including attractive and repulsive forces caused by surface charge and van der Waals forces. These calculations are usually made for impermeable spheres (Adler, 1981; Han and Lawler, 1992).

Both length and mass are important properties determining a particle’s fate. For this reason it is important to be able to describe the mass and length of a new particle formed by the joining of two old particles of known masses and lengths. Because mass is a fundamental conserved quantity, the mass of the new particle is the sum of the masses of the two old particles. Length is more problematic. The mass $m$ and radius $r$ of an aggregate are usually related by

$$r = Am^{1/d_{fr}}$$

(3)

where $d_{fr}$ is the fractal dimension, and $A$ is a constant (e.g., Sutherland, 1967; Logan and Wilkinson, 1990; Kilps et al., 1994; Jackson et al., 1997). For particles with constant density, such as liquid drops, $d_{fr} = 3$. Aggregates with solid components have fractal dimensions as low as 1.8 and are known as “fractals.”
Eq. 3 provides the means to relate mass and length for all aggregates, when there is only one source particle. It does not work to describe the properties of particle formed from two smaller particles when the smaller particles have different m to l relationships (equivalent to different values of A). Such situations occur when there is more than one class of source particle, such as in plankton systems where aggregates are formed from colloids, algal cells and fecal pellets. Jackson (1998) proposed that the quantity \( \lambda \equiv r^{d_f} \) is also conserved in aggregation reactions and can be used as a second particle property when describing particle aggregation with multi-source particles. The kinetics of coagulation can then be described and calculated using two dimensional particle size spectra. The techniques described in Jackson (1998) have been used to calculate the evolution of the particle size spectra in this work.

The values for the curvilinear and rectilinear formulations diverge when the two particles differ greatly in size. For differential sedimentation, the rectilinear kernel essentially is proportional to the square of the radius of the larger particle, while the curvilinear kernel is proportional to the square of radius of the smaller particle. The smaller value for the curvilinear kernel results from consideration of the flow field around the larger, faster falling particle, pushing away the smaller as it passes. Fractal aggregates require further consideration because their porous nature allows some flow through them and they do not push water as far away as they fall. The result is that values for coagulation kernels need to be intermediate between the rectilinear and curvilinear kernels to accurately describe marine situations.

**Brownian motion.** The coagulation kernel for Brownian motion of two particles describes the diffusion of 2 particles to each other. The formulation of Pruppacher and Klett (1980) is used here.

**Differential sedimentation.** The coagulation kernel for the rectilinear case is given by (Pruppacher and Klett, 1980)

\[
\beta_{d-s,ij} = \pi (r_i + r_j)^2 |v_j - v_i|
\]

(4)

The curvilinear kernel, for solid spheres and without any chemical attractive or repulsive forces, is smaller (Pruppacher and Klett, 1980):

\[
\beta_{d-c,ij} = 0.5 \pi r_i^2 |v_i - v_j|
\]

(5)

where \( r_j > r_i \). The effect of making this correction is greatest for small particles impacting large
Shear. The rectilinear coagulation kernel for turbulent shear is given by (Pruppacher and Klett, 1980)

\[ \beta_{sh-r,ij} = 1.3\Gamma (r_i + r_j)^3 \]  

(6) where the average shear rate \( \Gamma \) is given by

\[ \Gamma = \left( \frac{\epsilon}{\nu} \right)^{0.5} \]  

(7)

The curvilinear kernel is (Hill, 1992)

\[ \beta_{sh-c,ij} = 9.8 \frac{p^2}{(1 + 2p)^2} \Gamma (r_i + r_j)^3 \]  

(8) where \( p = r_i / r_j \) and again \( r_j > r_i \).

Effect of porous, fractal particles on coagulation kernels. Li and Logan (1997, 1997a) have experimentally determined the interaction rates between small, solid particles and larger aggregates, observing collision rates between those predicted by rectilinear and curvilinear kernels. They fit their results to curves which do not extrapolate well to the size range where both particles are the same size and where the differences between the curvilinear and rectilinear formulations are small. We have, therefore, modified the coagulation kernel to fit their observations but also to converge to the rectilinear solution when the particles are equal sized.

For shear, this fractal kernel is

\[ \beta_{sh-f,ij} = p^{0.88} \beta_{sh-r,ij} \]  

(9) where, again, \( p \) is the ratio of radii for small and large particles.

For differential sedimentation, this fractal kernel is

\[ \beta_{ds-f,ij} = p^{0.984} \beta_{ds-r,ij} \]  

(10)

There is one other correction that needs to be made. The curvilinear kernel assumes that larger particles fall faster than smaller ones, making their flow fields the controlling factor. When working...
with single source particles, this tends to be true. However, systems with multiple sources can have small, fast sinking particles overtaking large, slowly sinking ones, such as fecal pellets falling on colloidal aggregates. In this case, the flow field field of the larger particle does not push smaller particles away as it falls and the rectilinear kernel is the more appropriate kernel.

Including this second correction as well leads to

\[ \beta_{ts-f,ij} = p^{0.984} \beta_{ts-r,ij} \quad \text{if } (v_i - v_j) \cdot (r_i - r_j) \geq 0 \]
\[ = \beta_{ts-r,ij} \quad \text{if } (v_i - v_j) \cdot (r_i - r_j) < 0 \] (11)

**Particle dynamics**

For a heterogeneous mixture of particles in a mixed layer of depth \( M \) for which there is no single mass-length relationship, the number concentration of particles within a size range of \( r \) and \( r + dr \), \( m \) and \( m + dm \) can be expressed in terms of a 2-dimensional particle size spectrum \( n(m, r) \) as \( n(m, r) dm dr \), or, more conveniently, in terms of \( \lambda \) as \( n(m, \lambda) dm d\lambda \).

\[
\frac{dn(m, \lambda)}{dt} = \frac{dn(m, \lambda)}{dt} - 0.5 \alpha \int_0^m \int_0^\lambda \beta(m_1, \lambda_1, m - m_1, \lambda - \lambda_1)n(m_1, \lambda_1)n(m - m_1, \lambda - \lambda_1)dm_1d\lambda_1 \\
- \alpha n(m, \lambda) \int_0^\infty \int_0^\infty \beta(m, \lambda, m_1, \lambda_1)n(m_1, \lambda_1)n(m - m_1, \lambda - \lambda_1)dm_1d\lambda_1 \\
- v(m, \lambda)M^{-1}n(m, \lambda) 
\] (12)

where all the \( \beta, n, \) and \( v \) are functions of both particle mass and length (equivalent to \( \lambda \)), \( \alpha \) is the probability that a particle collision results in particles sticking together, \( v \) is particle settling velocity, and \( S \) is the biological source or loss term. The fundamental coagulation equations are summed over reactions between all possible particles, here involving double integrals rather than the more traditional single integrals because of the use of two dimensional, rather than the more traditional one dimensional, particle size spectra.

The coagulation equations can be solved numerically by assuming that the spectral shape over a defined particle mass range (a section) stays constant but the magnitude fluctuates (Gelbard et al., 1980). For a one-dimensional spectrum this is similar to representing the particle size spectrum as a histogram that approximates the shape of the spectrum, for which the heights of the bars
vary through time. By appropriate choice of histogram shapes, the time varying part can be made the total mass concentration of material within the region, in units such as $g\ m^{-3}$ or $\mu M\ N$. It is mathematically convenient to have the upper size range in each section be twice the lower bound. Thus, for a one-dimensional particle size spectrum the sectional bounds might collect all particles whose masses are 1-2, 2-4, 4-8, 8-16 pg, etc. For a two-dimensional size spectrum, the sectional boundaries form a grid in which the upper bound for any section is double the lower bound in either dimension. If $i$ and $j$ are the indices for the sections in the two dimensions, then $C_{ij}$ is the mass (or molar) concentration of particles in the $i,j$ section (Jackson, 1998). The problem of solving for the evolution of the particle size spectrum can be transformed to one of solving for all of the sectional concentrations using a set of coupled ordinary differential equations for $C_{ij}$ (Gelbard et al., 1980; Jackson, 1998).

Particle mass and fractal-transformed particle length ($\lambda$) are useful dimensional variables to use for the two dimensional spectra. In this case, the problem of solving for the evolution of the particle size distributions can be further simplified by assuming that coagulation can form particles only within a limited range of mass and $\lambda$ (the diagonal constraint; Jackson, 1998). That simplification has been used here.

The particle excess mass is used as the mass dimension for these calculations. The excess mass $\Delta m$ is the mass of a particle in excess of that of the water that is displaced by the particle:

$$\Delta m = m - \rho_f V_c$$

where $\rho_f$ is the fluid volume and $V_c$ is the particle’s conserved volume, the volume of fluid that is displaced by the solid part of the particle. Both excess mass and $\lambda$ are conserved when particles combine to form a new particle.

**Food web model**

The food web model is a modified version of the model developed by Fasham, Ducklow, and McKelvie (1990), hereafter known as FDM. This model has the advantage of considering detrital dynamics explicitly and of having been fairly well studied by others as well (e.g., Haney and Jackson, 1996).
The FDM model follows the evolution of concentrations for seven biologically important compartments — including phytoplankton \((P)\), zooplankton \((Z)\), bacteria \((B)\), nitrate \((N_r)\), ammonia \((N_d)\), dissolved organic nitrogen \((N_d)\), and detritus \((D)\) — within the surface mixed layer. Nitrogen is the model currency and the state variables have units of mmol N m\(^{-3}\) (\(\mu M\) N) while vertical fluxes have units of mmol N m\(^{-2}\) d\(^{-1}\).

The model implemented here has several modifications to FDM in order to incorporate coagulation interactions, including elimination of phytoplankton natural death, subdivision of dissolved organic matter release into a colloidal fraction and a “truly” dissolved fraction, and production of zooplankton feces of specified size. The colloidal release produces particles of fixed size which participate in coagulation interactions. Along with the phytoplankton produced by cellular division, the colloids and the feces form the three particle sources in the model.

In the original FDM model, changes in vertically-averaged concentrations of phytoplankton and detritus in the surface mixed layer are described by:

\[
\begin{align*}
\frac{dP}{dt} &= (1 - \gamma_1)\sigma P - GP - \mu_1 P - GP \\
\frac{dD}{dt} &= F_z - G_D - \mu_4 D + \mu_1 P - GD - \frac{v_D}{M} D
\end{align*}
\]  

(14)  

(15)

where \(\sigma\) is the specific production rate, \(\gamma_1\) is the fraction of production that is excreted, \(\mu_1\) is a natural mortality coefficient, \(G_P\) is the grazing loss rate, \(G\) incorporates changes in concentration caused by mixing across the thermocline and changes in the mixed layer depth, \(F_z\) is the rate of detrital production by zooplankton, \(G_D\) the rate of zooplankton feeding on detritus, \(\mu_4\) is the specific rate of detrital breakdown, \(M\) is the mixed layer depth, and \(v_D\) is the detrital sinking rate. The coupling of this food web model to a particle dynamics model requires modifying the equations describing changes in \(P\) and \(D\).

Each of the three source particles (single celled algae, colloids, and fecal pellets) is identified with a section that has the appropriate excess mass and length properties.

After the sectional transformations, changes in \(P\) can be represented as

\[
\frac{dP}{dt} = (1 - \gamma_1 - \gamma_c)\sigma P - GP - GP + \sum_{k=1}^{o} \sum_{l=1}^{q} \sum_{m=1}^{o} \sum_{n=1}^{q} \sum_{k=1}^{o} \sum_{l=1}^{q} \sum_{m=1}^{o} \sum_{n=1}^{q} \beta_{pkln} C_{kt} C_{mn} - P\bar{v}_p / M
\]  

(16)
where $\bar{\beta}_{ijklmn}$ represents the total interactions between section $(k,l)$ and $(m,n)$ that affect the $P$ section weighted by the section shape, $\bar{v}_p$ is the settling velocity weighted by the section shape for the phytoplankton section, and $\gamma_c$ is the fraction of algal productivity released as colloids. The major change from Eq. 14 is the elimination of natural mortality of phytoplankton, its replacement by coagulation and settling losses, and the separation of truly dissolved organic matter from colloidal matter.

Material in all the other sections is considered to be detrital, with $D = \sum_i \sum_j C_{ij} - P$. Detrital losses are proportional $C_{ij}$ for the non-phytoplankton sections:

$$\frac{dC_{ij}}{dt} = T_{ij} - \frac{C_{ij}}{D} G D - \mu_4 C_{ij} - GC_{ij} + \sum_{k=1}^{a} \sum_{l=1}^{q} \sum_{m=1}^{a} \sum_{n=1}^{q} \bar{\beta}_{ijklmn} C_{kl} C_{mn} - P\bar{v}_{ij}/M \quad (17)$$

where

$$T_{ij} = \begin{cases} 
F_z & \text{for the section containing focal pellets} \\
\gamma_c \sigma P & \text{for the section containing the colloids} \\
0 & \text{otherwise}
\end{cases}$$

The excess mass of algal particles is calculated to be consistent with the settling velocity relationship as a function of algal diameter (Smayda, 1970; Jackson, 1989); the excess mass of fecal pellets is calculated from the fecal pellet radius and an excess density (density of the particle less the water density) of 0.09 g cm$^{-3}$ (Small et al. 1979); the excess density of the colloidal particles is 0.046 g cm$^{-3}$; the density of the water is 1.02 g cm$^{-3}$. The fecal pellet diameter is assumed to be 10 $\mu$m, generally consistent with the pellet volume of a 200 $\mu$m copepod (Uye and Kanamé, 1994). These are the values for the lower bounds of the sections assigned to the particles. There is some variation introduced by the grid structure and its sectional boundaries.

The nitrogen content of individual algal cells is calculated using Mullin et al. (1966) and a C:N ratio of 106/16. The resulting ratio of excess mass to nitrogen content for phytoplankton is used to calculate the nitrogen content of all particles. For the 5 $\mu$m radius alga case, there is $2.4 \times 10^7$ mmol N per g excess mass.

Other assumptions are that only solitary algae divide, and that there is no disaggregation but there is a maximum size that an aggregate can reach which is fixed by the grid size. For the 30 x 30 sectional grid and the standard case, the grid spans particles with excess mass of $1.63 \times 10^{-14}$ to
1.75 \times 10^{-5} \text{ g and lengths } 4.39^{-5} \text{ to } 0.40 \text{ cm (} \lambda \text{ ranging from } 1.16 \times 10^{-5}-0.12 \text{ cm}^{2}\text{.} \) Particle settling velocities range from 0.002 to 558 \text{ m d}^{-1}.

**Numerical solution**

The system was usually solved on a 30 by 30 sectional grid (\( m \) and \( \lambda \)) using the double precision Fortran subroutine DVODE, available from NETLIB. Tests of the effect of grid size were made by using 25 by 25 and 30 by 30 sectional grids.

Simulations were run for 2 model years. The first year was used to set the initial condition for the second year, whose results were analyzed and are displayed here.

**RESULTS**

**Absence of coagulation**

In the absence of coagulation, there is a large zooplankton population whose concentration peaks at 0.86 \( \mu \text{M} \) after the spring phytoplankton bloom (Fig. 1, \( b\theta aq \) in Table 1). This is larger than the maximum phytoplankton and nitrate concentrations (0.42 and 0.51 \( \mu \text{M} \)). Fecal pellets constitute a significant fraction of the total nitrogen (maximum concentration of 0.15 \( \mu \text{M} \)). Note that this simulation does not have the mortality term for phytoplankton that the model of FDM did and, as a result, has a larger zooplankton concentration than that model.

The annual vertical flux is split almost evenly between settling of solitary algae (48%) and fecal pellets (52%). The average settling velocity is 0.8 m d\(^{-1}\). While there are fluctuations in the daily vertical flux, they are relatively small. Designating the ratio of maximum to minimum daily fluxes during a year as \( \psi \), the value of \( \psi = 0.36/0.19 = 1.9 \).

**Presence of coagulation**

In the presence of coagulation (using the fractal kernels, Eqs. 9, 11), there is a substantial change in the planktonic system (\( base \) in Table 1, Fig. 2). Phytoplankton nitrate concentrations are marginally lower, with maxima of 0.39 and 0.46 \( \mu \text{M} \). Zooplankton concentrations are much lower, showing a seasonal maximum of only 0.15 \( \mu \text{M} \), while the associated fecal pellets have a maximum of only 0.03 \( \mu \text{M} \). Aggregated particles dominate the vertical flux, with 64 mmol N m\(^{-2}\).
of the annual total of 114 mmol N m\(^{-2}\) y\(^{-1}\) (56\%), compared to 44 mmol N m\(^{-2}\) y\(^{-1}\) for the algae and 6 mmol N m\(^{-2}\) y\(^{-1}\) for the fecal pellets. Maximum average sinking velocity is 1.1 m d\(^{-1}\). Daily flux shows greater variability (\(\psi = 0.68/0.15 = 4.53\)).

**Effect of grid size**

There is no discernible difference in the total concentrations or fluxes when using grids of 25 by 25 (\textit{b25}, Table 1), 30 by 30 (\textit{base}, Table 1), or 35 by 35 (\textit{b35}, Table 1) cells with the fractal kernel formulation.

**Effect of coagulation kernel formulation**

The coagulation kernel that is used can have a very large effect on the results. The results for the curvilinear kernel (Eqs. 5, 8) are very different than those for the fractal kernel and are only slightly different than those for the simulation without coagulation (\textit{base}, Table 1). The annual flux is the same as in the absence of coagulation, although there is a modest contribution to the vertical flux from aggregates (25\%) that is accompanied by a decrease in the fecal pellet flux. Associated with the decrease in pellet flux, there is a slight decrease in the maximum zooplankton concentration, from 0.86 to 0.67 \(\mu\)M.

In contrast, the results for the rectilinear kernel (Eqs. 4, 6) show an extremely strong coagulation effect (\textit{baser} in Table 1, Fig. 3). Phytoplankton concentrations achieve their highest values of 0.16 \(\mu\)M only after the mixed layer shoals and zooplankton essentially disappear. Despite the low organism concentrations, the total annual flux increases to 335 mmol m\(^{-2}\) y\(^{-1}\), of which 96\% is in the form of aggregates. The maximum average particle velocity, 24 m d\(^{-1}\), occurs during the deep mixed layer phase rather than during the time of high phytoplankton concentrations. The daily flux is extremely variable (\(\psi = 2.21/0.20 = 11\)).

**Effect of algal size**

Halving the algal radius, to 2.5 \(\mu\)m, decreases the algal settling rate and the resulting algal flux (\textit{ba2p5}, Table 1, Fig. 4). There is smaller aggregate flux and greater fecal pellet flux but the peak settling velocity (0.64 m s\(^{-1}\)) reflects the smaller size of the settling particles and the smaller \(\psi\) (\(-2.38\)). The decreased loss of matter to settling stimulates the zooplankton population, which has
a maximum concentration of 0.7 $\mu$M.

Doubling the algal radius to 10 $\mu$m increases the single algal settling velocity (to 0.83 m d$^{-1}$) and particle aggregation, with aggregate flux accounting for 56% of the total $(bT0$, Table 1; Fig. 4). The zooplankton population is effectively eliminated. The daily flux is also more variable ($\psi = 6.0$). Peak particle velocity is 2.0 m d$^{-1}$.

**Effect of shear rate**

Making simulations at shears of 0.5 and 2. s$^{-1}$ $(bexp5$ and $bgz2$, Table 1; Fig. 5) as well as the shear of 1. s$^{-1}$ explores the importance of shear in the simulation. Increasing shear has little effect on the total annual flux, but does increase the peak daily flux to 0.79 mmol N m$^{-2}$ d$^{-1}$ and $\psi$ to 5.9. The fraction of the flux associated with aggregates increases, to 67%. Decreased shear leads to a slightly lower flux, but a significantly lower variation in daily flux, with $\psi = 2.9$. Phytoplankton concentration decreases with increased shear (Fig. 5). Zooplankton concentration is very sensitive to shear, with a large population at the low shear, a seasonal population at medium shear, and negligible zooplankton concentration at high shear.

**Effect of colloid release**

Setting the colloid release rate to 0 has a relatively small effect on the system $(bT0$, Table 1; Fig. 6). It does increase $\psi$ to 4.8 from 4.5 for base. Increasing the release rate by a factor of 4, from 2.5% to 10% of primary productivity $(bT2$, Table 1; Fig. 6), has a larger effect, decreasing the flux ratio to 4.0. In addition, it decreases the peak particle settling rate by 13%, slightly increases the total particle concentration and almost doubles the maximum zooplankton concentration.

If the colloid particles are larger, on the order TEP $(bT3p47$, Table 1; Fig. 7), there is a slight decrease in average settling rate.

**Effect of subsurface nitrate concentration**

Increasing the concentration of nitrate in the subsurface layer from 2 to 5 $\mu$M dramatically changes the system response $(bn05$, Table 1; Fig. 8). The system maintains a high nitrate concentration throughout the year, zooplankton concentration is very high (with a maximum of 2.1 $\mu$M N),
and phytoplankton concentration is relatively constant throughout the year (0.24-0.37 µM N). The maximum particle velocity is only 1.0 m d⁻¹ and occurs when the mixed layer is at its deepest. Aggregate flux is equal to the fecal flux, at 36% of the annual total. The value of ψ is 2.1.

Increasing the colloid size to a radius of 3.47 µm increases the integrated particle flux, from 149 to 197 mmol N m⁻² d⁻¹, and the maximum settling velocity to 1.4 m d⁻¹ (Fig. 9). The dominant form of the particle export changes through the year. In the winter-spring, most of the flux is in the form of aggregates; with the appearance of the summer zooplankton bloom, the fecal pellets dominate the flux. In either case, the aggregate and fecal pellet fluxes are comparable, while single algal cells provide a smaller fraction of the total.

**DISCUSSION**

Despite the utility of the two-dimensional particle size distribution in these calculations, this spectrum is not easily interpretable because it is difficult to include a time dimension when displaying results (e.g., Fig. 10). Collapsing the spectrum into the more traditional one-dimensional particle size spectrum can overcome this problem (Fig. 11). For example, the concentrations of solitary algae do not vary significantly, but the concentrations of aggregates larger than 100 µm show large seasonal variations for both the standard base case (Fig. 11a) and for the higher subsurface nitrate concentration case (bn05, Fig. 11b).

The abundance of fecal pellets associated with the higher zooplankton concentrations is noticeable in the spectra for bn05, for which there is a peak in concentration (Fig. 11b) and flux (Fig. 12b) associated with the fecal pellets at a diameter of 10 µm, although larger particles can dominate the flux. A substantial fraction of the particle flux involves aggregates which contain a fecal pellet as well as other material, such as phytoplankton. The amount of material settling out which is larger than the fecal pellets, particularly in the high subsurface nitrate case (Fig. 12b), implies that aggregation of fecal particles is an important part of process. In this sense, aggregation and zooplankton feeding/fecal pellet production are not purely competitive processes removing algae but can also interact to increase the vertical fluxes.
Implications for marine situations

A striking attribute of aggregation-controlled vertical flux is the greater variability not only in the average sinking velocity but also in the absolute flux, as seen by the values of $\psi$ being increased by aggregation from 3 to 6. Scharek et al. (1999) observed similar variations in the export of diatoms from the euphotic zone in the North Pacific, which they calculated as ranging from 0.5 to 1.8% d$^{-1}$ of the diatom standing stock. This variation in relative flux reflects an increase in settling rates which is similar to that observed in these simulations. Even though the average sinking velocity only increases by a factor of 2-3, there is a substantial number of very large, fast sinking particles produced. Interestingly enough, the annual fraction of the particle export in the form of aggregates remains fairly constant.

Models of coagulation in lakes show that long hydraulic residence times in lake simulations allow the formation of larger aggregates with faster sinking rates (O’Melia and Bowman, 1984). A similar effect can be observed in simulations with higher subsurface nitrate concentrations ($bn05$, Fig. 8), where the highest particle flux was associated with a deeper mixed layer. Here, the deeper mixed layer minimizes the loss rate per unit volume and allows the accumulation of larger aggregates (Figs. 11, 12). Deuser (1986) observed that the measured sediment trap flux was inversely correlated with the surface temperature 30 d earlier, noting that the cold surface temperatures were associated with deep mixed layers in the Sargasso Sea. Conte et al. (1998) observed that this material is predominantly derived from phytoplankton but is not associated with the spring phytoplankton bloom. Increased aggregation allowed by deeper mixed layers may explain the timing of their deep particle fluxes.

Differences in the timing between peaks in the surface particle concentration and peaks detected by sediment traps throughout the water column indicate that the dominant particles have settling rates of 50-100 m d$^{-1}$ or more (Deuser et al., 1981; Asper et al., 1992). Aggregation provides a means for small particles to fall this fast. While the average velocities in these simulations are substantially slower, further processing deeper in the water column in the form of preferential grazing or degradation of small particles or continued aggregation would increase the relative number of large particles and, hence, the average settling velocity.
The use of a two dimensional particle size distribution actually has an observational basis. Simultaneous measurements of length and fall velocity for suspended particles show wide ranges in particle excess mass or, equivalently, settling rate for a given length particle (e.g., Asper, 1987; Alldredge and Gotschalk, 1988; Syvitski et al., 1995; Hill et al., 1998; Pilskaln et al., 1998). For example, Hill et al. (1998) reported that velocities of aggregates composed of sediment particles varied by a factor of 7 (equivalent to the range in 3 sections). They argued that this range was the result of variable aggregate composition. In the plankton, Alldredge and Gotschalk (1988) measured sinking rates of aggregates and calculated excess densities that varied by a factor of thirty for the same particle length. Such observations are consistent with multiple source particles and with calculations made here.

Organic particles, either as small “colloids” or larger “TEP” particles (Alldredge et al., 1993), are not necessary for coagulation to be important, although they can enhance the coagulation rates and increase the peak settling rates (e.g., Jackson, 1995a). It must be noted that the simulations do not address the role of such particles if they are sticky (α = 1) while the algae are not because the simulations assume that all particles have the same probability of uniting upon contact.

The oligotrophic system marks one end of a continuum of situations in the ocean; bloom systems mark the other. The role that coagulation plays in repackaging particulate matter and speeding its descent varies in the two systems, largely because the difference in particle concentration changes the relative size of the process.

Model parameters

This study has shown that particle dynamics can fit into a plankton model, here the classic FDM description developed for Station “S” near Bermuda. Of particular interest is the fact that the standard model (base, Fig. 2) reproduces many of the features of that model. Replacing the natural algal mortality rate with coagulation losses allows a more mechanistic interpretation of algal losses than does the ad hoc natural mortality rate. Furthermore, the formation of aggregates produced an average sinking rate that was faster than that of the solitary algae but similar to the 1 m d⁻¹ that FDM found worked to best reproduce the observations. It is intriguing that a more recent parameterization of natural mortality rate uses a Monod rate expression (Fasham, 1993), replacing
the phytoplankton loss in FDM that is linear with concentration with one that is quadratic in phytoplankton concentration at low concentrations. Such quadratic rates may correspond to the quadratic nature of coagulation rates (Eq. 1).

The large number of poorly known constants involved in describing an oligotrophic food web can channel the results in unforeseen ways. In the original FDM model, the poorly observed natural mortality coefficient dominated the fate of phytoplankton (Haney and Jackson, 1996). With this model, the assumed conversion rate of detritus to DON has a specific rate of $\mu_4 = 0.05 \text{ d}^{-1}$. For detrital aggregation and sinking to dominate, the detrital loss rate given by the average sinking rate divided by the mixed layer depth $(v/M)$ must be greater than $\mu_4$. For a shallow summer mixed layer of 20 m, then $v$ must be greater than 1 d$^{-1}$. This imposed rate requirement cannot be met when the detrital concentrations are too low and the starting particles too small. For example, choosing $r_a = 0.5 \text{ \mu m}$ and $r_f = 1 \text{ \mu m}$ results in only a marginal increase in sedimentation ($bap5ft$), even if grazing on detritus is also turned off ($bap5ftr$). Eliminating bacterial dissolution does not necessarily lead to large vertical fluxes either. Parameterizing detrital dissolution by bacteria, presumably as a function of particle size and concentration, is an important challenge for understanding planktonic systems, particularly in oligotrophic regions. It may be important to distinguish the feeding preference of zooplankton for detritus. It may also be necessary to introduce higher trophic levels capable of producing the larger particles that sink faster.

In the simulations shown here, the smallest particle ($r_a = 2.5 \text{ \mu m}$) settled at a low rate, aggregates were a smaller fraction of the particle flux, and a large zooplankton population resulted. In contrast, the large alga ($r_a = 10 \text{ \mu m}$) showed the signs of coagulation controlling the particle dynamics. Boyd and Newton (1999) argued that observations of particle export from the near-surface region support the importance of large cells, particularly diatoms, in determining the flux rates. This conclusion is consistent with the importance of particle size in controlling the vertical flux associated with particle aggregation.

There is a sense in which adding the coagulation interactions substitutes a different set of assumed parameters, particularly the diameters and densities of the algae, colloids and fecal pellets that are the source particles, for the natural mortality and detritus sedimentation rates specified in FDM. However, these are important properties of real organisms. In fact, the particle dynamics
simulations highlight their importance to natural ecosystems. For a phytoplankter, it is not enough to describe it only by a nitrogen concentration. Its size and stickiness become properties that determine the fate of the organic matter. Similarly, it becomes important to distinguish fecal size and density from that of the general detrital material. Not only the physical properties of the organisms need to be addressed, but the importance of zooplankton grazing on detritus makes this an important process to understand. Models cannot assume that there is no differentiation between detritus and fresh algal material when zooplankton grazing can control the maximum effective size of detritus.

Among the relationships which will be useful will be the relationship between the size of a zooplankton grazer and that of its food, usually assumed to be at a ratio of 10, and the ratio of fecal pellet size to animal size (Uye and Kaname, 1994).

**Coagulation issues**

The form of the coagulation kernels is important to the results, as can be seen from the differences in results from using the rectilinear, curvilinear and fractal versions (base, basec, and base). The biggest difference between the curvilinear and rectilinear versions is in the interaction between large and small particles, with the rate being controlled by radii of the larger particles for the rectilinear and the smaller particle for the curvilinear. One consequence is that a disproportionate increase in the concentration of large particles, as from including disaggregation or from particles accumulating at the upper bound of the computed size range, causes the interactions with the largest particles to dominate for most particles. In effect, the large particles act as a snow fence, trapping smaller particles directly rather than having them grow to large size by interacting with like-sized particles. That process is evident in the size spectra for these calculations with the rectilinear kernel. That dominance of interactions with large aggregates is still present in the modification of Gonzalez and Hill (1998), who multiplied the rectilinear kernel by a constant factor of 0.01 to make it equivalent to the rates for interactions between fractal aggregates and single particles measured by Li and Logan (1997, 1997a).

Energy dissipation and, hence, shear varies with time and depth. MacKenzie and Leggett (1993)
found a relationship between energy dissipation rate, wind velocity $W$ and depth $z$:

$$\epsilon = 5.82 \times 10^{-9} W^3 z^{-1}$$

(18)

where $\epsilon$, $W$, and $z$ have units of W kg$^{-1}$, m s$^{-1}$, and m. (Note that the units of $\epsilon$ have been changed from the W m$^{-3}$ that they used.)

The vertically averaged shear $\bar{\Gamma}$ can be calculated by combining Eq. 18 with Eq. 7 and integrating vertically. The resulting expression is

$$\bar{\Gamma} = 1.53 \times 10^{-4} W^{1.5} \nu^{0.5} M^{-0.5}$$

(19)

where $M$ is the mixed layer depth and all units are MKS. For the BATS time series, Eq. 19 would imply average shear rates of 0.1-1 s$^{-1}$ (Fig. 13). Similar values can be calculated for the equatorial mixed layer (e.g., Wang et al., 1998), although the energy dissipation rate can be considerably higher in regions where bottom friction dominates (e.g., Horne et al., 1996).

The physical phenomenon of disaggregation is not explicitly considered here, but has been important in other situations (e.g., Jackson, 1995; Ruiz, 1997; Hill et al., 1998). The imposition of a maximum aggregate size in this implementation provides one of the functions of a disaggregation model. Such a maximum size had little effect for most of the simulations, as can be seen from the little difference that decreasing or increasing the maximum particle size by changing the grid size to 25 or 35 sections long in the base case, because there was very little mass in the largest particles (Fig. 2, 12, 14). However, in the case of the rectilinear kernel, there was a large accumulation of mass at the upper boundary of the calculation domain. For this situation, explicit inclusion of disaggregation is necessary to maintain the integrity of the system.

Another seasonally varying factor which has not been included here is temperature. Besides the well documented effect on biological metabolism, temperature also affects viscosity. For example, the kinematic viscosity of seawater ($\nu$) ranges from $0.0155$ to $0.0095$ cm$^2$ s$^{-1}$ for temperatures of 5 and 25°C (Jumars et al., 1993). Because the collision rates depend on the viscosity, they will be altered. More significantly, though, will be the change in settling velocity and, hence, vertical flux. Changes in vertical flux, in turn, affect particle concentrations, the dominant factor in determining particle contact rates. O’Melia (1980) has noted how the increase in viscosity and resulting decrease
in particle settling velocity for particles moving from a lake’s epilimnion to its hypolimnion increase particle concentrations despite constant particle fluxes (flux=velocity × concentration).

The additional complexity of solving the coagulation equations in conjunction to those describing biological dynamics has led to attempts to use simpler relationships. For example, Farley and Morel (1986) used simulations on the fate of an initially monodisperse solid to develop simple relationships between total particle concentration and vertical flux. These have been used by Honeyman and Santschi (1989, 1992) to calculate the removal rate of thorium from surface mixed layers by its adsorption onto colloidal particles which subsequently coagulate and settle out. Burd and Jackson (1997) re-solved Farley and Morel’s problem using newer coagulation kernels and fractal scaling for the mass-length relationship, finding a more complicated situation than that of the earlier work. Burd et al. (1999) were forced to solve the situation posed by Honeyman and Santschi numerically, but were able to predict the spectrum describing thorium distribution on particle of different sizes and compare their results with observations.

Attempts to include coagulation in food webs have also used simple relationships between algal concentration and removal rate, in part motivated by the second order relationship between particle collision and particle concentration (e.g., Doney et al., 1996). The results from the more complete calculations performed here show no such simple relationship (Fig. 14). There is no relationship between flux and algal concentration (Fig. 14a) and only a weak relationship with total particle concentration (Fig. 14b). This negative result suggests that it is premature to use simple parameterizations to represent the effect coagulation in planktonic food web.

CONCLUSIONS

The present study examines the expected result of considering coagulation processes in the more complicated situations that occur throughout the annual cycle of an oligotrophic plankton system. Among the findings are that coagulation does have a significant role in controlling particle fluxes out of the mixed layer, particularly in enhancing their episodic nature, and that this particle flux is related to particle abundance and, secondarily, depth of the mixed layer.
ACKNOWLEDGEMENTS

Steve Lochmann collaborated on an earlier version of this model. Adrian Burd provided many helpful comments and suggestions. This work was supported by the National Science Foundation OCE-9726077.

REFERENCES


Table 1: Particle export for different cases. $\psi$ is the ratio of maximum to minimum daily particle flux. Shown are the total annual particle flux as well as the flux of its three components: single algal cells, single fecal pellets, and aggregates. Also shown are the maximum daily fluxes and the maximum daily particle settling rate. The settling velocity for single algae in bap5f1, dap5f1, bap5f1r is 0.03 m d$^{-1}$; it is 0.38 m d$^{-1}$ for the standard $r_a = 10$ μm.

<table>
<thead>
<tr>
<th>Case</th>
<th>Treatment</th>
<th>Integrated annual flux</th>
<th>Maximum daily N flux</th>
<th>$\psi$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Total Alg. Fec. Agg.</td>
<td>vel m d$^{-1}$</td>
<td>mmol m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>mmol N m$^{-2}$ y$^{-1}$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>b0ag</td>
<td>no aggregation</td>
<td>101 47 54 0 0.80</td>
<td>0.36</td>
<td>1.9</td>
</tr>
<tr>
<td>base</td>
<td>standard case</td>
<td>114 44 6 64 1.06</td>
<td>0.68</td>
<td>4.5</td>
</tr>
<tr>
<td>b25</td>
<td>25x25 sectional grid</td>
<td>113 44 6 63 1.05</td>
<td>0.66</td>
<td>4.5</td>
</tr>
<tr>
<td>b35</td>
<td>30x30 sectional grid</td>
<td>114 44 6 64 1.06</td>
<td>0.68</td>
<td>4.5</td>
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<td>baser</td>
<td>Rectilinear kernels</td>
<td>335 13 0 322 23.97</td>
<td>2.21</td>
<td>11.0</td>
</tr>
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<td>basec</td>
<td>Curvilinear kernels</td>
<td>101 46 30 25 0.80</td>
<td>0.38</td>
<td>2.2</td>
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<tr>
<td>ba2p5</td>
<td>$r_a = 2.5$ μm</td>
<td>76 21 28 27 0.64</td>
<td>0.32</td>
<td>2.4</td>
</tr>
<tr>
<td>ba10</td>
<td>$r_a = 10$ μm</td>
<td>160 71 0 89 1.95</td>
<td>1.01</td>
<td>6.0</td>
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<tr>
<td>bgxp5</td>
<td>$\Gamma = 0.5$ s$^{-1}$</td>
<td>108 46 18 44 0.82</td>
<td>0.48</td>
<td>2.9</td>
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<tr>
<td>bgx2</td>
<td>$\Gamma = 2$ s$^{-1}$</td>
<td>113 35 2 76 1.41</td>
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<td>5.9</td>
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<td>bTx0</td>
<td>No colloid release</td>
<td>116 45 5 66 1.09</td>
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<tr>
<td>bTx4</td>
<td>4 x colloid release</td>
<td>107 42 8 57 0.96</td>
<td>0.59</td>
<td>4.0</td>
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<tr>
<td>bn05</td>
<td>N$_0$=5μM</td>
<td>149 43 53 53 1.00</td>
<td>0.62</td>
<td>2.1</td>
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<tr>
<td>bap5f1</td>
<td>$r_a = 0.5$ μm, $r_f = 1$ μm</td>
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<td>0.03</td>
<td>2.0</td>
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<tr>
<td>bap5f1r</td>
<td>$r_a = 0.5$ μm, $r_f = 1$ μm</td>
<td>7 3 1 3 0.05</td>
<td>0.03</td>
<td>2.0</td>
</tr>
<tr>
<td>p3 = 0</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>bref5</td>
<td>No grazing $r_{ij} &lt; 5$ μm</td>
<td>114 44 6 64 1.06</td>
<td>0.68</td>
<td>4.7</td>
</tr>
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<td>bref5T5X</td>
<td>No grazing $r_{ij} &lt; 5$ μm,</td>
<td>116 41 7 68 1.06</td>
<td>0.72</td>
<td>4.7</td>
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<td></td>
<td>4x release</td>
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<td></td>
<td></td>
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<td>bdet0</td>
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<tr>
<td>bT3p47</td>
<td>$r_c = 3.47$ μm</td>
<td>115 46 6 63 0.94</td>
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</tr>
<tr>
<td>bT3p47r</td>
<td>$r_c = 3.47$ μm,</td>
<td>110 46 3 61 0.94</td>
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<td>4.2</td>
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<tr>
<td></td>
<td>$\rho_c = 1.043$ g cm$^{-3}$</td>
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<tr>
<td>bT3xxx</td>
<td>$N_0 = 5$ μM,$r_a = 0.5$ μm,</td>
<td>197 43 73 81 1.42</td>
<td>0.82</td>
<td>2.4</td>
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<tr>
<td></td>
<td>$r_f = 1$ μm</td>
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Table 2: Notation. \( 1 \mu M = 1 \text{ nmol cm}^{-3} = 1 \text{ mmol m}^{-3} \).

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<th>Symbol</th>
<th>Meaning</th>
<th>Default value</th>
<th>Units</th>
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<tr>
<td>( B )</td>
<td>Bacterial concentration</td>
<td></td>
<td>( \mu M )</td>
</tr>
<tr>
<td>( c_i )</td>
<td>Number concentration of ( i ) particles</td>
<td></td>
<td>( \text{cm}^{-3} )</td>
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<tr>
<td>( C_{ij} )</td>
<td>Molar concentration of section ((i, j)) particles</td>
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<td>( \mu M )</td>
</tr>
<tr>
<td>( d_{fr} )</td>
<td>Fractal dimension</td>
<td>2.28</td>
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</tr>
<tr>
<td>( D )</td>
<td>Total detrital concentration</td>
<td></td>
<td>( \mu M )</td>
</tr>
<tr>
<td>( F_z )</td>
<td>Rate of fecal production</td>
<td></td>
<td>( \mu M ) \text{ N d}^{-1}</td>
</tr>
<tr>
<td>( G )</td>
<td>Phytoplankton, detrital loss rate from physical processes</td>
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<td>( \text{d}^{-1} )</td>
</tr>
<tr>
<td>( G_D )</td>
<td>Zooplankton grazing rate on detritus</td>
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<td>( \mu M ) \text{ N d}^{-1}</td>
</tr>
<tr>
<td>( m_i )</td>
<td>Mass of a particle</td>
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<td>g</td>
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<tr>
<td>( \Delta m_i )</td>
<td>Excess mass of a particle</td>
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<td>g</td>
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<td>( M )</td>
<td>Mixed layer depth</td>
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<td>( N_d )</td>
<td>Dissolved N concentration</td>
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<td>( \mu M )</td>
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<tr>
<td>( N_h )</td>
<td>Nitrate (new N) concentration</td>
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<td>( \mu M )</td>
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<tr>
<td>( N_0 )</td>
<td>Subsurface nitrate concentration</td>
<td>2.5</td>
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</tr>
<tr>
<td>( N_r )</td>
<td>Ammonia (regenerated N) concentration</td>
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</tr>
<tr>
<td>( p )</td>
<td>( r_i/r_j ), where ( r_j &gt; r_i )</td>
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<td>—</td>
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<tr>
<td>( P )</td>
<td>Phytoplankton concentration</td>
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<td>( \mu M )</td>
</tr>
<tr>
<td>( r_i )</td>
<td>Particle radius</td>
<td></td>
<td>( \mu m )</td>
</tr>
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<td>( r_a )</td>
<td>Algal radius</td>
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<td>( \mu m )</td>
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<td>( r_c )</td>
<td>Colloid radius</td>
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<tr>
<td>( r_f )</td>
<td>Fecal pellet radius</td>
<td>10</td>
<td>( \mu m )</td>
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<td>( R_{ij} )</td>
<td>Aggregate formation rate by collision of particles</td>
<td></td>
<td>( \text{cm}^{-3} \text{ s}^{-1} )</td>
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<tr>
<td>( S_x )</td>
<td>Rate of biological change in concentration of section ( x )</td>
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<td>( \mu M )</td>
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<tr>
<td>( t )</td>
<td>Time</td>
<td></td>
<td>s</td>
</tr>
<tr>
<td>( T_{ij} )</td>
<td>Rate of particle input</td>
<td></td>
<td>( \mu M ) \text{ N d}^{-1}</td>
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<tr>
<td>( v_i )</td>
<td>Particle fall velocity</td>
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<td>( \text{cm s}^{-1} )</td>
</tr>
<tr>
<td>( \bar{v}_{ij} )</td>
<td>Weighted fall velocity for section ( i, j )</td>
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<td>( \text{cm s}^{-1} )</td>
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<tr>
<td>( Z )</td>
<td>Zooplankton concentration</td>
<td></td>
<td>( \mu M )</td>
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### Notation: continued

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<td>$\alpha$</td>
<td>Probability that particles $i$ and $j$ stick</td>
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<tr>
<td>$\beta_{ij}$</td>
<td>Coagulation kernel for collision of particles $i$, $j$</td>
<td>$\text{cm}^3 \text{ s}^{-1}$</td>
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<tr>
<td>$\beta_{Bri,ij}$</td>
<td>Coagulation kernel for collision of particles $i$, $j$ for Brownian motion</td>
<td>$\text{cm}^3 \text{ s}^{-1}$</td>
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<tr>
<td>$\beta_{ds,ij}$</td>
<td>Coagulation kernel for collision of particles $i$, $j$ for differential sedimentation</td>
<td>$\text{cm}^3 \text{ s}^{-1}$</td>
<td>—</td>
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<tr>
<td>$\beta_{sh,ij}$</td>
<td>Coagulation kernel for collision of particles $i$, $j$ for shear</td>
<td>$\text{cm}^3 \text{ s}^{-1}$</td>
<td>—</td>
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<tr>
<td>$\bar{\beta}_{ijklmn}$</td>
<td>Sectional kernel for interactions between particles in sections $(k, l), (m, n)$ that affect $(i, j)$</td>
<td>$(\mu M N)^{-1} \text{ s}^{-1}$</td>
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<td>$\gamma_1$</td>
<td>Fraction of phytoplankton growth excreted as DON</td>
<td>0.025</td>
<td>—</td>
</tr>
<tr>
<td>$\gamma_c$</td>
<td>Fraction of phytoplankton growth excreted as colloids</td>
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<td>—</td>
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<tr>
<td>$\Gamma$</td>
<td>Shear rate</td>
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<td>$\text{s}^{-1}$</td>
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<td>$\bar{\Gamma}$</td>
<td>Shear rate averaged over the mixed layer</td>
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<td>$\text{s}^{-1}$</td>
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<td>$\epsilon$</td>
<td>Energy dissipation rate</td>
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<td>$\text{cm}^2 \text{ s}^{-3}$</td>
</tr>
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<td>Scaled length, $= r_{d,r}$</td>
<td>$\text{cm}^{d,r}$</td>
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<tr>
<td>$\mu_1$</td>
<td>Phytoplankton specific mortality rate</td>
<td>0.045</td>
<td>$\text{d}^{-1}$</td>
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<tr>
<td>$\mu_4$</td>
<td>Specific rate of detrital breakdown</td>
<td>0.05</td>
<td>$\text{d}^{-1}$</td>
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<tr>
<td>$\nu$</td>
<td>Kinematic viscosity</td>
<td>0.01</td>
<td>$\text{cm}^2 \text{ s}^{-1}$</td>
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<tr>
<td>$\rho_f$</td>
<td>Density of fecal pellet</td>
<td>1.11</td>
<td>g cm$^{-3}$</td>
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<tr>
<td>$\rho_a$</td>
<td>Density of alga</td>
<td>1.08</td>
<td>g cm$^{-3}$</td>
</tr>
<tr>
<td>$\rho_0$</td>
<td>Density of fluid</td>
<td>1.02</td>
<td>g cm$^{-3}$</td>
</tr>
<tr>
<td>$\rho_c$</td>
<td>Density of colloid</td>
<td>1.066</td>
<td>g cm$^{-3}$</td>
</tr>
<tr>
<td>$\sigma$</td>
<td>Phytoplankton average daily specific growth rate</td>
<td>$\text{d}^{-1}$</td>
<td>—</td>
</tr>
<tr>
<td>$\psi$</td>
<td>Maximum to minimum daily flux</td>
<td>$\text{—}$</td>
<td>—</td>
</tr>
<tr>
<td>$\Omega$</td>
<td>Detrital frac. of zoopl. death</td>
<td>0.33</td>
<td>—</td>
</tr>
</tbody>
</table>
FIGURE CAPTIONS

Figure 1: Results for the case of no aggregation ($\alpha = 0$: $h_{\text{agg}}$). A: concentrations of phytoplankton, zooplankton, nitrate, and detritus through time; B: vertical particle fluxes for solitary algal cells, fecal pellets, remaining particles (aggregates), and the total through time; C: average particle velocity of all material. Dotted line indicates the settling speed of a solitary alga; dashed line indicates the depth of the mixed layer.
Figure 2: Results for the base case of aggregation with the fractal coagulation kernels (base). A, B, C as in Fig. 1.
Figure 3: Results for the base case of aggregation with the rectilinear coagulation kernels (*baser*).
A, B, C as in Fig. 1.
Figure 4: Effect of varying algal radius. A: Concentrations of nitrate, phytoplankton and zooplankton; B: Fluxes of solitary algae, fecal pellets and aggregates. Algal radii were+: $r_a = 10 \mu m$; o: $r_a = 5 \mu m$; x: $r_a = 2.5 \mu m (ba10, base, and ba2p5)$. 

Figure 4: Effect of algal radius, a=2.5,5,10 mm
Figure 5: Effect of varying shear. A: Concentrations of nitrate for phytoplankton and zooplankton; B: Fluxes of solitary algae, fecal pellets and aggregates. Shear rates were: +: $\gamma = 0.5 \text{ s}^{-1}$; o: $\Gamma = 1 \text{ s}^{-1}$; x: $\Gamma = 2 \text{ s}^{-1}$ ($bgxp5$, base, and $bgx2$).

Figure 5: Effect of shear, $\Gamma=0.5,1,2 \text{ s}^{-1}$
Figure 6: Effect of varying colloid release rate. A: Concentrations of nitrate for phytoplankton and zooplankton; B: Fluxes of solitary algae, fecal pellets and aggregates. Release rates as a fraction of primary production were +: $\gamma_c = 0$; $\circ$: $\gamma_c = 0.025$; $\times$: $\gamma_c = 0.1$ ($bTx0,$ base, and $bTx4$).
Figure 7: Results for TEP (“colloid”) release as 3.47 µm particle. A: Concentrations of nitrate for phytoplankton and zooplankton; B: Fluxes of solitary algae, fecal pellets and aggregates. Conditions were: ○ standard release rate and density; × standard release rate but with reduced density; +: 4 times standard release rate and reduced density (bT3p47, bT3p47rho, and bT3rhox4).

Figure 7: Vary colloid size, release, density

- phyto.
- zoo.
- nitr.
- ○ bT3p47
- × bT3p47rho
- + bT3rhox4

- phyto
- fecal
- aggreg.
- ○ bT3p47
- × bT3p47rho
- + bT3rhox4

Time (d)
Flux (mmol-N m⁻² d⁻¹)
Concentration (µM-N)
Figure 8: Effect of increasing the subsurface nutrient concentration to $N_0 = 5 \mu M$ (thin, base line) from $N_0 = 2 \mu M$ (thick line).

Figure 8: $N_0=2, 5\mu M$.
Figure 9: Effect of combining the higher subsurface nutrient concentration $N_0 = 5 \ \mu M$ with TEP (colloid) release as $r_c = 3.47 \ \mu m$ particle. ($b T^{3xxx}$)
Figure 10: Two dimensional particle distribution at $t=0$ d for base. The results are shown as the total mass per section (A) and flux per section (B) rather than as the more mathematical two-dimensional particle size spectra. The upper bounds of sections in the $\lambda$ (length) direction are $2 \times (2^{1/d_f} = 1.36 \times)$ those of the lower bounds; excess mass of the upper bounds in the mass direction are also $2 \times$ those of the lower bounds.
Figure 11: Particle size spectrum through time as a function of particle radius. The one-dimensional particle size spectrum was calculated by first converting the molar concentration in each section to particle numbers, summing the number of particles in the different mass dimension for a given length range, and finally dividing this number of particles by the radius range of the sections. A: standard case ($N_0 = 2 \mu M$, base); B: higher subsurface nitrate concentration, $N_0 = 5 \mu M(bN05)$. 
Figure 12: Weighted particle flux spectrum through time as a function of particle radius. The one-dimensional flux spectrum was calculated by summing the mass flux per section in the different mass dimension for a given length range, and finally dividing this number of particles by the radius range of the sections. Weighting by the particle radius makes the area under a curve at a particular time proportional to integrated particle flux. A: standard case \((N_0 = 2 \, \mu M, \text{base})\); B: higher subsurface nitrate concentration, \(N_0 = 5 \, \mu M (bN05)\).
Figure 13: Wind forcing at the Bermuda Atlantic Time series station for 1996, as taken from the sampling vessel. Data were downloaded from the BATS data archive. A: Wind speed; B: Average shear in a 50 m mixed layer, estimated using Eq. 19.
Figure 14: Particle flux as a function of particle concentration. A: as a function of phytoplankton concentration; B: as a function of total particle concentration. Lower line represents the flux if the particles were falling at the speed of single algal cells (0.38 m d$^{-1}$); upper line represents the flux if the particles were falling at the speed of fecal pellets (1.66 m d$^{-1}$) (base, bN05, bT3xx, b0ag).