Influence of coagulation, sedimentation, and grazing by zooplankton on phytoplankton aggregate distributions in aquatic systems

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Abstract. Phytoplankton growing at the surface of lakes and oceans are removed from the water column by gravitational sedimentation and/or zooplankton grazing. Both of these processes are influenced by the aggregation state of the phytoplankton, which, in turn, may be altered through particle-particle coagulation. In this study, we present a mathematical analysis of these phenomena in an attempt to better understand the physical and biological factors that control phytoplankton concentrations in aquatic systems.

During phytoplankton blooms, grazer concentrations are relatively low, the concentration of phytoplankton in the mixed layer is high, and phytoplankton production at the surface is countered by coagulation and sedimentation. In this case, dynamic scaling theory indicates that the concentration of total phytoplankton aggregates $N_0$ and the volume fraction of phytoplankton $N_1$ should decay as power laws of depth $z$: $N_0 \sim z^{-\gamma}$ and $N_1 \sim z^{-e}$. The values of the power law exponents $\gamma$ and $e$ are determined by the physical and chemical processes responsible for coagulation and sedimentation in a given system.

Under nonbloom conditions, the concentration of grazers is relatively high, the phytoplankton concentrations are relatively low, and phytoplankton generated at the surface are quickly transferred to higher-trophic levels by grazing. In this case, $N_0$ and $N_1$ decay with depth in an approximately exponential fashion. These results suggest that the principle mechanism by which phytoplankton are removed from the water column in natural aquatic systems may be differentiated by the depth evolution of $N_0$ and $N_1$.

1. Introduction

On a global scale, phytoplankton are responsible for fixing $\sim 40 \times 10^9$ t of carbon per year, which is 40% of Earth's total primary production [Falkowski, 1994]. The fate of these organisms ultimately determines the fate of the carbon which they fix. Phytoplankton may aggregate with other phytoplankton, detritus, and settle under the influence of gravity [Allredge and Jackson, 1995]. The flux of these aggregates through the water column controls transport of carbon from the surface layers to the benthos, where the carbon may be remineralized, incorporated into sediments, or consumed by benthic organisms [Billett et al., 1983; Smetacek, 1985]. Alternatively, phytoplankton may be consumed by herbivorous grazers and enter the pelagic food web. In this case, the carbon and nutrients contained in the phytoplankton are passed on to higher-trophic levels.

There are many different processes that regulate the concentration of phytoplankton in natural aquatic systems, including growth conditions (light and nutrients) [Raymont, 1963a], zooplankton grazing [Banse, 1992], transport phenomena (ocean currents, wave action, upwelling, and gravitational sedimentation) [Weitenmann et al., 1989], and physicochemical phenomena (coagulation and uptake of trace metals) [Burd and Jackson, 1997; Fowler and Knauer, 1986]. These processes have an unequal impact on the fate of phytoplankton in different systems. For example, during the initial phase of a phytoplankton bloom, coagulation and gravitational sedimentation appear to control phytoplankton concentrations, while grazing is less important [Burd and Jackson, 1997]. During the well-stratified periods of summer, however, phytoplankton growth in the open ocean is nearly completely balanced by grazing [Banse, 1992]. The goal of this paper is to develop a theoretical framework for understanding how coagulation, gravitational sedimentation, and grazing by zooplankton control the vertical distribution of phytoplankton in natural aquatic systems. We accomplish this by solving the general dynamic equation (GDE) that describes these phenomena for a special case where the distribution of phytoplankton below the mixed layer achieves a steady state. Our results are interpreted in the context of dynamic scaling theory for coagulation and sedimentation of particles.

2. Model Development

Consider the water column illustrated in Figure 1. At the surface there is a mixed layer in which most of the primary production takes place [Falkowski, 1994]. The depth of the mixed layer varies from a few meters to a few hundred meters [Falkowski, 1994]. In this paper, we focus on the region below the mixed layer for the following reasons: (1) The mixed layer has been the subject of numerous theoretical investigations [Ackleh and Fitzpatrick, 1997; Burd and Jackson, 1997; Jackson and Lochmann, 1992], while the region below the mixed layer has received less attention, and (2) our results indicate that the manner in which the aggregate size distribution evolves with depth below the mixed layer may provide fundamental information regarding the physical, chemical, and biological processes that control phytoplankton levels there. For simplicity,
The particle distribution function, $n_j(z, t)$, represents the fluid concentration of phytoplankton aggregates composed of $j$ primary particles ($j$-mers); $K_{ij}$ is the rate constant for coagulation between $i$-mers and $j$-mers; and $R_s$ and $R_g$ are the sedimentation and grazing removal terms, respectively. In this equation, the temporal change in the concentration of $j$-mers (term on left-hand side) depends on their formation by coagulation of particles of size $i$ and $j-i$ (first term on right-hand side), loss by coagulation with all other sized aggregates (second term on right-hand side), removal from the fluid phase by gravitational sedimentation (third term on right-hand side), and grazing by zooplankton (last term on right-hand side). Our goal is to derive from this GDE mathematical expressions for the phytoplankton aggregate size distribution, $n_j$, the concentration of total phytoplankton aggregates, $N_0 = \sum_j n_j$, and the volume fraction of phytoplankton which is proportional to $N_0 = \sum_j j n_j$. In sections 2.1, 2.2, and 2.3 we develop mathematical expressions for $K_{ij}$, $R_s$, and $R_g$.

2.1. Coagulation Kernel

The coagulation kernel $K_{ij}$ appearing in (1) represents the rate constant for the coagulation between $i$-mers with $j$-mers. Its magnitude reflects the transport processes that bring aggregates into proximity and the physical and surface-chemical interactions that occur between aggregates upon close approach. To account for these processes mathematically, the coagulation kernel is often expressed as the product of a collision frequency function $\beta_{ij}$ and an attachment efficiency $\alpha_{ij}$:

$$K_{ij} = \alpha_{ij} \beta_{ij}$$

where $\beta_{ij}$ represents the collision frequency between $i$-mers and $j$-mers under one or more transport mechanisms and $\alpha_{ij}$ represents the fraction of these collisions that result in aggregation. Commonly employed collision frequency functions are listed in Table 1.

Kernels may also be described in terms of more general mathematical properties. For example, van Dongen and Ernst [1985] (hereafter referred to as VDE) classify kernels on the basis of two parameters, $\lambda$ and $\mu$, which were calculated for each kernel by assuming that both the hydrodynamic radius and the collision cross-section radius scale with aggregate size as $r_i = i^{0.5} r_1$. Values $\lambda$ and $\mu$ describe the homogeneity and the small $i/j$ limit of the collision frequency, respectively. DLA and RLA are diffusion and rate limited aggregation, respectively. Value $\epsilon$ is the turbulent energy dissipation rate, $v$ is the kinematic viscosity of the fluid, $T$ is the absolute temperature, $k_b$ is the Boltzman constant, $r_1$ is the radius of a monomer, $\mu_0$ is the dynamic viscosity of the fluid, $p_f$ is the density of the fluid, and $\omega$ is an exponent characterizing the surface area of an aggregate.

### Table 1. Expressions for Several Collision Frequencies

<table>
<thead>
<tr>
<th>Mechanism</th>
<th>Collision Frequency, $\beta_{ij}$</th>
<th>$\lambda$</th>
<th>$\mu$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fluid shear</td>
<td>$1/(\epsilon/v)^{0.5} (r_i + r_j)^2$</td>
<td>$3/D$</td>
<td>0</td>
</tr>
<tr>
<td>Rectilinear</td>
<td>$10(\epsilon/v)^{0.5} (r_i + r_j)^2 r_i$, where $r_i \ll r_j$</td>
<td>$3/D$</td>
<td>0</td>
</tr>
<tr>
<td>Curvilinear</td>
<td>$0.5 \pi (r_i + r_j)^2</td>
<td>w_i - w_j</td>
<td>1 + 1/D</td>
</tr>
<tr>
<td>Differential settling</td>
<td>$0.5 \pi (r_i + r_j)^2</td>
<td>w_i - w_j</td>
<td>$</td>
</tr>
<tr>
<td>Rectilinear</td>
<td>$2k_b T / 3p_f \mu_0 (1/r_i + 1/r_j)(r_i + r_j)$</td>
<td>$0$</td>
<td>$-1/D$</td>
</tr>
<tr>
<td>Curvilinear</td>
<td>$2k_b T / 3p_f \mu_0 (1/r_i + 1/r_j)(r_i + r_j)$</td>
<td>$1$</td>
<td>0</td>
</tr>
<tr>
<td>Brownian diffusion, DLA</td>
<td>$2k_b T / 3p_f \mu_0 (1/r_i + 1/r_j)(r_i + r_j)$</td>
<td>$1$</td>
<td>0</td>
</tr>
<tr>
<td>RLA</td>
<td>$K_{ij}(i)^{\omega}$</td>
<td>$2\omega$</td>
<td>$\omega$</td>
</tr>
</tbody>
</table>

Values $\lambda$ and $\mu$ were calculated for each kernel by assuming that both the hydrodynamic radius and the collision cross-section radius scale with aggregate size as $r_i = i^{0.5} r_1$. Values $\lambda$ and $\mu$ describe the homogeneity and the small $i/j$ limit of the collision frequency, respectively. DLA and RLA are diffusion and rate limited aggregation, respectively. Value $\epsilon$ is the turbulent energy dissipation rate, $v$ is the kinematic viscosity of the fluid, $T$ is the absolute temperature, $k_b$ is the Boltzman constant, $r_1$ is the radius of a monomer, $\mu_0$ is the dynamic viscosity of the fluid, $p_f$ is the density of the fluid, and $\omega$ is an exponent characterizing the surface area of an aggregate.
where $\mu$ is the dynamic viscosity of the fluid and the hydrodynamic radius, $R_h$, represents the radius of a sphere that experiences the same drag force as the aggregate at the same translational velocity. In general, the hydrodynamic radius of an aggregate grows with aggregate size $j$ according to the following power law relationship [Miyazima et al., 1987; Rogak and Flagan, 1990]:

$$R_h \sim r_j j^\mu$$

where $r_j$ is the primary particle radius and the magnitude of exponent $\alpha$ depends on the degree to which primary particles in the aggregate occupy the embedded space, or the aggregate’s fractal dimension, $D$. The following relationship between $\alpha$ and $D$ is often assumed [Rogak and Flagan, 1990]:

$$\alpha = 1/D$$

Combining (8) and (9), we obtain the following expression for the drag force:

$$F_D = 6\pi \mu_r r_j j^\omega w_j$$

An expression for the terminal fall velocity of a $j$-mer can be obtained by assuming an equality between the left and right-hand sides of (11) and setting (11) equal to (7):

$$w_j = w_1 j^{1-\omega}$$

where

$$w_1 = \frac{v_1 (\rho_p - \rho_f) g}{6 \pi \mu_r r_1}$$

### 2.3. Grazing

The removal of phytoplankton aggregates by zooplankton in the water column can be represented mathematically as

$$R_g = k_j(z)n_j$$

where $k_j(z)$ is defined as the rate at which a population of zooplankton removes $j$-mers per unit time at a particular depth, $z$. The grazing rate constant depends on the clearance rate for $j$-mers, $\psi_j$ (with units of volume/time/grazer), and the concentration of grazers, $G(z)$, present at depth $z$:

$$k_j(z) = \psi_j G(z)$$

A number of researchers have studied the relationship between the size of a food particle and the rate it is cleared from suspension by zooplankton, $\psi$ [e.g., Frost, 1972; Gaudy, 1974; Gonzalez et al., 1990; Monger and Landry, 1991; Mullin, 1963; Paffenhöfer, 1971; Richman and Rogers, 1969; Wimpenny, 1973]. Monger and Landry [1990] used a “force-balance model” to theoretically examine this relationship for passive feeding microzooplankton, like zooflagellates, and determined that the clearance rate of a grazer on a particle increases with the particle’s radius: $\psi \propto \text{radius}$. Because phytoplankton aggregates are fractal in nature [Logan and Wilkinson, 1990], we adopted the hydrodynamic radius to relate the clearance rate to the size of a phytoplankton aggregate: $\psi \propto R_h \propto j^\omega$. Accordingly, the following expression applies for the clearance rate of $j$-mers:

$$\psi_j = \psi_1 j^\omega$$

where $\psi_1$ is the clearance rate of a single phytoplankton particle and the exponent $\alpha$ determines how the hydrodynamic radius varies with the number of constituent particles (see (9) and (10)). The magnitude of $\psi_j$ depends on the physical feeding mechanisms employed by the zooplankton under consideration. The size, swimming speed, and number of cilia, fla-
gella, and pseudopodia will determine the volume of water processed by the zooplankton [Kiefer and Berwald, 1992]. Examples of clearance rates of zooplankton for different size phytoplankton can be found in, or extrapolated from, the studies by Frost [1972], Monger and Landry [1991], and Gonzalez et al. [1990]. In formulating a mathematical expression for grazing, we have assumed that (1) the zooplankton present are passive feeders that encounter food by direct interception, (2) the nutritional value attributed to the phytoplankton is high, and (3) the clearance rate increases linearly with the aggregate’s hydrodynamic radius. With respect to the last assumption, it has been found that for any individual zooplankton species there is a limited range of food sizes for which the clearance rate increases with prey size [Kiefer and Berwald, 1992]. For food particles that are too small or too large, it is difficult for an individual zooplankton to handle the prey because of physical constraints. Hence the relationship employed here should be regarded as a first approximation of a complex phenomenon that is only partially understood at the present time [Hansen et al., 1997].

The concentration of grazers $G$ in the water column varies seasonally, daily, regionally, and with depth [Raymont, 1963b]. This spatiotemporal variability in zooplankton concentration is controlled by many factors, including primary production rates, presence of predators, nutrient availability, and sunlight intensity [Raymont, 1963c]. Diel migration of zooplankton affects the vertical distribution of most zooplankton [Raymont, 1963d]. After sunset, some species of zooplankton migrate to the surface layers to feed when there is little danger of being seen by a predator. During daylight hours the zooplankton retreat to greater depths. In this study, we do not explicitly take into account the diel migration of zooplankton but rather consider two “static” grazer profiles that may be representative of night and day conditions (see Figure 1). For the exponential distribution the concentration of grazers declines exponentially from a maximum of $G_0$ directly below the mixed layer:

$$G(z) = G_0 e^{-z/\delta}$$

(16)

The parameter $\delta$ represents the characteristic length scale over which the grazer concentration drops a factor 1/e. For the unimodal distribution the grazer concentration increases with depth from $G = 0$ at $z = 0$, reaches a maximum of $2G_0/e^2$ at $z = 2\delta$, then declines exponentially for $z > 2\delta$:

$$G(z) = G_0 2(z/\delta)^2 e^{-z/\delta}$$

(17)

3. Mathematical Solutions

After substituting previously derived expressions for $K_{ij}$, $R_\bullet$, and $R_p$ into (1) and letting the unsteady term go to zero, we obtain the following GDE for the system illustrated in Figure 1:

$$0 = \frac{K_{ij}}{2} \sum_{r=1}^{i-j} [i(j-i)]^n n_{ij} - K_{ij} \sum_{r=1}^{i-j} (ij)^n n_{ij} - w_j^{1-\alpha} d n_j / dz$$

$$- \psi_j j^\alpha G(z) n_j$$

(18)

To minimize the number of separate variables that require consideration, the above equation can be recast in a nondimensional form by multiplying all terms by $2/K_{11}N_0^2(0)$:

$$0 = \sum_{r=1}^{i-j} [i(j-i)]^n \bar{n}_{ij} - 2 \sum_{r=1}^{i-j} (ij)^n \bar{n}_{ij} - j^{-\alpha} \frac{d \bar{n}_j}{dz}$$

$$- \bar{\psi}_j j^\alpha \bar{G}(z) \bar{n}_j$$

(19)

The reduced variables in this equation are defined as follows:

1. Value $\bar{n}_j = n_j/N_0(0)$ represents the concentration of $j$-mers at some depth normalized by the concentration of total aggregates at $z = 0$.

2. Value $\bar{G}(z) = G(z)/G_0$ represents the characteristic growth timescale $\gamma_G$ for the scavenging of single particles by grazers at $z = 0$.

3. Value $f(z/\delta)$ is a function that determines the shape of the grazer distribution with depth. The parameter $\delta = \delta/z/\tau_\gamma$ represents the characteristic time for a single phytoplankton particle to settle through the portion of the water column where grazers are most abundant divided by the characteristic timescale for coagulation $\tau_\gamma$. The function $f$ takes on the following forms for the exponential and unimodal distribution, respectively: $f(z) = e^{-z}$ and $f(z) = \frac{1}{2} (1 + e^{-z})$.

Equation (19) represents an infinite set of coupled differential equations for which no solutions are presently known. Attempts to solve this equation numerically are complicated by the so-called “finite domain” problem, in which an infinite number of aggregate size classes must be integrated on machines with finite memory [Kobenst and Duncan, 1986]. Although several numerical schemes have been proposed to address the finite domain problem [e.g., Lawler et al., 1980; Williams, 1981], each is subject to the limitations and errors inherent in such efforts.

An exact solution to (19) can be obtained for the choice of $\alpha = \omega = 1/2$. To a first approximation, $\alpha$ is related to the fractal dimension of aggregates through (10), and therefore a choice of $\alpha = 1/2$ corresponds to a fractal dimension of $D = 2$. Logan and Wilkinson [1990] have measured the fractal dimension of marine aggregates and found that $D$ falls in the range of $1.26 < D < 2.14$; hence, our choice of $D = 2$ is within natural limits. The choice $\omega = 1/2$ implies that our coagulation kernel has a homogeneity $\lambda = 1$ and $\mu = 1/2$. Ball et al. [1987] have shown that $\lambda = 1$ and $\mu = 0$ for reaction-limited aggregation (RLA) in which many particle-particle collisions occur for every sticking event. Our kernel fulfills the homogeneity requirement for RLA when $\omega = 1/2$ but fails to match the condition on $\mu$. Because $\mu > 0$ our solution will underestimate the reactivity between small and large clusters relative to RLA. It has been postulated that the collision efficiency favors the coagulation between equal-sized clusters in natural aquatic systems [McCave, 1984] which would be consistent with $\mu > 0$, as assumed here. The choice of $\lambda = 1$ is also not too different from the homogeneity of the kernel for orthokinetic coagulation, for which $\lambda = 1.5$ and $\mu = 1$ if $D = 2$ (see Table 1). Although the values of the parameters $\lambda$ and $\mu$ for orthokinetic coagulation do not exactly match the values for the kernel employed in this study, the basic mathematical properties of both kernels are the same; that is, interactions between clusters of the same size increase with size, and coagulation occurs predominately between clusters of the same size. The choice of the constant $K_{11}$ would ultimately determine whether the ker-
The mathematical solutions for the particle size distribution, total particle size, and volume fraction are derived in the appendix and given as follows:

\[
\tilde{n}_j(\tilde{z}) = \frac{x^{j-1}}{(1 + x)^{j-1}} I(\tilde{z} = 0) I(\tilde{z})
\]  

(20a)

\[
\frac{N_0(\tilde{z})}{N_0(0)} = Li_{-\frac{1}{2}} \left[ x \frac{1}{(1 + x)^{\frac{1}{2}}} \frac{I(\tilde{z} = 0)}{I(\tilde{z})} \right] \frac{1}{x(1 + x)}
\]  

(20b)

\[
\frac{N_1(\tilde{z})}{N_1(0)} = Li_{-\frac{1}{2}} \left[ x \frac{1}{(1 + x)^{\frac{1}{2}}} \frac{I(\tilde{z} = 0)}{I(\tilde{z})} \right] \frac{1}{x(1 + x)}
\]  

(20c)

In these expressions, \(Li[y]\) is the polylogarithmic function,

\[
Li[y] = \sum_{i=1}^{\infty} \frac{y^i}{i^\alpha}
\]  

(21)

\(I(\tilde{z})\) is an integrating factor determined by the grazer distribution,

\[
I(\tilde{z}) = \exp \left[ \int \tilde{G}_0 f(\tilde{z}) \, d\tilde{z} \right]
\]  

(22)

and \(x\) is a scaled depth,

\[
x = \int_0^{\tilde{z}} \frac{I(\tilde{z} = 0)}{I(\tilde{z})} \, d\tilde{z}
\]  

(23)

These solutions are valid for any choice of the spatial distribution of grazers \(G(z)\), so long as it is a continuous function of depth.

4. Model Predictions

4.1. Predictions for \(N_0\) and \(N_1\)

Grant et al. [1996] showed that when particles undergo steady state coagulation and settling, the aggregate size distribution predicted by the GDE develops a shape that is invariant with depth (i.e., "self-similar") and independent of the particle concentration at \(z = 0\) (i.e., "universal"). In this case, the aggregate size distribution can be written in the following factored form:

\[
n_i \approx s(z)(r(z))\eta \xi(\eta)
\]  

(24)

where \(\eta\) is a reduced form of the aggregate size, \(\eta = j/r(z)\), \(s(z)\) and \(r(z)\) are functions of depth, and \(\xi\) determines the "shape" of the aggregate size spectrum. Substituting this factored form of the aggregate size distribution back into the GDE for steady state particle coagulation and sedimentation, a similarity analysis reveals that \(N_0\) and \(N_1\) should both decay like power laws with depth, where the power law exponents are determined by the homogeneity of the governing coagulation kernel \(\lambda\) and the way the hydrodynamic radius varies with aggregate size \(\alpha\):

\[
N_0 \approx \tilde{z}^{-\gamma} \quad \gamma > 0
\]  

(25a)

\[
N_1 \approx \tilde{z}^{-\epsilon} \quad \epsilon > 0
\]  

(25b)

where \(\gamma = (2 - \alpha)(3 - 2\alpha - \lambda)\) and \(\epsilon = (1 - \alpha)(3 - 2\alpha - \lambda)\).

From a practical point of view, these results suggest that when these two moments of the aggregate size distribution are plotted in a double logarithmic format against depth, they should appear as straight lines with slopes that reflect the underlying coagulation and sedimentation mechanisms operative in a particular system.

When Grant et al. [1996] tested this idea on phytoplankton volume distributions published by Weilenmann et al. [1989] for Lake Zurich, Switzerland, they found that \(N_0\) and \(N_1\) both decayed like power laws with depth. However, interpretation of the power law exponents was complicated by the fact that it was not clear what effect grazers might have on the similarity predictions for \(N_0\) and \(N_1\). For the model solution derived in the present paper (see (20a), (20b), and (20c)), we have assumed that \(\alpha = 1/2\) and \(\lambda = 1\). Therefore, if grazers were not present in the water column, we would expect that \(N_0\) and \(N_1\) would decay like power laws of depth with exponents given by \(\epsilon = 0.5\) and \(\gamma = 1.5\) (see equations (25a) and (25b)).

In Figure 2, we present model predictions for \(N_0\) and \(N_1\) corresponding to three different grazer distributions: no grazers (first column), exponentially distributed grazers (second column), and unimodally distributed grazers (third column). For the case where there are no grazers, our solutions for \(N_0\) and \(N_1\) are given by (20b) and (20c) with

\[
I(\tilde{z}) = 1
\]  

(26a)

\[
x = \tilde{z}
\]  

(26b)

The resulting expressions are plotted against reduced depth \(\tilde{z}\) in Figure 2d. Consistent with power law expressions for \(N_0\) and \(N_1\), these two moments appear linear when plotted in the double logarithmic format employed in the figure. The power law exponents, as represented by the slope of the curves in Figure 2d, can be computed directly from our solutions, and these values are plotted in Figure 2g. As predicted by similarity theory, the power law exponents for \(N_0\) and \(N_1\) \((\gamma \text{ and } \epsilon \text{, respectively})\) achieve constant values of 1.5 and 0.5, respectively.

When zooplankton are present in the water column, the variables \(x\) and \(I(\tilde{z})\) appearing in (20a)-(20c) take on the following expressions for the exponential distribution,

\[
x = \tilde{z} - e^{-\tilde{z}} \left[ E[\tilde{G}_0 \tilde{\delta}] - E[\tilde{G}_0 e^{-\tilde{z}}] \right]
\]  

(26d)

and for the unimodal distribution,

\[
x = \left[ e^{\tilde{z} - e^{-\tilde{z}} \tilde{G}_0 \tilde{\delta}} - e^{-\tilde{z} - e^{-\tilde{z}} \tilde{G}_0 \tilde{\delta}} \right] / (2\tilde{G}_0 \tilde{\delta}) \tilde{G}_0 e^{-\tilde{z} - e^{-\tilde{z}} \tilde{G}_0 \tilde{\delta}}
\]  

(26f)

where \(E[y]\) = \(\int_{e^{-\tilde{z}}} \tilde{G}_0 \tilde{\delta} f(y) \, dy\).

Plots of \(N_0\) and \(N_1\) for these two different grazer distributions are shown in the second and third columns of Figure 2, for the choice of \(\tilde{G}_0 = 2 \times 10^{-5}\) and \(\tilde{\delta} = 10^2\). The same total number of grazers are present in the water column in these two example grazer distributions. The fact that there appears to be more grazers associated with the exponential distribution is an artifact of the logarithmic presentation. Interestingly, the presence of grazers in the water column only affects the depth evolution of \(N_0\) and \(N_1\) at intermediate depths \((10^3 < \tilde{z} < 10^4)\). The reason grazers do not affect \(N_0\) and \(N_1\) for \(\tilde{z} < 10^4\)
follows from our mathematical formulation of the grazing process: We assume that the clearance rate increases in proportion to the hydrodynamic radius of the phytoplankton aggregates. Hence scavenging of the phytoplankton occurs most efficiently at intermediate depths where the phytoplankton are present in large clusters. At intermediate depths \((10^4 < \bar{z} < 10^7)\), the moments deviate significantly from the power law behavior predicted by similarity theory, as is manifested by the "bumps" in the curves for \(\tilde{N}_0\) and \(\tilde{N}_1\) (Figures 2e and 2f) and the excursions in the calculated power law exponent values (Figures 2h and 2i). Presumably, if the phytoplankton leaving the mixed layer were aggregated, grazers would impact the values of \(\tilde{N}_0\) and \(\tilde{N}_1\) at a shallower depth.

For \(\bar{z} > 10^7\) the moments appear to recover their power law behavior, and the power law exponents reestablish the values predicted by similarity theory. At these large depths, the grazer concentrations have dropped to near zero and therefore grazing rates are low, although this observation alone cannot account for the reestablishment of the power laws. The power laws for \(\tilde{N}_0\) and \(\tilde{N}_1\) are reestablished for \(\bar{z} > 10^7\) because of the "universality" of steady state coagulation and sedimentation. As the phytoplankton aggregates settle out of the region where grazing has the most impact, coagulation and sedimentation are the dominant processes, and \(\tilde{N}_0\) and \(\tilde{N}_1\) have no "memory" of grazing that occurred at shallower depths.

The plots presented in Figure 2 are for a particular choice of the parameters \(\tilde{G}_0\) and \(\delta\). The extent to which zooplankton grazing perturbs the power laws for \(\tilde{N}_0\) and \(\tilde{N}_1\) depends on the product \(\tilde{G}_0 \times \delta\). Also, the reduced depth at which the grazers impact \(\tilde{N}_0\) and \(\tilde{N}_1\) is determined by the magnitude of \(\tilde{G}_0\). Figures 3 and 4 illustrate these points. In Figure 3 we have...
plotted the power law exponents calculated for the exponentially distributed grazers for $G_o = 10^{-2}$ and for three different choices of the parameter $G_o \times \delta$. This last parameter represents the characteristic time $\delta/w$, that single phytoplankton spend settling through the portion of the water column dominated by grazers, divided by the characteristic time $\tau_o$ for the scavenging of single phytoplankton particles by grazers at $z = 0$. Grazing has little influence on the power law behavior of $N_o$ and $N_1$ when the settling time is short and the grazing time is large (i.e., $G_o \times \delta = 0.1$ in Figure 3). As $G_o \times \delta$ is increased above this value, the magnitude of the perturbation becomes larger, and it extends over a larger range of depths. When $G_o \times \delta$ is very large (>10), most of the phytoplankton are lost to grazers and both $N_o$ and $N_1$ decay with depth according to the following expressions for exponentially distributed grazers:

$$N_o, N_1 \approx \exp\left[\bar{G}_o \delta (e^{-\delta} - 1)\right] \quad (27a)$$

and for unimodally distributed grazers

$$N_o, N_1 \approx \exp\left[\bar{G}_o \delta (e^{-\delta} + 2e^{-\delta} - 2\delta^2)/2\delta^2 - 1\right] \quad (27b)$$

If $G_o \times \delta$ is sufficiently large to perturb the power law behavior of $N_o$ and $N_1$, the reduced depth at which the perturbation occurs increases with decreasing $G_o$, as illustrated for two choices of this parameter in Figure 4.

To summarize, $N_o$ and $N_1$ evolve with depth differently depending on whether sedimentation or grazing is the dominant sink for phytoplankton. In the former case, $N_o$ and $N_1$ are predicted to decay like power laws of depth with exponents that can be mathematically related to the underlying physical and chemical processes responsible for coagulation and sedimentation. In the latter case, $N_o$ and $N_1$ decline with depth in an approximately exponential fashion. For the mixed case, where both removal processes are important, the depth evolution of $N_o$ and $N_1$ depends in detail on the relative magnitude of grazers and phytoplankton at the surface, the spatial distribution of grazers, and clearance rates of the dominate zooplankton species considered.

What does the model tell us about the likelihood that power laws for $N_o$ and $N_1$ will occur in ocean or lakes systems? To address this question we, (1) compiled estimates for each of the model parameters assuming either bloom or nonbloom conditions (see Table 2), (2) assumed that the collision frequency function can be estimated from the rectilinear formulation of the shear kernel (see Table 1), (3) assumed that the zooplankton are distributed exponentially with depth with $\delta = 100$ m, and (4) assumed that the maximum number of grazers found during bloom conditions is an order of magnitude less than that used for the nonbloom conditions.

![Figure 4. The effect $G_o$ has on the power law behavior of $N_o$ and $N_1$ when grazers are distributed exponentially and $G_o \times \delta = 5$.](image)

Table 2. Hypothetical Ocean Parameters

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\delta$</td>
<td>100 m$^2$</td>
</tr>
<tr>
<td>$\beta_{1,1}$</td>
<td>$10^{-19}$ m$^2$/s particles$^b$</td>
</tr>
<tr>
<td>$\alpha_{1,1}$</td>
<td>1.0</td>
</tr>
<tr>
<td>$d_{i}$</td>
<td>2.0 $\mu$m$^d$</td>
</tr>
<tr>
<td>$\psi_1$</td>
<td>$0.2$ g/cm$^3$c</td>
</tr>
<tr>
<td>$w_i = d_i(\Delta \rho)/18 \mu_w$</td>
<td>$1 \times 10^{-15}$ m$^3$/grazer s$^d$</td>
</tr>
<tr>
<td>$K_{11} = \alpha_{1,1} \beta_{1,1}$</td>
<td>$10^{-19}$ m$^3$/particles</td>
</tr>
</tbody>
</table>

*Estimate of depth below mixed layer where grazer numbers fall to $1/e$ of their maximum value.

Following Burd and Jackson [1997], we use a shear rate of $s/v = 1.0$ s$^{-1}$ for the rectilinear formulation of the shear kernel (see Table 1).

We assume every collision between phytoplankton results in a sticking event.

Diameter of A. anophagefferens reported by Smaaya and Villareal [1989] for a bloom event in Narragansett Bay.

Burd and Jackson [1997] estimate $\rho_p = 1.2$ g/cm$^3$ is typical for algal cells. We take $\rho_p = 1.0$ g/cm$^3$.

Obtained by extrapolating data of Monger and Landry [1991].

Concentration of algal cells during nonbloom conditions approximated to be $3 \times 10^9$ s$^{-1}$ for the rectilinear formulation of the shear kernel (see Table 1).

Prior to a spring bloom, the concentration of zooplankton is relatively low. Here we choose a concentration $1 \times 10^9$ s$^{-1}$ that is typical for nonbloom conditions.

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m below the bottom of the mixed layer, and the similarity predictions for $\gamma$ and $\epsilon$ are sustained over the rest of the water column. In contrast, for the nonbloom condition (Figure 5a), $N_0$ and $N_1$ do not achieve power law status except for physically unreasonable depths in $>10$ km below the bottom of the mixed layer. These predictions are consistent with previous suggestions that coagulation and sedimentation will dominate phytoplankton dynamics only during bloom events [Billet et al., 1983; Riebesell, 1991a, b; Wassmann et al., 1990]. Importantly, our results suggest that the power law behavior of $N_0$ and $N_1$ predicted for phytoplankton blooms may reveal much about the underlying physical and chemical processes at work.

4.2. Aggregate Size Distribution

In this section, we examine how coagulation, sedimentation, and grazing influence the phytoplankton aggregate size distributions that evolve with depth. As mentioned earlier, when no zooplankton are present in the water column, the aggregate size distribution $\tilde{N}_r$ adopts a self-similar form below some critical depth and the size distribution can be written in the factored form given by (24). For the case where there are no grazers present in the water column, $I(2) = 1$, and the expressions for $\tilde{N}_r(s)$ and $\tilde{N}_r$ reduce to those given by (28a) and (28b). These results indicate that the aggregate size distribution that develops in the presence of grazers can still be described as self-similar and that the exact nature of the functions $s(\tilde{z})$ and $\tilde{n}$ depends in detail on the vertical distribution of zooplankton, as represented through the functionality of $I(2)$.

4.3. Phytoplankton Partitioning

What factors determine whether carbon fixed at the surface enters the pelagic food web or settles to the benthos? Our mathematical solutions provide a first-order answer to this question. The fraction of phytoplankton leaving the mixed layer that is lost to zooplankton is given mathematically as follows:

$$F = \int_0^\infty \left( \tilde{G}_z f(z/\delta) \sum_{r=1}^n j \tilde{n}_r \right) dz$$

(30)

If we substitute our solutions for $\tilde{n}_r$ into (30), we obtain the following simple result, which is valid for both exponentially and unimodally distributed grazers:

$$F = 1 - \exp(-\tilde{G} \times \delta)$$

(31)
This equation predicts that the flux of phytoplankton to higher trophic levels is controlled exclusively by the product $G_0 \times \delta$ (see Figure 7). When this parameter is unity, the phytoplankton mass is roughly equally partitioned between the benthos and zooplankton. When $G_0 \times \delta > 1$, the majority of phytoplankton leaving the mixed layer are recycled to higher-trophic levels via zooplankton, and when $G_0 \times \delta < 1$, most of the phytoplankton aggregates fall to the bottom to be incorporated into sediments or consumed by benthic organisms. It is important to acknowledge that our model does not incorporate the mineralization of phytoplankton by bacterial degradation; this process may play a major role in determining how the planktonic carbon is partitioned in the aquatic community [Landry, 1992].

5. Conclusions

Much progress has been made over the years in elucidating the individual processes that affect phytoplankton concentrations in natural aquatic systems. In this study, we investigated the combined effect these processes have on phytoplankton distributions by directly solving the GDE that describes their coagulation, sedimentation, and removal by zooplankton grazing.

In solving this GDE, it was necessary to make several simplifying assumptions, which limit the solution’s applicability to natural systems. One of the potentially restrictive assumptions is that the particle size distribution maintains a steady state throughout the water column. In practice, both the phytoplankton distributions and the zooplankton profiles will fluctuate on diel and seasonal timescales. However, our solutions may still apply if the timescale associated with the relaxation of the particle size distributions to their steady state condition is sufficiently short, and the total concentration of grazers at the surface ($N_0(z = 0)$) and grazer distribution ($G(z)$) vary slowly with time. Further research is needed to determine if these “quasi-steady state” conditions are likely to prevail in natural systems. We also assume that single phytoplankton particles flux from the mixed layer at a constant rate. In reality, aggregation occurs in the mixed layer and aggregates may flux...
from this region as well. However, because of the universality of coagulation and sedimentation, the particle size distributions that develop at depth should have no memory of the aggregation state of phytoplankton near the surface.

When zooplankton concentrations are low, our solution to the GDE can be described using the language of dynamic scaling theory. Namely, the aggregate size distribution develops a shape that is self-similar and universal, and the total particle concentration $N_0$ and the particle volume fraction $N_1$ decay like power laws of depth. The power law exponents can be directly related to the physical and chemical processes responsible for coagulation and sedimentation. When grazers are present in the water column at high concentrations, the phytoplankton size distributions are still self-similar, but $N_0$ and $N_1$ decay exponentially with depth. From a practical point of view these results suggest a simple methodology for distinguishing between systems that are dominated by coagulation and sedimentation on the one hand and zooplankton grazing on the other hand. In the former case, $N_0$ and $N_1$ should decay like power laws of depth with exponents that are within the bounds dictated by similarity theory (see (25a) and (25b)), while in the latter case, both moments should decay exponentially with depth.

Our model also provides a conceptual framework for determining whether phytoplankton settling out of the mixed layer are consumed by zooplankton or escape to the benthos. The partitioning of phytoplankton between these two pathways is determined by the magnitude of a single dimensionless number $G_0 \times \delta$, which represents the ratio of timescales for sedimentation and for grazing. When $G_0 \times \delta$ is computed for oceans, we find that its magnitude is in the range where small changes in the values of key system variables (like the concentration of phytoplankton at the surface) have a significant influence on the fraction of phytoplankton partitioned between these two pathways.

**Appendix**

In this appendix, we derive the expressions for $\bar{N}_0$, $\bar{N}_1$, and $\bar{N}_2$ presented in the text. We begin by moving the third term on the right-hand side of (19) to the left-hand side and rewriting the equation in terms of a new dependent variable $p_j$.

\[
\frac{dp_j}{d\bar{z}} = \sum_{i=1}^{j-1} [(j - i)]^{a+\alpha-1} p_i p_{j-i-1} - 2 \sum_{i=1}^{\infty} (ij)^{a+\alpha-1} p_i p_j - \bar{G}_0 f(\bar{z} / \delta) j^{a+\alpha-1} p_j \tag{A1}
\]

The explicit dependence of the right-hand side on $i$ and $j$ can be eliminated by choosing $\omega = \alpha = 1/2$.

\[
\frac{dp_j}{d\bar{z}} = \sum_{i=1}^{j-1} p_i p_{j-i-1} - 2 \sum_{i=1}^{\infty} p_i p_j - \bar{G}_0 f(\bar{z} / \delta) p_j \tag{A2}
\]

This equation can be further simplified by applying an integrating factor $I(\bar{z})/I(\bar{z} = 0)$, where

\[
I(\bar{z}) = \exp \left[ \int_{\bar{z}}^{1} \bar{G}_0 f(\bar{z} / \delta) d\zeta \right] \tag{A3}
\]

and defining a new dependent variable $b_j = p_j I(\bar{z})/I(\bar{z} = 0)$.

\[
\frac{I(\bar{z})}{I(\bar{z} = 0)} \left( \frac{db_j}{d\bar{z}} \right) = \sum_{i=1}^{j-1} K_{i,j} b_i b_{j-i-1} - 2 \sum_{i=1}^{\infty} K_{i,j} b_i b_j \tag{A4}
\]

A change of variables is made such that $d/dx = I(\bar{z})/I(\bar{z} = 0)$.$d/d\bar{z}$:

\[
\frac{db_j}{dx} = \sum_{i=1}^{j-1} K_{i,j} b_i b_{j-i-1} - 2 \sum_{i=1}^{\infty} K_{i,j} b_i b_j \tag{A5}
\]

which corresponds to

\[
x = \int_{0}^{1} \frac{I(\bar{z} = 0)}{I(\bar{z})} d\zeta \tag{A6}
\]

Equation (A5) is to be solved subject to the boundary conditions

\[
b_j(\bar{z} = 0) = 1 \tag{A7a}
\]

\[
b_{j>2}(\bar{z} = 0) = 0 \tag{A7b}
\]

These boundary conditions imply that all particles entering the system at $z = 0$ are present as single particles. Equation (A5) is mathematically identical, or "isomorphic," to von Smoluchowski's [1917] equation for the coagulation of particles for a constant kernel for which the solution is given as follows:

\[
b_j = \frac{x^{j-1}}{(1 + x)^{j-1}} \tag{A8}
\]

From the definition of $b_j$ and $p_j$ we recover the solution presented in the text (see (20a)). This solution collapses to the solution derived previously for the case where there is no biological removal, $\bar{G}_0 = 0$ [Grant et al., 1996]. Expressions for $N_0$ and $N_1$ (see (20b) and (20c)) follow from their respective definitions.

**Notation**

- $d_1$: diameter of a single phytoplankton [L].
- $D$: fractal dimension of aggregates.
- $f(\bar{z} / \delta)$: function that determines the shape of the grazer distribution.
- $F$: fraction of phytoplankton leaving the mixed layer that is lost to zooplankton.
- $F_{Dj}$: drag force experienced by a $j$-mer [ML/T²].
- $F_{Gj}$: gravitational force experienced by a $j$-mer [ML/T²].
- $g$: gravitational acceleration [L/T²].
- $G_0$: determines the maximum number of zooplankton in the water column [1/L³].
- $\bar{G}_0$: reduced form of the maximum zooplankton concentration $G_0$.
- $G(z)$: concentration of zooplankton [1/L³].
- $I(z)$: integrating factor determined by the grazer distribution.
i, j, k number of constituent particles in an aggregate.

\( k_s \) rate at which a population of zooplankton removes j-mers [1/T].

\( K_{i,j} \) kernel for the coagulation between phytoplankton aggregates of containing j and i constituent particles [L^2/T].

\( n_j \) concentration of phytoplankton j-mers [1/L^3].

\( \bar{n}_j = n_j/N_0(0) \) reduced concentration of j-mers.

\( N_0 = \sum_j n_j \) the total concentration of phytoplankton aggregates [1/L^3].

\( \bar{N}_0(z) = N_0(z)/N_0(0) \) reduced form of phytoplankton concentration.

\( N_1 = \sum_j j \nu_j n_j \) the volume fraction of phytoplankton [1/L^3].

\( \bar{N}_1(z) = N_1(z)/N_1(0) \) reduced form of the volume fraction.

\( \bar{N}_{0.5} = \sum_{j=1} \bar{N}_j \) reduced form of 1/2th moment of the aggregate size distribution.

\( r_i \) radius of single phytoplankton [L].

\( R_h \) hydrodynamic radius of an aggregate [L].

\( R_s \) removal rate of phytoplankton aggregates by zooplankton [1/T^L].

\( R_e \) removal rate of aggregates via sedimentation [1/T^L^3].

\( s_0 \) the effective surface area of an aggregate containing i primary particles [L^2].

\( s(z) \) function that relates \( n_j \) to \( \xi(\eta) \) [1/L^3].

\( \omega \) gravitational settling velocity of a j-mer [L/T].

\( x \) scaled depth [L].

\( \bar{z} = \tau_e/\tau_c \) reduced depth.

Greek letters

\( \alpha \) exponent relating cluster size to hydrodynamic radius.

\( \alpha_{i,j} \) attachment efficiency for the coagulation between aggregates containing j and i phytoplankton.

\( \beta_{i,j} \) collision frequency function for coagulation between aggregates containing j and i phytoplankton [L^3/T].

\( \delta \) length scale for grazer distribution [L].

\( \delta = \delta/\omega \) reduced form of the length scale \( \delta \).

\( e \) exponent describing power law behavior of \( N_j \).

\( \gamma \) exponent describing power law behavior of \( N_i \).

\( \Gamma \) shear rate [1/T].

\( \eta \) reduced form of the aggregate size.

\( \lambda \) homogeneity of coagulation kernel.

\( \mu \) an exponent governing the small i/j limit of \( K_{i,j} \).

\( \mu_e \) dynamic viscosity of the water [M/LT].

\( \rho_p \) density of a phytoplankton particle [M/L^3].

\( \rho_f \) density of the fluid [M/L^3].

\( \tau_e = 2/[K_1 N_0(0)] \) characteristic timescale for coagulation [T].

\( \tau_g = 1/G_0 \omega \) characteristic timescale for grazing [T].

\( \tau_s = \omega/\omega_j \) characteristic timescale for settling [T].

\( \nu_1 \) volume of a single phytoplankton [L^3].

\( \omega \) exponent characterizing aggregate surface area.

\( \xi(\eta) \) "shape" of the normalized aggregate size distribution.

\( \psi_d \) clearance rate of a j-mer [L^3/T].

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