



Rapid formation and sedimentation of large aggregates is predictable from coagulation rates (half-lives) of transparent exopolymer particles (TEP)

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Abstract—Two hypotheses have been proposed to account for the precipitous formation of large, rapidly settling aggregates at the termination of phytoplankton blooms in nature; aggregation due primarily to cell–cell collisions, and aggregation resulting from the presence of abundant transparent exopolymer particles (TEP), a recently discovered class of particles formed from polysaccharides excreted by phytoplankton. The hypothesis of TEP-driven coagulation in three disparate systems, a freshwater lake, a coastal ocean, and a saltwater mesocosm was evaluated, by comparing TEP abundance to several related factors including phytoplankton concentrations, measured sediment fluxes, and abundances of large aggregates. The timing of large aggregate formation and sedimentation events was related to coagulation rates expressed in terms of particle half-lives, $t_{1/2}$, calculated as the time for TEP or phytoplankton to decrease to half their concentration through shear coagulation. While TEP have been previously investigated only in marine systems, it is reported here that TEP also can be present in high concentrations (860 ml^{-1}) in freshwater lakes (Lake Constance, Germany) and that high fluxes of particulate organic matter at depth coincide with the disappearance of abundant TEP from overlying waters. The half-lives of TEP in the three different systems indicate that large aggregate formation and massive sedimentation events following diatom blooms occur when the TEP half-life decreases to less than a few days. By comparing TEP and phytoplankton half-lives in these systems, it is concluded that the formation of rapidly sinking aggregates following blooms of mucous-producing diatoms is primarily controlled by concentrations of TEP, not phytoplankton.

INTRODUCTION

While mass flocculation and subsequent sedimentation of phytoplankton, especially diatoms, as large, rapidly sinking aggregates at the termination of blooms, occur ocean-wide and represent a major global sink for carbon (Smetacek, 1985; Fowler and Knauer, 1986), the mechanism of bloom aggregation has been unclear. Although earlier models concluded that particle collisions in the deep ocean were too infrequent to produce large aggregates relative to time scales for biological processes (McCave, 1984), a coagulation model developed by Jackson (1990) demonstrated that cell–cell collisions of phytoplankton under bloom conditions were sufficient to produce large aggregates. According

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to this cell-collision model, unaggregated phytoplankton concentrations would be limited to a maximum, or critical concentration, C_{cr} , since above C_{cr} removal by aggregation would exceed increases in phytoplankton due to its growth rate. Although this cell-cell collision coagulation model has been found to be consistent with coagulation in some natural systems (Kjørboe *et al.*, 1994), these models often predict that mass flocculation of phytoplankton should occur at cell concentrations much higher than those actually observed to aggregate in nature (Riebesell, 1991; Hill, 1992).

An alternative hypothesis to explain rapid diatom bloom aggregation was proposed by Alldredge *et al.* (1993) based on their discovery in marine systems of a class of highly abundant, but nearly invisible, particles called transparent exopolymer particles (TEP). TEP are produced when dissolved polysaccharide chains excreted by phytoplankton align via cation bridging and become particulate. TEP range from submicron to several hundred microns in size and occur at abundances up to thousands per milliliter (Alldredge *et al.*, 1993). According to the TEP-collision paradigm, marine snow-sized aggregates (aggregates >0.5 mm) are formed primarily by the coagulation of TEP with each other. The inclusion of phytoplankton and other particles into aggregates is dominated by collisions of TEP with these other particle types and not by phytoplankton-phytoplankton collisions. Thus, aggregation proceeds at a rate dependent on the abundance and size of TEP rather than on the concentration of phytoplankton.

While the TEP hypothesis has been found to be consistent with TEP abundance and the onset of aggregation and sinking of a diatom bloom (*Chaetoceros* and *Nitzschia* spp.) off coastal California (Passow *et al.*, 1994), the cell-cell collision model has been shown to be consistent with the maximum cell densities measured during a *Skeletonema* bloom in a Danish fjord (Kjørboe *et al.* 1994), although TEP concentration were not measured in the latter study.

In order to contrast these two hypotheses of the mechanisms responsible for the formation of large aggregates of phytoplankton, we examined data on the abundance of TEP and phytoplankton, visual appearance of large aggregates, and sedimentation rates from a wide range of systems. The coagulation rate of TEP in each system was normalized for difference in TEP size and concentration using a half-life calculation based on coagulation rate of homogeneously-sized particles in a turbulent sheared environment.

BACKGROUND

Several approaches have been used to model particle size distributions undergoing coagulation. One approach is to describe the size distribution of suspended aqueous particles by a continuous function $n(v)$, where $v = \pi d^3/6$, and d is the particle diameter. The number concentration dN of particles in a size interval dv is related to $n(v)$ by $dN = n(v) dv$. The change in the concentration of suspended particles of volume v in the water is a function of the rate of particle production by coagulation of particles smaller than v , and particle losses due to sinking and coagulation into particles larger than v . Neglecting particle losses due to sinking, this can be expressed mathematically (Friedlander, 1977; Hunt, 1982) as

$$\frac{\partial n(v)}{\partial t} = \frac{1}{2} \int_0^v \alpha \beta(v', v - v') n(v') n(v - v') dv' - \int_0^\infty \alpha \beta(v, v') n(v) n(v') dv' \quad (1)$$

where β is the collision kernel describing the rate that particles are brought into contact by

Brownian, shear or differential sedimentation, α the sticking coefficient defined as the fraction of collisions that result in particle attachment, and v' the size of a particle smaller than v that, upon collision with a particle of size $v-v'$, forms a particle of size v . Equation (1) can not be solved analytically, and two approaches have been used to provide approximate solutions. These include using direct numerical solutions (which have not been experimentally verified) and asymptotic solutions for later times (Hunt, 1982). Partial solutions to equation (1) have been obtained using self-preserving transformations (Hunt, 1982; Jiang and Logan, 1991) although these are only applicable to steady-state processes.

Particle size distributions also have been analyzed by direct numerical solution of equations describing particle concentrations measured in different size intervals. Jackson (1990) proposed that algal floc formation could be modeled using

$$\begin{aligned}\frac{dC_1}{dt} &= \mu C_1 - \alpha C_1 \sum_{i=1}^{\infty} C_i \beta_{1i} (1 + \delta_{1i}) \\ \frac{dC_i}{dt} &= 0.5\alpha \sum_{j=1}^{i-1} C_j C_{i-1-j} \beta_{j,i-j} - \alpha C_i \sum_{j=1}^{\infty} C_j \beta_{ij} (1 + \delta_{1i}) \quad (\text{for } i \neq 1)\end{aligned}\quad (2)$$

where C_1 is the concentration of single phytoplankton cells, C_i and C_j the concentration of particles containing i and j algal units, β_{ij} the coagulation kernel describing the frequency of collisions between particles, and δ_{ij} the Kronecker delta used to account for the loss of two particles when both colliding particles are of the same size. This approach included particle growth, described by a first-order growth rate constant μ , but did not include particle formation (or collisions) of algal cells with other particles in the size distribution.

The calculation of particle coagulation rates can be simplified by assuming that the rate is controlled primarily by collisions between particles of similar size. This argument of few collisions between dissimilar-sized particles has been used by others (Jackson, 1990; Han and Lawler, 1992; Jackson and Lochman, 1993) based on coagulation calculations using curvilinear collision functions.

Critical number model

In order to predict a maximum number of single-celled phytoplankton in a system undergoing coagulation, Jackson (1990) simplified equation (2) to

$$\frac{dC_1}{dt} = \mu C_1 - 2\alpha \beta_{11} C_1^2 \quad (3)$$

Derivation of equation (3) required that collisions between similar-sized particles determined particle coagulation rates, and that coagulation proceeded at a rate proportional to collisions between phytoplankton cells and not between phytoplankton and other particles in the water column. Defining the critical concentration of cells, C_{cr} , as the cell concentration when growth exactly balances coagulation, or when $dC/dt = 0$, produced

$$C_{cr} = \frac{\mu}{2\alpha \beta_{11}} \quad (4)$$

Using the collision kernel of $\beta_{11} = 1.3Gd^3$, produced

$$C_{cr} = \frac{0.38\mu}{\alpha Gd^3} \quad (5)$$

where the, G is the mean shear rate, and d the particle diameter.

Simplifications for monodisperse suspensions

If a particle suspension contains particles all of the same size or is monodisperse, then equation (1) can be simplified for a non-settling suspension coagulating by either Brownian (Friedlander, 1977) or shear (Swift and Friedlander, 1964; Birkner and Morgan, 1968) coagulation. For a monodisperse suspension, particle settling velocities are equal and there is no coagulation by differential sedimentation.

Birkner and Morgan (1968) experimentally verified that the initial coagulation rate of a monodisperse suspension of a completely destabilized suspension ($\alpha = 1$) could be expressed as a first order expression

$$\frac{dC}{dt} = -k_t C \quad (6)$$

where C is the total particle concentration in the size interval examined, $k_t = 2.48\Phi G$ is a collision rate constant for coagulation by turbulent shear, $\Phi = N_o v_p$, where $v_p = \pi d^3/6$ is the volume of the primary particles forming the monodisperse suspension, and N_o is the initial number of particles. A similar expression was verified by Swift and Friedlander (1964) for laminar shear coagulation. The simplified expression proposed by Birkner and Morgan (1968) works since over short periods of time the average volume of all particles is nearly constant, and therefore, $k_t = \beta N_o$ remains constant. The first-order rate expression is therefore identical to a second-order rate expression for small changes in total particle concentration. Equation (6) differs from the last term in equation (3) by a factor of 2 since all particles remain within the size spectra included in the definition of C during coagulation, while in equation (3) two particles are removed into other size fractions described by C_{ij} after a successful collision.

METHODS

Theory

All of the above approaches have some limitations for describing particle coagulation in natural waters. For example, there is no known method to develop a continuous particle size function, $n(v)$ capable of describing a size distribution containing phytoplankton cells with and without spines, chains of cells, detrital particles, TEP, etc. While Jackson (1995) has further developed his numerical model to describe particle spectra in a well mixed tank, the general equations are still limited by differing particle characteristics such as variable mass to volume ratios and sticking coefficients; in addition. TEP has not been included in model formulations as a unique type of particle.

Simplified coagulation equations can provide insight into the coagulation process even though they fail to describe the total particle spectra with time. The critical concentration model, for example, provides a measure of the maximum number of single phytoplankton

cells that can easily be compared to measured values. However, it fails to account for coagulation between other particles and for the fact that individual phytoplankton cells in natural systems can vary widely in size.

The approach proposed in this study to analyze coagulating systems is also based on a similarly simplified view of particle size spectra. In order to estimate relative coagulation rates of different types of particles, the system is viewed here as being composed of different types of particles that interact only with other particles of similar size and type. The assumption of only similar-sized particle collisions is justified from calculations made by others (Jackson and Lochman, 1993; Han and Lawler, 1992). Based on this view, a single phytoplankton can only coagulate with another phytoplankton of similar size and stickiness, small aggregates of cells can collide and stick only to other small aggregates, and TEP can collide and stick only to each other. Recognizing that even particles of the same type will have their own size distribution, it is assumed that particle sizes can be described by a mean concentration, \bar{C} , and mean size, l .

Using these assumptions, rates of coagulation of similar types of particles in the suspension with each other are approximated using a modified form of the monodisperse coagulation rate expression as

$$\frac{d\bar{C}}{dt} \approx -\alpha k_t \bar{C} \quad (8)$$

The rate that two similar-sized particles collide is a function of their size, but there is no defined method to adjust the collision frequency for non-spherical particles (such as phytoplankton cells with spines or highly amorphous TEP). In order to use equation (8) here, we define the particle volume as that of a sphere of similar size, or $v_p = \pi l^3/6$. Using this approximation in the definition of k_t , we obtain

$$\frac{d\bar{C}}{dt} = -(1.3\alpha G \bar{C}_o l^3) \bar{C} \quad (9)$$

where all variables in the bracketed term are assumed to be constant over short time intervals. Since α is the constant used to reconcile observed rates ($d\bar{C}/dt$) once all other parameters are defined, any error in l will be incorporated into the estimate of α .

The amount of time to reduce the concentration of particles by half through coagulation is calculated by integration of equation (9).

$$t_{1/2} = \frac{\ln 2}{1.3\alpha G \bar{C}_o l^3} \quad (10)$$

The half-life, $t_{1/2}$, serves as a useful measure of the time scale for coagulation of one type of particle relative to the time scales for other processes, such as the coagulation of other types of particles, growth of individual cells, and particle losses due to ingestion by particle feeders or sinking out of the mixed layer. If marine snow-sized particles are formed primarily through collisions between TEP, then the timing of rapid aggregate formation should be a function of the rate of collisions between similar-sized TEP particles. Since high concentrations of marine snow aggregates have been observed to form within only a few days, it is expected that half-lives of the particles forming marine snow aggregates will decrease to time scales of less than a few days. Thus, it should be possible to determine the types of particles forming marine snow aggregates by identifying particles that are

coagulating rapidly enough to account for the time scales observed for marine snow aggregate formation.

Experimental

In order to test the hypothesis that TEP aggregation rates were sufficiently rapid to account for marine snow formation, half-lives of TEP were calculated in three different systems: surface waters in a coastal ocean; surface waters in a freshwater lake; and in a saltwater mesocosm.

The size and concentrations of TEP in coastal surface waters (upper 10 m) off California (34° 20' N, 119° 50' W) during a diatom bloom dominated by *Chaetoceros* and *Nitzschia* spp. were measured at different stages of aggregation (Passow *et al.*, 1994), and were used here to calculate TEP half-lives.

The relationship between TEP in surface waters and organic matter sedimentation was examined in Lake Constance, Germany (47° 49' N, 09° 08' E) during a spring bloom in 1993. TEP were quantified as described by Passow *et al.* (1994) from 5 ml samples collected in the upper 6 m of the water column except that wet filters stained with alcian blue were vacuum dried and mounted on frosted slides (Cytoclear, Poretics Corp.). Sedimentation rates were measured using plexiglass sediment traps 10 cm in diameter and 100 cm long (deployed in quadruplicate) anchored at a depth of 50 m that were retrieved twice a week (see Simon *et al.*, 1993). Macroscopic aggregates (lake snow) were quantified as described in Grossart and Simon (1993).

Half-lives of TEP and phytoplankton also were compared during a phytoplankton bloom, dominated by *Chaetoceros* and *Nitzschia* spp., under controlled conditions in a 1400 liter mesocosm experiment (see Alldredge *et al.* (1995) this issue). The 1.2 m diameter mesocosm contained 1150 liters of sand-filtered seawater from the Santa Barbara Channel, California, inoculated with 50 liters of unfiltered seawater and spiked with nutrients to attain initial nutrient concentrations of 46 μM NO_3 , 3 μM PO_4 , and 110 μM SiO_4 . The mesocosm was maintained at 15°C and 14 h light: 10 h dark artificial illumination, and mixed with a plexiglass propeller at 2.6 rpm, producing an average shear rate of $G = 1.3 \text{ s}^{-1}$. Phytoplankton and TEP ($>5 \mu\text{m}$) were microscopically sized and enumerated [see Passow and Alldredge (1995) this issue]. Aggregate sizes were determined by nondestructively photographing slabs of water $5.2 \times 7.7 \times 1 \text{ cm}$ in size illuminated by a strobe through transparent ports in the tank wall. Photographic negatives were analyzed with computerized image analysis as described in Alldredge *et al.* (1995).

RESULTS

Coastal ocean

TEP concentration in surface waters ($<10 \text{ m}$) increased to a maximum of 590 ml^{-1} on 24 June and thereafter decreased in concentration due to their coagulation (Table 1). The coagulation of TEP with cells was reflected in increasing TEP sizes from 20 to $1000 \mu\text{m}$ and an increasing percentage of diatom cells tangled with TEP as the bloom flocculated. The half-life of TEP prior to the appearance of large flocs was >2 days, but during the period when large numbers of marine snow aggregates appeared (26–29 June), TEP half-lives were reduced to less than one day ($t_{1/2}$ of 0.03 to 0.05 days).

Table 1. Mean TEP concentration and half-lives in the upper 10 m during a diatom bloom in 1992 dominated by *Chaetoceros* and *Nitzschia* spp. off California (34°20'N, 119°50'W) in different stages of aggregation. (Data adapted from Passow et al., 1994. Calculated values assume $G = 1 \text{ s}^{-1}$ and $\alpha = 1$.)

Date	Flocculation State	Size (μm)	Concentration (ml^{-1})	Half-life (days)	Phytoplankton in TEP (%)
19 June	Unfocculated	20	380	3.4	8
24 June	Early flocculation	26	590	1.0	38
26 June	Flocculating	100	220	0.04	79
29 June	Flocculating	95	160	0.07	90

Freshwater lake

TEP not only occurred abundantly in freshwater but its loss from surface waters was correlated to the sedimentation of a diatom bloom dominated by *Stephanodiscus hantzschii*, *St. astrea*, and *Cyclotella bodanica*. TEP reached a maximum concentration of 860 ml^{-1} and an average size of $20 \mu\text{m}$, resulting in a half-life of only 1 day on 22 April (Fig. 1). By 29 April, only 70–90 TEP ml^{-1} remained in surface waters and macroscopic aggregates (lake snow) increased 3 to 4-fold to 5–10 liter^{-1} in deeper waters (15 to 25 m). Sedimentation rates increased 8 fold over this period (Fig. 1) and trap material contained large amounts of TEP, indicating that TEP had facilitated rapid sedimentation of phytoplankton.

Experimental mesocosm

High concentrations of both TEP and phytoplankton were produced in the mesocosm over the 14 day experiment. TEP were present at the highest concentrations on Day 7, decreasing from 1400 ml^{-1} to 500 ml^{-1} on Day 10. On Day 11 phytoplankton particles (primarily chains), and total phytoplankton concentrations reached maximums of 2000 particles, and 20,000 cells ml^{-1} , respectively. Large aggregates ($>1 \text{ mm}$) reached measurable concentrations on Day 10 and increased dramatically by Day 12 (Fig. 2).

The wide range in cell sizes and the high concentrations of cells in chains makes it difficult to conclude whether the estimate of a critical concentration of cells in the tank was accurate. Based on the increases in total (attached and free-living) phytoplankton abundances between Days 7–10, the growth rate of phytoplankton was $\mu = 0.44 \text{ day}^{-1}$. Using this growth rate and assuming that all cells were sticky ($\alpha = 1$), the critical cell concentration according to equation (1) could have been in the range of 12 to 12,000 ml^{-1} assuming average phytoplankton cell sizes of 5 to $50 \mu\text{m}$. This range in C_{cr} is too wide to conclude whether this maximum cell concentration was ever reached. Furthermore, this approach neglects to consider the abundance of cells growing in chains. Although total phytoplankton cell concentrations in the mesocosm reached 20,000 ml^{-1} , many cells grew as chains. When phytoplankton in chains and clusters of cells are used to define a 'phytoplankton particle', the maximum concentration is lowered to 2000 ml^{-1} . Thus, the analysis based on C_{cr} is inconclusive.

A more useful approach to determine whether phytoplankton or TEP were a more dominant factor in the formation of marine snow-sized particles is to calculate which type

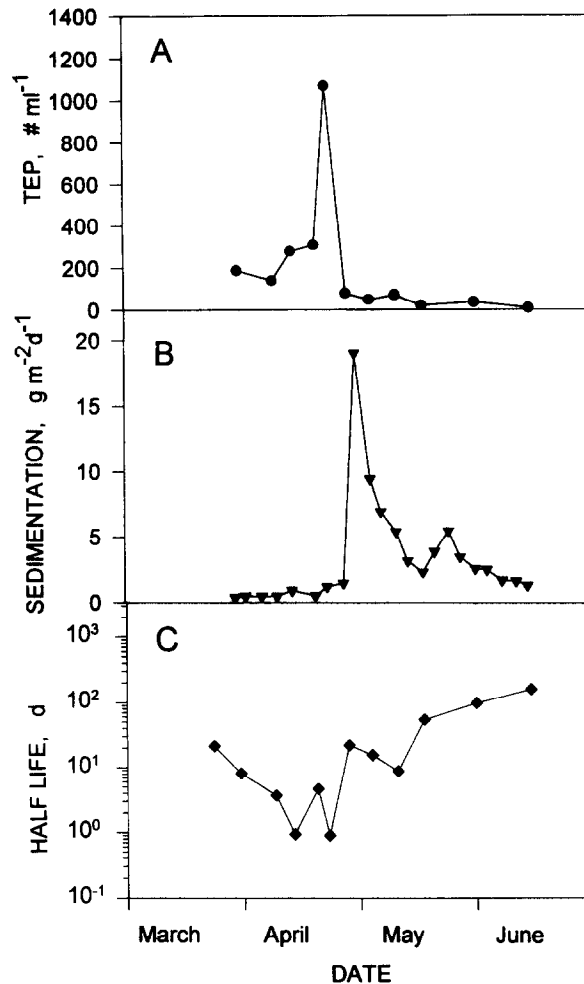


Fig. 1. (A) The concentration of TEP; (B) sedimentation rates of particulate mass; and (C) the half lives of TEP particles in surface waters of Lake Constance during the spring of 1993. The peak in sedimentation follows the peak and disappearance of TEP from surface waters. Short half-lives (<1 day) support high TEP coagulation rates. (Calculations assume $G = 1 \text{ s}^{-1}$ and $\alpha = 1$.)

of particle had the greatest coagulation rate (shortest half-life). For this calculation, it is necessary to estimate sticking coefficients for TEP and phytoplankton particles. The α for TEP can be estimated using the rate of decrease in TEP. Since this approach neglects new production of TEP, this underestimates α . Between Days 7 and 10 the concentration of TEP decreased [Fig. 2(B)] while the average size of TEP increased from 20 to 112 μm indicating TEP was coagulating with itself during this period. From the decreases in TEP concentration and equation (2), α of TEP was calculated to be 0.21.

Since phytoplankton particle concentrations were still increasing prior to the appearance of large numbers of aggregates $>1 \text{ mm}$ (Days 10–12), the sticking coefficient for phytoplankton particles cannot be estimated in the same manner as TEP. The magnitude of the sticking coefficient must have been much less than 1 (as assumed above for

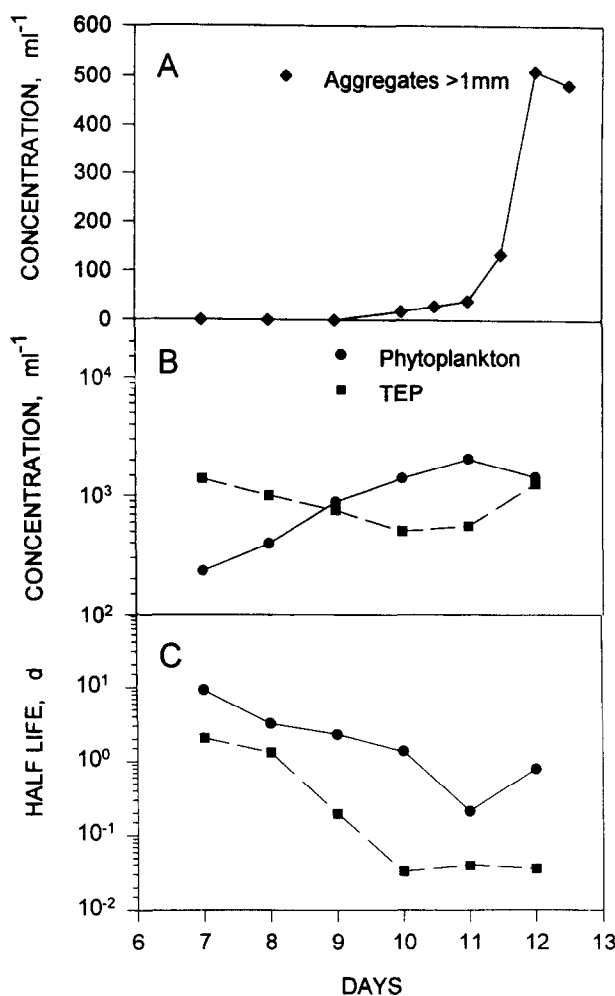


Fig. 2. (A) Size distributions, (B) concentrations, and (C) half-lives of TEP and phytoplankton particles in the mesocosm.

phytoplankton cells) in order to have produced the high concentrations of phytoplankton particles in the tank. Let us define the overall rate of change of particle concentration as the difference between particle growth (due to cell division, particle coagulation, etc.) and particle loss due to coagulation, as

$$\frac{d\bar{C}}{dt} = r_f - r_c \quad (11)$$

where r_f is the rate of particle formation, and r_c is the rate particle concentrations decrease due to coagulation. Based on the method used to characterize the average size of phytoplankton particles, the rate of phytoplankton particles growth between Days 7 and 9 was exponential, or $r_f = \gamma \bar{C}$, where $\gamma = 0.67 \text{ day}^{-1}$ [Fig. 2(B)]. Using this observed growth

rate and equation (7) to describe the rate of particle removal, we can approximate the rate of particle change as

$$\frac{d\bar{C}}{dt} = \gamma\bar{C} - \alpha k_t \bar{C} \quad (12)$$

Equation (12) can be used to estimate the maximum concentration of phytoplankton particles possible in the tank when $d\bar{C}/dt = 0$. Substituting in the definition of k_t , the maximum number of particles, \bar{C}_{\max} , is

$$\bar{C}_{\max} = \frac{0.77\gamma}{\alpha G l^3} \quad (13)$$

Using the $\gamma = 0.67 \text{ day}^{-1}$, $G = 1.3 \text{ s}^{-1}$, the measured maximum phytoplankton particle concentrations of 2000 ml^{-1} on Day 11, and $l = 53 \text{ }\mu\text{m}$, α can be calculated as the only unknown in equation (1) as 0.015. If $\alpha = 1$, then \bar{C}_{\max} would have been 31 ml^{-1} , a value well below the observed concentration of phytoplankton particles.

Using these values of α for phytoplankton particles and TEP, the minimum half-lives (equation (10)) of phytoplankton particles were always an order of magnitude longer than half-lives of TEP particles [Fig. 2(C)]. TEP half-lives on Day 8 were only 1 day, and further decreased to $t_{1/2} = 0.01$ day on Day 10, a value similar to that observed in the coastal ocean system during marine-snow formation. The persistence of high concentrations of phytoplankton in the mesocosm prior to the appearance of marine-snow sized aggregates can therefore be reconciled with the timing of the onset of aggregation by recognizing that large aggregate formation could not occur until TEP reached sufficient sizes and concentrations on Day 10 to produce mm-sized aggregates. The timing of phytoplankton aggregate formation was thus less related to cell of phytoplankton particle concentrations than to abundance and coagulation rates of TEP.

DISCUSSION

The feature common to the freshwater, marine and mesocosm studies is the simultaneous presence of high concentrations of TEP and large numbers of diatoms. The demise of these blooms due to mass flocculation and sedimentation always coincided with large coagulation rates (small half-lives) of TEP. These three separate studies indicate that when large ($20 \text{ }\mu\text{m}$) TEP reached concentrations around $500 \text{ particles ml}^{-1}$, aggregation between TEP and other particles in the water column could rapidly form large, fast settling aggregates of lake or marine snow and result in a predictable pulse of carbon to deep sediments. The data from Lake Constance demonstrate a direct correlation between disappearance of TEP from surface waters and increased flux of particulate matter at depth. Thus, assessment of the size distribution and abundance of TEP in surface waters over time may allow prediction of rates of aggregate formation and of the timing and magnitude of particulate flux to the benthos in the presence of certain phytoplankton species.

The major importance of TEP for aggregation of diatom blooms appears to be the high sticking coefficient of TEP compared to cells (Passow *et al.*, 1994). Most diatom species previously investigated have low cell-cell stickiness coefficients, usually $<10^{-2}$ to 10^{-3} (Kiørboe *et al.*, 1990; Kiørboe and Hansen, 1993), consistent with the low phytoplankton

particle α 's calculated here. In contrast, TEP are highly sticky with $\alpha > 10^{-1}$, possibly approaching 1. This high stickiness facilitates rapid aggregation rates in phytoplankton blooms when both TEP and phytoplankton are abundant.

The high stickiness of TEP may also effect aggregation rates under non-bloom conditions. TEP form the matrix of all types of marine snow-sized aggregates so far examined in the ocean (Alldredge *et al.*, 1993) suggesting that TEP are a major mechanism of aggregate formation for many types of aquatic particulate matter. At lower particle abundances, the half-life of TEP would be days to weeks resulting in slower rates of aggregation and the gradual, rather than pulsed, sedimentation more typical of non-bloom conditions. Since TEP by themselves are primarily water and have low sinking velocities (Passow *et al.*, 1994; Passow and Alldredge, in press), the nature of sedimenting particulate material will be largely determined by the more substantive particles aggregated by TEP.

The presence of TEP may not be necessary to explain the aggregation of all phytoplankton blooms (Kiørboe *et al.*, 1994) since not all phytoplankton species produce TEP abundantly, and since not all species of phytoplankton may stick to TEP (Kiørboe and Hansen, 1993; Passow and Alldredge, in press). However, our results suggest that aggregation of blooms in marine surface waters dominated by diatoms, especially chain-forming *Chaetoceros* and *Nitzschia*, are most likely regulated by the abundance of TEP produced from exopolymers secreted by them. The export of carbon due to the formation and subsequent sedimentation of marine and lake snow is predictable from TEP size distributions in the presence of these mucous-producing diatoms. Thus, the abundance and nature of TEP is central to understanding the cycling and loss of carbon in the world's lakes and oceans.

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