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Maximum phytoplankton concentrations in the sea

Abstract—A simplification of plankton dynamics using coagulation theory provides predictions of the maximum algal concentration sustainable in aquatic systems. These predictions have previously been tested successfully against results from iron fertilization experiments. We extend the test to data collected in the North Atlantic as part of the Bermuda Atlantic Time Series program as well as data collected off Southern California as part of the Southern California Bight Study program. The observed maximum particulate organic carbon and volumetric particle concentrations are consistent with the predictions. The results imply that physical processes control maximum particle concentrations in planktonic systems.

Planktonic systems in the ocean are controlled by a myriad of physical, chemical, and biological processes. Coagulation, known to be important in the dynamics of clouds, air pollution, and water treatment, is emerging as important in controlling particle dynamics in the ocean as well. Coagulation is the process by which small particles collide and stick to form new, larger particles. By many such collisions, material originally colloidal in size, as well planktonic algal cells, can become visible to the naked eye. Particle size is an important property because it controls the rate at which material falls out of the surface layer. Understanding the factors that control it is important for our understanding of the ocean.

Physical coagulation theory describes the rates at which different mechanisms bring particles together to calculate the rates at which particle size distributions change and particles fall. Such mechanisms depend on the sizes and concentrations of the colliding particles. This concentration dependence has led to an emphasis on describing the role of coagulation in regulating the maximum concentration of an algal bloom: coagulation rate increases with particle concentration squared and will eventually balance algal growth rate and thus puts an upper limit on cell concentration. For such a rapidly growing, initially monodisperse system, the maximum algal concentration attainable can be simply estimated as a function of the cell growth rate, the turbulent shear rate, the probability of two colliding particles sticking (“stickiness”), and the algal diameter (initially derived in Jackson 1990, corrected in Jackson 2005). The applicability of the maximum algal concentration has been tested in natural phytoplankton blooms (Riebesell 1991*a,b*; Kjørboe et al. 1994) as well in more recent iron addition experiments (Boyd et al. 2002, 2005; Jackson et al. 2005), and coagulation theory has

generally proved efficient in predicting maximum algal concentrations.

In this article, we explore if there is a general maximum phytoplankton volumetric concentration in the upper ocean that can be predicted from coagulation theory. We test the theory on two different data sets, The Bermuda Atlantic Time Series (BATS, Michaels et al. 1994) and the Southern California Bight Study (SCBS, Eppley 1986), and show that maximum volumetric particle concentrations in the euphotic zone are consistent with those predicted using coagulation theory.

Methods

The critical concentration is a simplified way to predict the maximum concentration of an algal bloom in a mixed layer that is controlled by coagulation. Among the relevant assumptions here are that only single algal cells are interacting with each other, that relevant shear and particle accumulation rates are averages for the mixed layer, and the rapid settling of large particles balances the growth of the small. Originally expressed in terms of particle number concentration (Jackson 1990), it has been recast in terms of phytoplankton volumetric concentration. The maximum or critical volumetric phytoplankton concentration for algal cells is (Jackson 2005; Jackson et al. 2005)

$$V_{cr} = \pi\mu(8\alpha\gamma)^{-1}$$

where μ is the phytoplankton specific accumulation rate, α is the particle stickiness, and γ is the average shear rate. If other algal losses are small, μ is the phytoplankton specific growth rate. V_{cr} can be converted to a critical concentration of particulate organic carbon (POC), C_{cr} , for a given POC:phytoplankton volume value, assuming that POC is predominantly phytoplankton. We estimated the average specific accumulation rate of the total particle pool as the ratio of primary production (PP) to POC, $\mu_{POC} = PP/POC$. Particle volume was calculated assuming the POC:volume relationship determined for the SCBS data. The value for α was set to 1.

We used different data sets with different limitations to test the prediction (Table 1). BATS, in conjunction with the Bermuda Bio-Optical Project, provides one of the most complete records of phytoplankton variability available. We were able to calculate average specific growth rates over the mixed layer, average particle concentrations, and average wind speeds for the site. This enabled us to

Table 1. Data used for different analyses. The n for the SCBS data are for samples with particle volume and with POC measurements. ML, mixed layer average; Disc, discrete samples; +, information used; -, information not used.

	ML (BATS)	Disc (BATS)	Disc (SCBS)
Wind speed	+	-	-
Mixed layer depth	+	-	-
Average POC	+	-	-
Average μ_{POC}	+	-	-
Ave C_{cr}	+	-	-
Disc POC	-	+	+
Disc μ_{POC}	-	+	+
Disc particle volume	-	-	+
Discrete C_{cr}	-	+	+
n	49	573	466/1718

estimate maximum particle concentrations and compare them with observations.

Data for BATS are available at <http://bats.bbsr.edu/>. We downloaded data for temperature (T) and salinity (S) as well POC and PP determined from ^{14}C -uptake measurements. We calculated vertical density profiles from T, S data. We determined the base of the mixed layer as the shallowest depth where the density gradient exceeded 0.009 kg m^{-2} . POC and PP were averaged over the mixed layer. Wind data collected in the area from 1994 to 2002 were provided by Tom Dickey of the University of California, Santa Barbara, from the Bermuda Bio-Optical Project. We estimated the daily average wind speed by calculating the mean wind speed measurements taken for 1 d at intervals of less than 1 min.

Average shear rate for the surface mixed layer was calculated using the average wind speed for a given day using the relationship of MacKenzie and Leggett (1993) to estimate the average energy dissipation rate $\varepsilon = a W^3 Z^{-1}$, where W is the average wind velocity, Z is the average mixed layer depth, and $a = 5.82 \times 10^{-6} \text{ kg m}^{-3}$. The average shear rate was estimated as $\gamma = (\varepsilon \rho_0^{-1} \nu^{-1})^{0.5}$, where ν is the kinematic viscosity, and ρ_0 is the density of seawater. Average shears from different days were combined to test the effect of historic shears. There were 49 cruises for which the requisite water column and wind data were available to estimate the average shear, POC, and specific growth rate within the mixed layer. The wind-derived estimates of γ for BATS were used to compute mixed layer averages of predicted (C_{cr}) and particulate concentrations. The value of μ_{POC} was estimated as the ratio of PP and POC averaged through the surface mixed layer.

We also tested the utility of the critical concentration parameter for individual samples, for which we did not average over depth and for which we did not have wind samples by using BATS and SCBS data. The mean and standard deviation of the shears calculated from wind and mixed layer data above were $0.20 \pm 0.16 \text{ s}^{-1}$. To make these calculations, we assumed $\gamma = 0.1 \text{ s}^{-1}$. There were 573 individual depth-specific samples from BATS with the necessary POC and carbon fixation data for the period

1994–2002, of which 407 had a specific growth rate greater than 0.005 d^{-1} .

Data on POC, PP, and particle volume for SCBS have been described in Eppley (1986) and Eppley et al. (1977). The POC:volume ratio for the SCBS sample, 0.17 g C cm^{-3} , was used to calculate the critical POC concentration data for the more numerous POC samples. The value of μ_{POC} was estimated as the PP:POC values for individual samples. For SCBS, there were 466 usable samples with measurements of particle volume and 1,718 with usable POC values.

Results

The BATS data set for values averaged through the mixed layer data corresponds most closely to the simple coagulation model used to derive C_{cr} . The ratio of observed to predicted POC ($\text{POC} : C_{cr}$) was always $\ll 1$, indicating that average POC concentration never exceeded C_{cr} (Fig. 1). The average $\text{POC} : C_{cr}$ was 0.044 if the shear for the sample day was used and 0.046 if the average of 3 d ending on the sampling day was used. The average ratio increased to 0.06 if the maximum shear over the 3-d period was used and 0.07 if the maximum was for the preceding 6-d period.

When the POC values from individual bottle samples at BATS were compared to the C_{cr} calculated using an assumed constant value for γ , POC was less than C_{cr} whenever the associated $\mu_{POC} > 0.005 \text{ d}^{-1}$ (Fig. 2). POC values for some samples with $\mu_{POC} < 0.005 \text{ d}^{-1}$ did exceed C_{cr} , but samples with such low growth rates are typically at the bottom or below the euphotic zone and cannot be considered to be phytoplankton dominated. For comparison, the minimum value of μ_{POC} averaged over the mixed layer was 0.06 d^{-1} (Fig. 1). Despite the range in the $\text{POC} : C_{cr}$ ratio, the reported values of POC were relatively constant, $2.0 \pm 0.8 \mu\text{mol L}^{-1}$. Most of the variation in the ratio was driven by the variation in μ_{POC} . Nevertheless, C_{cr} was not exceeded in the productive region.

The SCBS data included volumetric data for some cruises, but had insufficient data on wind and mixed layer thickness to compare the average particle concentration to C_{cr} . The measured particle volumes exceeded V_{cr} only 5.6% of the time (Fig. 3B), whereas the more numerous POC values exceeded C_{cr} in 6.5% of the samples (Fig. 3A). In either case, the maximum particle concentration increased with increasing μ_{POC} in a way consistent with the predicted V_{cr} and C_{cr} . The mean and standard deviation for POC concentrations were much higher in the SCBS region ($12.4 \pm 13.8 \mu\text{mol L}^{-1}$) than at BATS and more likely to approach the C_{cr} .

Discussion

The critical concentration was originally derived to explain the steady-state results for a simple simulated system in which only single cells divided at a constant rate (Jackson 1990). In this original system, single cells were a large fraction of the total particulate biomass and C_{cr} provided a useful index for estimating system properties at steady state. Alterations to the system, such as might be

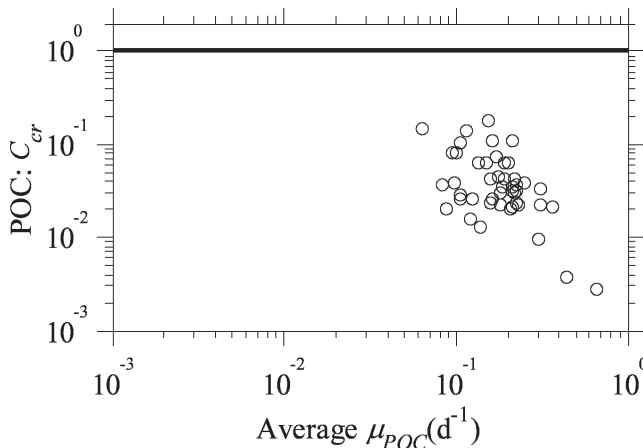


Fig. 1. Ratio of observed to predicted POC concentration averaged over the mixed layer as a function of the average POC specific growth rate at the BATS site. Average shear rate was calculated using the maximum wind speed for the sample date and the 2 preceding days. All particle concentrations were less than the predicted maxima.

caused by allowing algae growth in aggregates, change the relative importance of single cells (e.g., Jackson 1995). Preliminary simulations suggest that the effect of allowing continued algal growth in aggregates would change biomass distribution but would not cause large changes to total biomass (G. A. Jackson unpubl. data). A proper accounting of the effect of algal growth in aggregates in chains would require better descriptions of disaggregation rates as well as of particle collision rates of chains (Jackson and Lochmann 1993). Consideration of the complexity of any planktonic system requires relative elaborate coupled coagulation and ecosystem models. To the extent that aggregates can also form significant pools of particulate matter, C_{cr} provides an underestimate of the total POC concentration in planktonic systems. Although only a single index for complicated systems, C_{cr} is easy to calculate and, as noted here, provides remarkable useful predictions.

The SCBS region is an eastern boundary current region, with the associated upwelling that can lead to higher algal concentrations (e.g., Eppley et al. 1977) than in the oligotrophic Bermuda region of the Atlantic. Particle concentrations that are limited by coagulation rarely develop in the latter region but frequently in the former. For this reason, the SCBS region provides a better test of the predictions. If critical POC ranges from $2 \mu\text{mol L}^{-1}$ C to $100 \mu\text{mol L}^{-1}$ C and nitrogen and carbon content are related by the Redfield ratio of 6.6, then the values of critical concentration calculated for the region are equivalent to $0.12\text{--}16 \mu\text{mol L}^{-1}$ NO_3 , well within the range of concentration for our samples, which had mean nitrate and particulate organic nitrogen (PON) concentrations of $7.4 \mu\text{mol L}^{-1}$ and $1.7 \mu\text{mol L}^{-1}$ for these samples.

An understanding of the role that algal concentration and aggregate settling rates have on particle export is important for predicting the effect of iron fertilization on carbon export. By addition of iron to high-nitrate, low-chlorophyll waters, experimentalists hope to stimulate

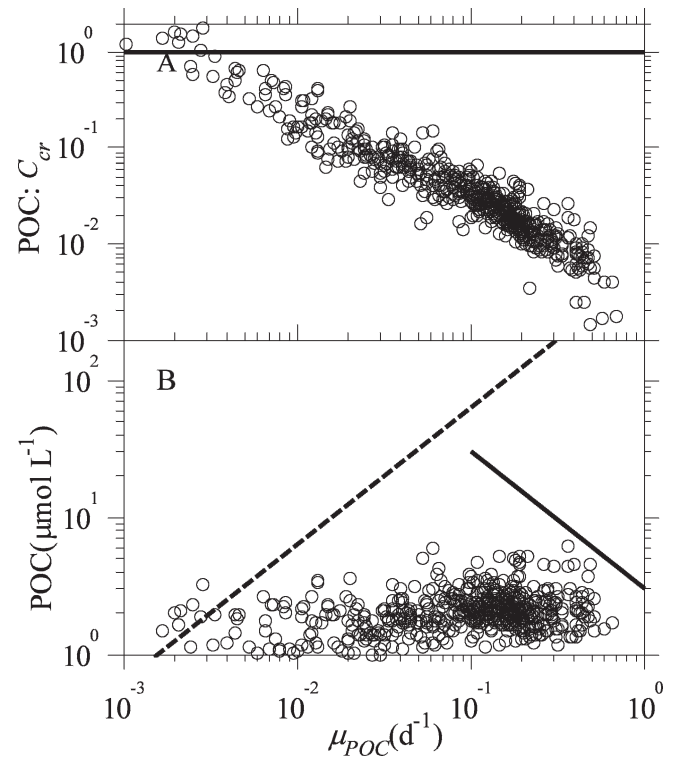


Fig. 2. Predicted versus observed POC concentrations for discrete samples at BATS calculated as for the SCBS data (Fig. 3), with an assumed shear rate of 0.1 s^{-1} . Primary production measurements were interpolated to depths for which there were POC samples to calculate μ_{POC} . (A) Ratio of observed to predicted concentrations. Solid line shows where the concentrations are equal. (B) Actual concentrations. The dashed line represents the maximum POC concentration predicted for these parameter values. The solid line shows the slope expected if there were a spurious correlation associated with plotting POC as a function of PP: POC.

phytoplankton growth and carbon export from the surface (e.g., de Baar et al. 2005). Iron addition has increased algal concentrations and in some, but not all, cases increased the export. Calculation of expected critical concentrations has helped to understand the maximum plant populations observed as well as the extent of particle sedimentation (Boyd et al. 2002, 2005; Jackson et al. 2005).

The critical concentration and its dependence on shear illustrate another way that physical processes affect phytoplankton populations. Because wind velocity and mixed layer depth affect the average shear, they influence coagulation rates and couple oceanic and atmospheric processes. Storms with high winds can have dramatic effects. Ø. Fiksen (pers. comm.) observed a decrease in chlorophyll concentration associated with the passage of a storm during a spring bloom in the Norwegian Sea. Observed chlorophyll concentration dropped from 3.9 mg L^{-1} to 0.6 mg L^{-1} ; the critical concentrations of chlorophyll, estimated from observed wind speeds and mixed layer depths, and modeled growth rates (not shown) decreased from 6 mg L^{-1} to 1.1 mg L^{-1} . The similarity of the absolute concentrations as well as the relative changes for the predicted and observed situations is striking and

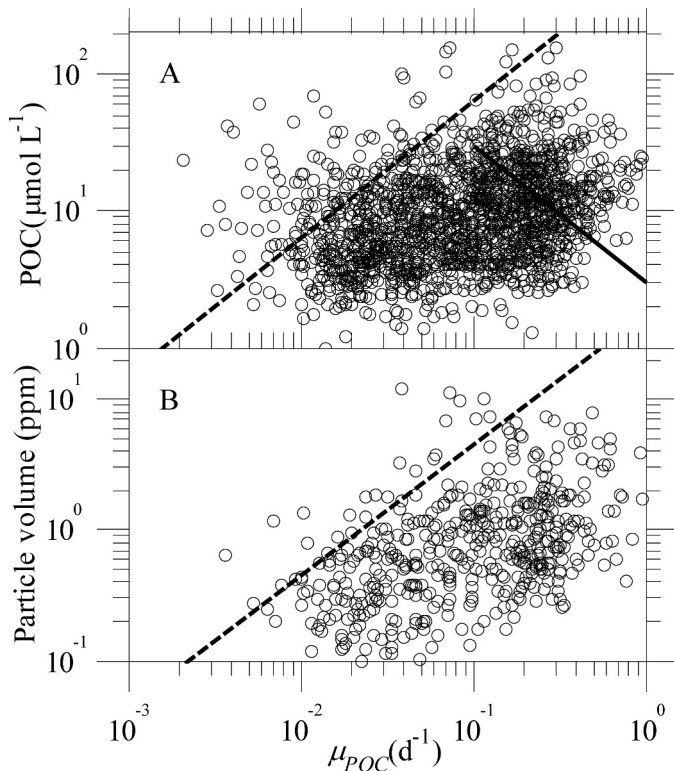


Fig. 3. Predicted versus observed particle concentrations for discrete samples from SCBS data. (A) POC concentration as a function specific growth rate of POC (μ_{POC}). (B) Particle volume as a function of μ_{POC} . Shear (γ) = 0.1 s^{-1} , stickiness (α) = 1; POC:vol = 0.17 g C cm^{-3} . The dashed line represents the maximum POC concentration predicted for these parameter values. The solid line shows the slope expected if there were a spurious correlation associated with plotting POC as a function of PP:POC.

further supports the relevance of these ideas to real planktonic systems.

The observed mixed layer average POC concentrations were consistent with the C_{cr} predicted using vertically averaged shear and growth rates. Such averaging mixes the high growth rate regions near the surface with slower growing regions deeper. When we calculated C_{cr} for deep discrete samples using specific growth rates from deep samples, we used μ values less than the average. As a result, the values of C_{cr} were less than would be calculated with average mixed layer values. It should not be surprising that some POC concentrations were greater than C_{cr} for the discrete samples. What is satisfying is that the general trend of the maximum particle concentration was consistent with that predicted by C_{cr} .

One of the problems with making these comparisons is the limited number of data sets with the requisite information on particle volume, algal specific growth rate, wind velocity, and mixed layer depth. The observations from iron fertilization experiments have provided one of the best documented observation sets and are generally consistent with the predictions. Our analysis suggests that predictions made for less extensive data observations, in which we need to assume several parameters including

shear rate and C:volume ratio to make the comparisons, are still remarkably useful.

The field observations summarized here demonstrate that particle concentration in the ocean rarely, if ever, exceeds that predicted by coagulation theory. The observed maximum particle concentrations suggest that coagulation in conjunction with the enhanced settling rate of larger aggregates does place an upper bound on oceanic phytoplankton and, by extension, particle concentrations. Obviously, phytoplankton concentration can be—and often is—much less the maximum predicted by coagulation theory, either because phytoplankton concentration is limited by other factors, typically zooplankton grazing or low concentrations of inorganic nutrients, or because the system has not yet reached steady state.

In addition to the model assumptions, there are parameter values assumed in the absence of better information. All of these comparisons assume that the stickiness was one. As lower stickiness (Kjørboe et al. 1990; Kjørboe and Hansen 1993) would lead to higher critical concentrations, the calculations are conservative. The fact that we do not see evidence of significantly higher V_{cr} in our results or in the results of various iron fertilization experiments (e.g., Boyd et al. 2002, 2005) suggests that the stickiness in most natural matter may effectively be one. In this, the presence of other particles, such as transparent exopolymeric particle (TEP) (e.g., Passow 2002), may counteract any inherently lower values of algal stickiness.

The application of the critical concentration to discrete data rather than mixed layer averages involves at least two significant expansions from conditions of the original model: the comparison with individual samples rather than mixed layer averages and the comparison with total POC using μ_{POC} rather than just phytoplankton biomass and specific growth rate. The fact that the simple formula for phytoplankton works for the situations suggests that the concept of coagulation regulation of particulate concentration in the ocean is a robust one.

Whereas the original coagulation model was formulated for phytoplankton abundances, we have compared it to POC and total particle volume. At the high concentrations at which coagulation becomes important in limiting phytoplankton populations, phytoplankton growth rates exceed losses to traditional processes, such as zooplankton grazing and viral mortality (e.g., Evans and Parslow 1985). POC is predominantly phytoplankton, and the assumed correspondence between phytoplankton and POC is reasonable.

Many processes clearly are important in structuring pelagic food webs, but our analysis suggests that coagulation and associated faster sinking of aggregates put an upper bound on concentrations of particles in the ocean. Other processes that regulate food web structure and function must operate within that constraint. Light and self-shading also place an upper bound on particle concentration, but also work in conjunction with algal losses from sinking, respiration, or grazing mortality. For example, Mitchell et al. (1991) used an updated version of Sverdrup's (1953) critical depth model with a more sophisticated photosynthesis model to predict the maxi-

mum particle concentrations. However, they needed to invoke unmeasured algal losses to fit observations of phytoplankton concentrations. Interactions in the plankton are a combination of physical and biological processes; factors besides zooplankton feeding can determine the fate of organic material.

At high particle concentrations, coagulation and resulting increased average particle sinking rate place fundamental limits on planktonic systems. At lower concentrations, they still function in conjunction with other processes traditionally considered in the sea.

George A. Jackson¹

Department of Oceanography
Texas A&M University
College Station, Texas 77843

Thomas Kjørboe

Danish Institute for Fisheries Research
Kavalergaarden 6, DK-2920
Charlottenlund, Denmark

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¹ Corresponding author (gjackson@tamu.edu).

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