A hidden cost of mucus production by phytoplankton: Viscosity hinders nutrient uptake

Bryce G. Inman

Scripps Institution of Oceanography, University of California San Diego, La Jolla, California

Scientific Significance Statement
Phytoplankton secrete sticky mucus that facilitates interactions with bacteria and drives carbon sequestration in the oceans. However, no negative physiological consequences of mucus production have been identified. I show that viscous mucus increases the nutrient concentration gradient but lowers the nutrient uptake by phytoplankton, which could impede their growth and productivity. Because mucus production varies dramatically among phytoplankton taxa, viscous mucus may represent an adaptive strategy that provides ecological benefits, outweighing the loss of nutrient uptake. By steepening the concentration gradient, mucus may allow mutualistic bacteria to survive near phytoplankton without being starved of shared nutrients. This work also identifies a feedback loop through which late-stage blooms—producing more mucus when nutrients are scarce—may accelerate their own decline by viscous inhibition of nutrient uptake.

Abstract
Diverse phytoplankton exude polysaccharides that can form a viscous mucus layer surrounding their cells, facilitating complex chemical exchanges with bacteria. An unexplored ramification of mucus production is the influence of its viscosity on the diffusion of nutrients such as vitamins to the cell. Here, I use simulations to demonstrate that mucus viscosity increases the nutrient concentration gradient but always reduces the flux to the cell. Uptake is marginally improved during nutrient pulses, as the mucus acts like a sponge by retaining nutrients near the cell. Lower uptake in the presence of mucus presents a fitness cost that any ecological benefits of mucus must outweigh. I derive a relationship between mucus viscosity and nutrient uptake that can be used to test hypotheses of mutualistic interactions between phytoplankton and bacteria. This work emphasizes the need for empirical measurements of macronutrient diffusion through mucus layers and provides a framework for interpreting those results.

Marine phytoplankton produce mucus that can surround their cells or disperse as filaments into the water column (Myklestad 1995; Passow 2002). Diatoms, dinoflagellates, haptophytes, chlorophytes, and cyanobacteria secrete 2–50% of carbon fixed during photosynthesis (Thornton 2014). Of those exudates, a substantial portion is high molecular weight polysaccharides that may increase the local viscosity (Jenkinson 1986; Biddanda and Benner 1997; Aluwihare and

*Correspondence: binman@ucsd.edu

Associate editor: Stephen Monismith

Author Contribution Statement: BGI designed the research, performed the analyses, and wrote the manuscript.

Data Availability Statement: The source code for the numerical simulations is available at https://github.com/bryceinman/pvw.

Additional Supporting Information may be found in the online version of this article.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
Phytoplankton exudates attract heterotrophic bacteria that engage in complex ecological interactions (Larsson and Hagström 1979; Amin et al. 2012, 2015; Seymour et al. 2017). Within the “phycosphere,” some bacteria can remineralize limiting nutrients and produce vitamins for the benefit of phytoplankton (Azam and Ammerman 1984; Legendre and Rassoulzadegan 1995; Croft et al. 2005; Durham et al. 2015). Other bacteria can attack phytoplankton cells or compete with phytoplankton for inorganic nutrients (Cole 1982; Bratbak and Thingstad 1985; Joint et al. 2002; Mayali and Azam 2004). Azam and Smith (1991) suggested that the mucus layer keeps bacteria close enough for chemical exchange but also acts as a physical barrier to prevent direct contact with the cell surface in case of bacterial attack.

The current understanding of viscous exudates is that they facilitate ecological interactions but present no significant physiological consequences to the phytoplankton (Thornton 2014; Mühlenbruch et al. 2018). However, the macromolecules found in mucus decrease the local molecular diffusivity of inorganic nutrients, vitamins, and other relatively small molecules required by phytoplankton and associated bacteria. The degree to which mucus reduces the diffusivity depends on viscosity, molecular crowding, porosity of the polymer medium, and other factors (see SI Discussion). Ploug and Passow (2007) measured the molecular diffusivity of dissolved H2 directly and O2 indirectly in diatom aggregations. They found that mucus lowered the diffusivity of those gases by 5–10%. However, Dauty and Verkman (2004) have shown that the diffusion of small solutes is not slowed by viscosity in the same way as larger solutes. Therefore, mucus may reduce the diffusivity of larger molecules such as vitamins and siderophores to a greater extent.

Until the diffusivities of molecules larger than O2 are experimentally quantified in the phycosphere, a linear relationship between viscosity and diffusivity is a useful approximation: the results presented in this work can easily be reinterpreted to accommodate future findings. To this end, I assume that the molecular diffusivity of nutrients is described by the Stokes–Einstein relation,

$$D = \frac{k_B T}{6\pi \eta A}$$

where $D$ is the molecular diffusivity in m$^2$ s$^{-1}$, $k_B = 1.38 \times 10^{-23}$ J K$^{-1}$ is the Boltzmann constant, $T$ is the temperature in kelvin, $\eta$ is the dynamic viscosity of the medium in kg m$^{-1}$ s$^{-1}$, and $A$ is the effective radius of a single solute molecule (Einstein 1905; Sutherland 1905; Von Smoluchowski 1906). Increasing the viscosity $\eta$ reduces the diffusivity $D$ of any nutrients in the vicinity. Recent experiments demonstrate that the mucus layer surrounding phytoplankton can increase the local viscosity up to a factor of 10 above seawater (Guadayol et al. 2021), decreasing the diffusivity by a factor $\leq 10$.

When nutrients are scarce, uptake is primarily determined by the diffusive flux to the cell surface,

$$J = -D \nabla C$$

where $\nabla C$ is the spatial gradient of nutrient concentration normal to the cell in kg m$^{-4}$. When nutrients are more plentiful, the rate of nutrient uptake by phytoplankton can also depend on the number of uptake sites and the rate of nutrient transport into the cell (Bonachela et al. 2011; Casey and Follows 2020). Here, I assume that nutrients are limited and the mucus layer changes nutrient uptake to a cell through the influence of viscosity on the diffusivity in Eq. 1. These results can be applied to cells that are not nutrient-limited by including terms for the number and affinity of uptake sites in Eq. 2 (e.g., Casey and Follows 2020, Eq. 10).

In this work, I use theory and numerical models to investigate the effects of mucus on nutrient uptake by idealized spherical phytoplankton. Both steady and time-dependent uptakes during nutrient pulses are considered. I find that viscous mucus increases the concentration gradient of nutrients at the cell’s surface, but not enough to compensate for the decrease in diffusivity. Mucus thus causes a net reduction in the steady-state nutrient uptake rate. During nutrient pulses, viscous mucus retains elevated nutrient levels near the cell for longer, improving nutrient uptake above the steady-state rate. However, in both steady and pulsed cases, a naked cell receives more nutrients than a mucus-covered cell.

### Results

#### Steady nutrient uptake

Mucus gradients have been detected near living diatoms, dinoflagellates, and haptophytes in laboratory experiments (Guadayol et al. 2021). Although frequently anisotropic, the average mucus layer viscosity appears to decrease exponentially away from the cell until it is undetectable at distances 2–18 $\mu$m away from the cell surface. The authors found that mucus increased the local viscosity by a factor of 1–10 above seawater within this layer. For a spherical phytoplankton cell of radius $a$ with spherically symmetric mucus production, I define a mucus layer via the viscosity $\eta'$:

$$\eta = \eta_S + \eta_M (\eta_M - 1) e^{-(r-a)/L_M}$$

where $\eta_S$ is the background viscosity of seawater (Sharqawy et al. 2010; Nayar et al. 2016), $1 \leq \eta_M \leq 10$ is the factor increase in viscosity caused by mucus, $r$ is the radial coordinate, and $L_M = 18 \mu$m is the length scale that determines the thickness of the mucus layer. For an intermediate cell size of $a = 10 \mu$m, varying the viscosity factor $\eta_M$ and normalized thickness $L_M/a$ yield mucus profiles of $\eta'$ as shown in Fig. 1A.
The prime notation indicates the quantity is normalized by its background value far from the cell.

The mucus-induced increase in viscosity reduces the molecular diffusivity of a nutrient through the Stokes–Einstein relation (Eq. 1). The diffusivity at the surface of the cell is lowered by a factor of \( D'(a) = \eta'_M \) (Fig. 1B). The thickness of the mucus layer \( L_{M/a} \) determines the radial extent of the diffusivity reduction moving away from the cell’s surface. A heat flux from the cell due to respiration or photosynthesis can potentially increase the diffusivity \( D \) in Eq. 1; this effect is minimal and is addressed in SI Methods. The diffusivity profiles \( D(r) \) are used to numerically solve the steady diffusion equation for the nutrient concentration profiles in Fig. 1C (see the Methods section, Eq. 9).

The reduction in diffusivity changes the shape of the nutrient concentration profile, retaining higher concentrations closer to the cell compared to the constant-diffusivity (no mucus) case. Within 10 \( \mu \)m of the cell surface (equivalent to the cell radius), \( 2 \leq \eta_M \leq 10 \) mucus increases the nutrient concentration by up to 20–130% above that of a naked cell. The nutrient-depleted layer is typically defined as the distance from the cell at which the concentration reaches 90% of its maximum value (Karp-Boss et al. 1996). A layer of \( 2 \leq \eta_M \leq 10 \) mucus reduces the thickness of the nutrient-depleted layer to 3–8 \( a \) (cell radii) compared to 9\( a \) for a cell without mucus. The concentration profile \( C(r) \) and associated gradient \( \partial C/\partial r \) depend more on the viscosity close to the cell \( \eta_M \) than the thickness of the mucus layer \( L_M \).

Uptake of limiting nutrients by phytoplankton then depends on whether the reduction of diffusivity by mucus is compensated by steepening of the nutrient gradient in Eq. 2. The ratios of these quantities for experiments with mucus compared to controls without mucus are defined, respectively, as

\[
G_E = \frac{\partial C(a)/\partial r}{\partial C_C(a)/\partial r}, \quad D_E = \frac{D(a)}{D_C} \quad \text{and} \quad J_E = D_E G_E
\]  

where \( G \) is the concentration gradient at the cell surface, the subscript “\( C \)” refers to the control without mucus, and the control diffusivity \( D_C \) is constant everywhere. These ratios are primarily controlled by the \( \eta_M \) and \( L_{M/a} \) mucus parameters. As the viscosity of the mucus increases, the concentration gradient ratio \( G_E \) increases and the diffusivity ratio \( D_E \) decreases (Fig. 2A). Increased gradients are not balanced by the decreased diffusivity, and so viscosity enhancement always lowers the flux of nutrients to the cell, that is, \( J_E < 1 \). For a given viscosity, a thicker mucus layer \( L_{M/a} \) reduces both the gradient and flux (Fig. 2B). As the layer thickness increases, the relationship between \( L_{M/a} \) and \( J_E \) weakens. This implies that the viscosity near the cell has a greater effect on nutrient uptake than the thickness of the layer. Note that for the same layer thickness \( L_M \), the flux to a larger cell (small \( L_{M/a} \)) is greater than to a smaller cell (large \( L_{M/a} \)).

To understand why decreased diffusivity is never compensated by gradient enhancement, I consider a form of \( D \) for which the diffusion Eq. 9 has an analytical solution at steady state:

\[
D = D_C - D_C \frac{(1 - \eta_{M/a}) a^2}{r^2}
\]  

Here, the viscosity reduces the diffusivity by a factor of \( D_E = \eta_{M/a}^{-1} \) at the surface of the cell. The profile of the analytical \( D \) is similar to the numerical \( D \) with thickness \( L_{M/a} = 0.2 \) (2 \( \mu \)m). Assuming nutrients are immediately taken up by the phytoplankter (i.e., \( C(a) = 0 \)) and maintain their ambient concentration at infinity \( (C(\infty) = C_\infty) \), the steady-state solution to Eq. 9 is
and $7$ can apply to other cell sizes when $\eta_M$ do not change during the nutrient pulse. The concentration near the cell climbing by a factor of $\eta_M^{-1}$ here, Eq. 8 can accommodate different relationships between viscosity and diffusivity that are determined in future work. This is accomplished by simply substituting $\eta_M^{-1}$ in Eq. 8 with $D_E(\eta_M)$. An extension of this analysis to cells of arbitrary shape is provided in the SI Discussion.

**Time-dependent nutrient pulse**

Rapid nutrient fluctuations at the scale of phytoplankton can occur when nearby cells lyse, zooplankton egest, or turbulence stirs chemical gradients (Stocker 2012). An example of a brief nutrient pulse originating $9a$ away from cells of radius $a = 10 \mu m$ is shown in Fig. 3 (see the Methods section, Eq. 11). The nutrient concentration near a control cell with constant diffusivity is compared to a cell surrounded by a layer of mucus with viscosity $\eta_M = 10$ and thickness $L_M/a = 0.2$ (Fig. 3A). This high viscosity enhancement is chosen to help visualize differences from the control. The simulation begins at $t = 0$ s with the diffusivity and concentration profiles at steady state as shown in Fig. 1. The diffusivity profiles do not change during the nutrient pulse. The concentration increases at the edge of the domain ($t = 0.98$ s, Fig. 3A), climbing by a factor of $C_0' = 100$ after $1$ s. The pulse diffuses toward the cell ($t = 1.25$ s) and increases the concentration near the cell’s surface before relaxing ($t = 2.3$ s) back toward a steady state.

A time course of nutrient flux (normalized by the steady-state value) shows that the pulse reaches the control cell slightly before the cell with a mucus layer (Fig. 3B), because viscous mucus slows the diffusion of nutrients. This causes an initial decrease in the ratio of the mucus-to-control fluxes, $J_E$, from the steady-state value (Fig. 3C). The mucus subsequently retains elevated nutrient concentrations near the cell, prolonging the flux enhancement compared to the control and increasing the ratio $J_E$ at time $t = 2.3$ s. Mucus behaves like a sponge for a pulsed nutrient, with a net increase in $J_E$ for the duration. However, $J_E$ is still always less than 1, so the actual flux to the cell with mucus is always less than the flux to the control.

Varying mucus viscosity or thickness does not alter the form of $J_E$ for a given nutrient pulse (SI Fig. S3). The magnitudes of fluctuations from steady state $J_E$ increase with both mucus viscosity $\eta_M$ and thickness $L_M$, consistent with the sponge-like behavior just described. The shape and magnitude of $J_E$ fluctuations change with pulse duration $P_d$ (Fig. 4A). For a $\eta_M = 2$ and $L_M = 2 \mu m$ mucus layer, the fluctuations of $J_E$ skew toward a net increase above steady state up to $P_d = 1$ s. This is the optimal duration for such a mucus layer to maintain elevated nutrient gradients compared to the control at

\[
C = C_\infty - C_\infty \frac{\text{arcoth}(r/a \sqrt{1-\eta_M^{-1}})}{\text{arctanh} \left( \sqrt{1-\eta_M^{-1}} \right)}
\]

The gradient and flux can then be obtained as a function of $\eta_M$ alone:

\[
G_E = \frac{\eta_M \sqrt{1-\eta_M^{-1}}}{\text{arcoth} \left( \sqrt{1-\eta_M^{-1}} \right)}
\]

and

\[
J_E = \frac{\sqrt{1-\eta_M^{-1}}}{\text{arctanh} \left( \sqrt{1-\eta_M^{-1}} \right)}
\]
the tail end of the pulse. For longer pulse durations \( P_d > 1 \) s, the \( J_E \) fluctuations diminish toward the steady-state value. The difference between steady-state and time-dependent results are negligible when \( P_d > 10 \) s for cells of radius \( a = 10 \) μm because the change in nutrient concentration outside the mucus layer is slower than the diffusion of nutrients through the mucus layer. A similar cutoff is \( P_d > 0.1 \) s for \( a = 1 \) μm and \( P_d > 10^3 \) s for \( a = 100 \) μm. Increasing the pulse magnitude \( C_p \) increases the relative flux to a cell surrounded by mucus during the tail end of a pulse (Fig. 4B). In all cases, the mean of the fluctuations of \( J_E \) from steady state are positive, indicating a net increase in uptake compared to steady state for a cell surrounded by a viscous layer. Still, the net flux of nutrients is always less for a cell surrounded by mucus than one without mucus.

### Discussion

Nutrient uptake by phytoplankton depends on the molecular diffusivity and concentration gradient of the nutrient. A viscous mucus layer enveloping a phytoplankter reduces the molecular diffusivity and increases the concentration gradient of nutrients near the cell surface. Phytoplankton cells radiate a small amount of heat that can increase the local diffusivity. However, heat flux from the cell does not generally offset the viscous reduction of diffusivity in the Stokes–Einstein equation (SI Discussion). The steady flux of nutrients to phytoplankton is always reduced by a viscous mucus layer despite increased concentration gradients, as demonstrated by Eq. 8.

Ploug and Passow (2007) found that mucus in diatom aggregates reduced the diffusivity of H₂ and O₂ by 5–10%. This corresponds to a 1–2% reduction in the flux of nutrients to a cell with a thin \( L_M = 2 \) μm viscous layer. However, experimental evidence suggests that larger solutes like vitamins and siderophores would experience a greater reduction in diffusivity within the same viscous layer (Dauty and Verkman 2004). In the range of mucus viscosities and layer thicknesses...
measured by Guadayol et al. (2021), I estimate that the flux of macronutrients is reduced by as much as 80% for an $a = 10 \mu m$ cell with a $\eta_M = 10$ factor increase in viscosity and $L_M = 10 \mu m$ thick mucus layer. The more conservative scenario of $a = 10 \mu m$, $\eta_M = 2$, and $L_M = 2 \mu m$ reduces macronutrient flux by 10%. The difference between the results of Ploug and Passow (2007) and the estimates for larger molecules presented here emphasizes the need for experimental quantification of the relationship between viscosity and diffusivity of macronutrients in the viscous phycosphere.

During a nutrient pulse, the flux to a cell surrounded by mucus vs. a naked cell improves compared to steady state. This is because the viscous layer acts like a sponge, retaining pulsed nutrients near the cell for longer than a cell without mucus. A mucus layer provides the greatest advantage to an $a = 10 \mu m$ cell when the nutrient pulse lasts for seconds and increases the nutrient concentration by more than a factor of 100. However, $f_E < 1$ during the pulse and so the overall flux to a cell with a viscous layer is always lower than to a naked cell.

For limiting nutrients, phytoplankton growth rate is proportional to nutrient uptake (Morel 1987; Bonachela et al. 2011). A 10–80% reduction in macronutrient uptake increases the doubling time for a phytoplankton population by 15–500%. This constraint on growth rates represents a significant loss of fitness for phytoplankton in the open ocean where nutrients are scarce. Mucus production varies significantly between taxonomic groups (Guadayol et al. 2021). If there is no ecological benefit from mucus, I would expect that the loss of fitness over evolutionary time scales would minimize mucus production across taxa. Because diverse and common taxa secrete mucus, increasing the local viscosity may be an adaptation that provides significant ecological benefits. Mucus may not just be a byproduct of the photosynthetic machinery that holds “no biological advantage to the phytoplankton,” as has been historically asserted (Fogg 1966, 1983; Bjørnsen 1988).

Recent research has revealed complicated signaling, metabolic shifts, and chemical exchanges between phytoplankton and bacteria in close proximity (Amin et al. 2009, 2015; Durham et al. 2015). While some chemicals are exchanged for mutual benefit, other nutrients utilized by both phytoplankton and bacteria represent a source of competition. Without mucus, the nutrient-depleted layer surrounding a phytoplankton cell reaches 10–100s of microns away from the cell. This presents a problem for keeping helpful bacteria near the phytoplankton cell: nonmotile bacteria may be “starved” of shared nutrients. Mucus reduces the size of the nutrient-depleted region, elevating the concentrations of shared nutrients by a factor of 1.2–2.3 within $10 \mu m$ of the phytoplankton cell (Fig. 1C). Therefore, I propose that mucus production may represent a method for sharing limiting nutrients with bacteria that produce other beneficial compounds. If mutualistic bacteria release beneficial chemicals as a pulse within the mucus layer, the sponge-like behavior of mucus viscosity may enhance the uptake of those chemicals by the phytoplankton.

Near the end of a bloom, the combined mucus production of a dense phytoplankton population can increase the bulk viscosity of seawater by a factor of 10 or 100 (Aldredge et al. 1993; Jenkinson 1993; Jenkinson and Biddanda 1995; Seuront et al. 2006). As nutrients become limited within the bloom, elevated viscosity from neighboring cells further inhibits nutrient uptake. Whatever benefit a single phytoplankton cell gained from associated bacteria in its own mucus layer may not outweigh the loss of nutrient uptake caused by the excess viscosity of a dense bloom. In addition, phytoplankton produce more mucus during nutrient stress (Fogg 1983). Excess mucus viscosity results in lower nutrient acquisition, which leads to more mucus. This feedback loop could contribute to the rapid decline of phytoplankton blooms during their late stages. At the same time, phytoplankton that compete with the dominant species also experience reduced uptake rates from the bulk viscosity, possibly preventing succession at the climax of a bloom. The reduction of nutrient uptake because of mucus does not refute other potential benefits of exudation, such as preventing viral infection, “farming” bacteria that generate useful compounds, or deterring grazers (Malej and Harris 1993; Legendre and Rassoulzadegan 1995; Murray 1995). Rather, the combination of ecological advantages permitted by mucus must outweigh the reduction in fitness caused by lowered nutrient flux. This reduction in fitness is well-characterized by the analytical $f_E$ in Eq. 8 and may be useful for parameterizing trait-based models of phytoplankton dynamics.

**Methods**

A spherical phytoplankton cell of radius $a$ is surrounded by a spherically symmetric mucus layer. The equation governing diffusion of a nutrient to a phytoplankton cell in a quiescent fluid assuming spherical symmetry is

$$\frac{\partial C}{\partial t} = \frac{1}{r^2} \frac{\partial}{\partial r} \left( D r^2 \frac{\partial C}{\partial r} \right)$$  \hspace{1cm} (9)

where $C(r)$ is the nutrient concentration, $r$ is the radial coordinate, and $D$ is the molecular diffusivity of the nutrient in seawater. Mucus exuded by the cell causes variation in the diffusivity in the radial direction and Eq. 9 can only be solved analytically for limited functional forms of $D(r)$. To accommodate varying mucus profiles and time-dependent nutrient pulses, Eqs. 1 and 9 are solved numerically in the domain between the surface of the cell $r = a$ and an outer boundary $r = b$. The outer boundary is located at $b = 100a$ for steady state simulations and $b = 10a$ for time-dependent simulations.

I assume the phytoplankton cell takes up nutrients as quickly as possible and the concentration boundary conditions are $C(a) = 0$ and $C(b) = C_b$. If uptake is limited by the number or affinity of uptake sites on the surface of the cell, the nutrient concentration at the surface can increase as $0 < C$
(a) < Cb. While this changes the nutrient concentration profile, the gradient Gt and flux Fr ratios are the same as in the C (a) = 0 case. Therefore, the effect of mucus on the nutrient flux to a cell is independent of uptake site limitations. At steady state, Eq. 9 reduces to

$$\frac{\partial C}{\partial t} = \frac{C_b}{\gamma Dr^2}$$  \hspace{1cm} (10)

where \(\gamma = \int_0^b D^{-1} r^{-2} dr\) is numerically integrated. The time-dependent solution of Eq. 9 is calculated using a Forward Time Central Space scheme that is first order in time and second order in space. A pulse of nutrients is introduced at the outer boundary via

$$C(b,t) = C_b + (C_P - C_b) e^{-\left(\frac{r}{fl}\right)^2}$$  \hspace{1cm} (11)

where \(C_P\) is the maximum nutrient concentration during the pulse, \(P_i\) is the time at which the maximum occurs, and \(P_d\) scales the duration of the pulse.

Error analysis and other details are available in the SI Methods.

References

Alldredge, A. L., U. Passow, and B. E. Logan. 1993. The abundance and significance of a class of large, transparent organic particles in the ocean. Deep Sea Res. Part 1 Oceanogr. Res. Pap. 40: 1131–1140. doi:10.1016/0967-0637(93)90129-q

Aluwihare, L. I., and D. J. Repeta. 1999. A comparison of the chemical characteristics of oceanic DOM and extracellular DOM produced by marine algae. Mar. Ecol. Prog. Ser. 186: 105–117.

Amin, S. A., D. H. Green, M. C. Hart, F. C. Kupper, W. G. Sunda, and C. J. Carrano. 2009. Photolysis of iron-siderophore chelates promotes bacteria-algal mutualism. Proc. Natl. Acad. Sci. 106: 17071–17076.

Amin, S. A., and others. 2015. Interaction and signalling between a cosmopolitan phytoplankton and associated bacteria. Nature 522: 98–101.

Amin, S. A., M. S. Parker, and E. V. Armbrust. 2012. Interactions between diatoms and bacteria. Microbiol. Mol. Biol. Rev. 76: 667–684.

Azam, F., and J. W. Ammerman. 1984. Cycling of organic matter by bacterioplankton in pelagic marine ecosystems: Microenvironmental considerations, p. 345–360. In M. Fasham [ed.], Flows of energy and materials in marine ecosystems. Springer.

Azam, F., and F. Malfatti. 2007. Microbial structuring of marine ecosystems. Nat. Rev. Microbiol. 5: 782–791.

Azam, F., and D. Smith. 1991. Bacterial influence on the variability in the ocean’s biogeochemical state: A mechanistic view, p. 213–236. In S. Demers [ed.], Particle analysis in oceanography. NATO ASI Series. Springer-Verlag.

Azam, F., D. C. Smith, G. F. Steward, and Å. Hagström. 1994. Bacteria-organic matter coupling and its significance for oceanic carbon cycling. Microb. Ecol. 28: 167–179.

Biddanda, B., and R. Benner. 1997. Carbon, nitrogen, and carbohydrate fluxes during the production of particulate and dissolved organic matter by marine phytoplankton. Limnol. Oceanogr. 42: 506–518.

Bjørnsen, P. K. 1988. Phytoplankton exudation of organic matter: Why do healthy cells do it? Limnol. Oceanogr. 33: 151–154.

Bonachela, J. A., M. Raghib, and S. A. Levin. 2011. Dynamic model of flexible phytoplankton nutrient uptake. Proc. Natl. Acad. Sci. USA 109: 3190.

Bratbak, G., and T. Thingstad. 1985. Phytoplankton-bacteria interactions: An apparent paradox? Analysis of a model system with both competition and commensalism. Mar. Ecol. Prog. Ser. 25: 23–30.

Casey, J. R., and M. J. Follows. 2020. A steady-state model of microbial acclimation to substrate limitation. PLoS Comput. Biol. 16: e1008140.

Cole, J. J. 1982. Interactions between bacteria and algae in aquatic ecosystems. Annu. Rev. Ecol. Syst. 13: 291–314.

Croft, M. T., A. D. Lawrence, E. Raux-Deery, M. J. Warren, and A. G. Smith. 2005. Algae acquire vitamin B12 through a symbiotic relationship with bacteria. Nature 438: 90–93.

Dauty, E., and A. S. Verkman. 2004. Molecular crowding reduces to a similar extent the diffusion of small solutes and macromolecules: Measurement by fluorescence correlation spectroscopy. J. Mol. Recognit. 17: 441–447.

Durham, B. P., and others. 2015. Cryptic carbon and sulfur cycling between surface ocean plankton. Proc. Natl. Acad. Sci. USA 112: 453–457.

Einstein, A. 1905. On the motion of small particles suspended in liquids at rest required by the molecular kinetic theory of heat. Ann. Phys. 17: 549–560.

Fogg, G. 1966. The extracellular products of algae. Oceanogr. Mar. Biol. 4: 195–212.

Fogg, G. E. 1983. The ecological significance of extracellular products of phytoplankton photosynthesis. Bot. Mar. 26: 3–14.

Guadayol, Ò., T. Mendonca, M. Segura-Noguera, A. Wright, M. Tassieri, and S. Humphries. 2021. Microrheology reveals microscale viscosity gradients in planktonic systems. Proc. Natl. Acad. Sci. 118: e2011389118.

Jenkinson, I. R. Oceanographic implications of non-newtonian properties found in phytoplankton cultures. Nature. 1986;323: (6087):435–437. doi:10.1038/323435a0

Jenkinson, I. R. 1993. Bulk-phase viscoelastic properties of seawater. Oceanol. Acta 16 (4):317–334.

Jenkinson, I. R., and B. A. Biddanda. 1995. Bulk-phase viscoelastic properties of seawater relationship with plankton components. J. Plankton Res. 17: 2251–2274. doi:10.1093/plankt/17.12.2251
Joint, I., P. Henriksen, G. A. Fonnes, D. Bourne, T. F. Thingstad, and B. Riemann. 2002. Competition for inorganic nutrients between phytoplankton and bacterioplankton in nutrient manipulated mesocosms. Aquat. Microb. Ecol. 29:145–159.

Karp-Boss, L., E. Boss, and P. A. Jumars. 1996. Nutrient fluxes to planktonic osmotrophs in the presence of fluid motion. Oceanogr. Mar. Biol. 34:71–107.

Larsson, U., and A. Hagström. 1979. Phytoplankton exudates release as an energy source for the growth of pelagic bacteria. Mar. Biol. 52:199–206.

Legendre, L., and F. Rassoulzadegan. 1995. Plankton and nutrient dynamics in marine waters. Ophelia 41:153–172.

Malej, A., and R. P. Harris. 1993. Inhibition of copepod grazing by diatom exudates: A factor in the development of mucus aggregates? Mar. Ecol. Prog. Ser. 96:33–42.

Mayali, X., and F. Azam. 2004. Algicidal bacteria in the sea and their impact on algal blooms. J. Eukaryot. Microbiol. 51:139–144.

Morel, F. M. M. 1987. Kinetics of nutrient uptake and growth in phytoplankton. J. Phycol. 23:137–150.

Mühlenbruch, M., H. P. Grossart, F. Eigemann, and M. Voss. 2018. Mini-review: Phytoplankton-derived polysaccharides in the marine environment and their interactions with heterotrophic bacteria. Environ. Microbiol. 20:2671–2685.

Murray, A. G. Phytoplankton exudation: exploitation of the microbial loop as a defence against algal viruses. Journal of Plankton Research. 1995;17: (5):1079–1094. doi:10.1093/plankt/17.5.1079

Myklestad, S. M. Release of extracellular products by phytoplankton with special emphasis on polysaccharides. Science of The Total Environment. 1995;165: (1-3):155–164. doi:10.1016/0048-9697(95)04549-g

Nayar, K. G., M. H. Sharqawy, L. D. Banchik, V. Lienhard, and H. John. 2016. Thermophysical properties of seawater: A review and new correlations that include pressure dependence. Desalination. 390: 1–24. doi:10.1016/j.desal.2016.02.024

Passow, U. 2002. Transparent exopolymer particles (TEP) in aquatic environments. Prog. Oceanogr. 55:287–333.

Ploug, H., and U. Passow. 2007. Direct measurement of diffusivity within diatom containing transparent exopolymer particles. Limnol. Oceanogr. 52:1–6.

Seuront, L., D. Vincent, and J. G. Mitchell. 2006. Biologically induced modification of seawater viscosity in the Eastern English Channel during a Phaeocystis globosa spring bloom. J. Mar. Syst. 61:118–133.

Seymour, J. R., S. A. Amin, J. B. Raina, and R. Stocker. 2017. Zooming in on the phycosphere: The ecological interface for phytoplankton-bacteria relationships. Nat. Microbiol. 2:2–7.

Sharqawy, M. H., V., J. H. Lienhard, and S. M. Zubair. 2010. Thermophysical properties of seawater: A review of existing correlations and data. Desalin. Water Treat. 16:354–380. doi:10.5004/dwt.2010.1079

Stocker, R. 2012. Marine microbes see a sea of gradients. Science 338:628–633.

Sutherland, W. 1905. A dynamical theory of diffusion for non-electrolytes and the molecular mass of albumin. Lond. Edinb. Dublin Philos. Mag. J. Sci. 9:781–785. doi:10.1080/1478640509463331

Thornton, D. C. 2014. Dissolved organic matter (DOM) release by phytoplankton in the contemporary and future ocean. Eur. J. Phycol. 49:20–46.

Von Smoluchowski, M. 1906. Zur kinetischen theorie der brownscen molekularbewegung und der suspensionen. Ann. Phys. 326:756–780.

Acknowledgments

I thank Peter J.S. Franks, Óscar Guadayol, and Stuart Humphries for helpful discussions and suggestions. This work was supported by a grant from the Simons Foundation (732155, BGI). Additional support was provided by the Scripps Institution of Oceanography. Simulations were conducted on the Comet and Expanse resources located at the San Diego Supercomputer Center through the generous support of NSF XSEDE grant TG-OCE160016.

Submitted 29 June 2021
Revised 10 January 2022
Accepted 19 January 2022