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Title: Marine snow viscosity regulates microbial degradation and the ocean carbon sink

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Abstract: Bacterial degradation of marine snow aggregates is a major component of global carbon cycling. Whether aggregate carbon is released in the upper ocean or is sequestered at depth depends on its sinking speed and degradation rate. However, little is known about the physical constraints of bacterial colonization and degradation of individual aggregates. Using molecular rotors to measure the nanoscale viscosity field of natural aggregates, we show that aggregates are highly structured microhabitats with less-viscous regions that are accessible for colonization and more-viscous regions that correlate to a barrier to bacterial infiltration. By quantifying the viscosity degradation rate, we demonstrate that more viscous aggregates take longer to degrade, sink farther, and contribute more to carbon sequestration, revealing a microscale physical constraint of the global ocean carbon pump.

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Main Text: Marine snow – a flurry of heterogeneous organic particles sinking to the deep ocean – accounts for 70% of ocean carbon export (1). Marine snow originates in the upper water column from phytoplankton exudates and blooms, zooplankton fecal matter and carcasses, viral cell lysis, and other debris (2–4). The combined spatial and temporal variability of marine snow sources and dynamic ocean conditions makes predicting the efficiency of the carbon pump challenging, a topic that has been the focus of decades of research (5–7). Fundamentally, marine snow sinking speeds and bacterial degradation rates determine whether the organic matter is recycled in the upper ocean or contributes to the ocean carbon sink: rapid decomposition by bacteria releases carbon dioxide back into the sunlit shallows where it was originally fixed by photosynthesis; faster sinking transports particulate organic carbon toward the seafloor where it is sequestered for hundreds to thousands of years (8–14). Despite the fundamental importance of these two rates, little is known about the physical structure of marine snow and how it impacts bacterial colonization and degradation over time (15–17).

Observations of the distribution of marine snow in the water column using sedimentation traps, marine snow catchers, and imaging profilers have repeatedly shown a substantial decline in the flux of particulate organic matter as a function of depth (18–24), a relationship known as the Martin curve (25). This empirical description of the vertical attenuation of the oceanic carbon flux is frequently used in carbon budgets and modern climate models (26). The collective microscale interactions between microbes and marine aggregates that influence the Martin curve are not well understood and may explain variability or deviations from the canonical attenuation curve in different ocean regions (26–29). Improving our understanding of bacterial degradation of the physical structure of marine snow is critical for predicting the efficiency of ocean carbon fluxes in an Earth climate system that is undergoing rapid changes (30).

Marine snow typically contains transparent mucus material that comprises the majority of the particle or acts as a glue for dead cells, ballast minerals, and other solid detritus (31). The sources of marine snow differ in their chemical composition and density (32, 33), and so the material properties of marine snow from different ecosystems may display considerable variability. The material properties of marine snow have not been measured directly, but indirect evidence suggests that the mucus is viscous. Phytoplankton increase the microscale viscosity of the phycosphere near their cells by exuding extracellular polymeric substances (EPS), a precursor to marine snow (34, 35). An “invisible comet tail” of viscous, low-density mucus can slow the sinking speed of marine snow particles (36). Such studies rely on tracking seeded microspheres to estimate viscosities and flow; these microspheres do not readily penetrate into mucus and preclude concurrent observations of bacteria which are similar in size to the microspheres. Bacteria rapidly colonize marine snow and collectively produce hydrolytic enzymes to digest the descending particles (37). To date, methods used to simultaneously visualize bacteria and marine snow (e.g. alcian blue, catalyzed reporter deposition–fluorescence in situ hybridization) require fixation, filtration, washing, or drying, which damage the fragile structures of the mucus and distort three-dimensional spatial relationships (31, 38, 39).

To overcome these limitations, we developed a method to measure the 3D nanoscale viscous structure of individual marine snow particles (“mucus aggregates”) using molecular rotors and confocal microscopy (40). A molecular rotor fluoresces when twisting of a functional group is slowed by crowding of the local environment by nonsolvent molecules. Microviscosities measured with molecular rotors (referred to as “viscosity” herein) correlate with but are not the same as hydrodynamic viscosities (fig. S1). These viscosity-sensing dyes readily penetrate into mucus to reveal the interior physical structure of undisturbed marine aggregates. Combined with a nucleic

acid stain to locate bacteria, we can quantify bacterial colonization and the associated transformation of viscosity within individual aggregates over time. Notably, this method is ratiometric and normalized to background fluorescence and viscosity standards to account for variability in dye concentration, temperature, and other environmental and optical artifacts (see materials and methods). The molecular rotor viscosity measurements showed excellent agreement with independent microrheological measurements of aggregates from the same species, verifying the reliability of the method in a complex biofluid (see supplementary materials). In this work, we present the first 3D quantitative view of the viscous structure – the “mucoscape” – of mucus aggregates from laboratory diatom cultures and environmental samples. We found that viscosity (relative to seawater) within aggregates correlates to a physical constraint on colonization and degradation by bacteria. Bacteria can readily colonize lower-viscosity “surface” regions, but are not found in higher-viscosity inner “barrier” regions until they are broken down below a viscous threshold. By quantifying the rate of viscosity degradation, we show that marine snow viscosity is a notable, previously unrecognized rate determinant of the ocean carbon sink.

Bacteria and the viscous microhabitat of marine aggregates

The molecular rotors revealed a high degree of spatial variability in the relative viscosity of the exterior of a mucus aggregate sampled from a laboratory culture of the centric diatom, *Chaetoceros affinis* (Fig. 1A, blue color scale, and movie S1). Nanoscale heterogeneity composed of bulges and crevasses – smaller than the bacteria – was visible across the exteriors and inside of all laboratory aggregates analyzed (N=30 aggregates; Fig. 1B and movie S2). Despite the heterogeneity, viscosity tended to increase toward the interior of aggregates (Fig. 1C). The median relative viscosity of all aggregates was 2.1 and the 95th percentile viscosity was 12.4, compared with 1.0 and 1.2, respectively, for the background volume outside of the aggregates (seawater). Bacteria (~1 μm) were located near the “surface” regions of the aggregates as individuals or clusters (Fig. 1, B and D). Aggregate volumes ranged from 548 to 10,100 μm^3 , with a mean of $3300 \pm 478 \mu\text{m}^3$. Larger millimeter-scale aggregates were abundant in the cultures, but smaller aggregates were chosen for analysis to maximize spatial resolution of both the viscosity and the bacteria.

To better understand bacterial associations with aggregate viscosities, we quantified properties within 0.3 μm of the bacterial cells (orange color scale, Fig. 1B). The probability of a given viscosity occurring in the proximity of bacteria in contact with the aggregate differed from that of bacteria not in contact with the aggregate (Fig. 2A). The most probable viscosity for aggregate-colonizing bacteria was 1.25 (N = 2843 bacteria) compared with 1.00 for bacteria outside the aggregates (N = 3607 bacteria). Hence, a viscosity of ~1.25 correlates to a “surface” to bacteria and can be used to determine the portions of mucus aggregates that are physically accessible for colonization. Bacteria likely remain on these surface regions by binding to aggregate polymers using lectins embedded in their cell membranes (41, 42). The ratio of the probability of a viscosity occurring in the proximity of bacteria versus the rest of the aggregate volume is shown in Fig. 2B. A probability ratio >1 indicates a preferential association of the bacteria with an aggregate viscosity, whereas a probability ratio <1 indicates that bacteria are less associated with those viscosities within the aggregate. The probabilities are equal at a viscosity of ~2, signifying that viscosities >2 are increasingly inaccessible to bacteria. Bacteria are half as likely to encounter an aggregate viscosity of 4, which correlates to a physical “barrier” to bacteria. Elastic properties of the mucus may also contribute to bacterial colonization patterns but are not quantified with the molecular rotor assay. Analysis of viscosity gradients within the aggregates supports similar definitions of accessible surfaces and inaccessible barriers for bacteria (fig. S9).

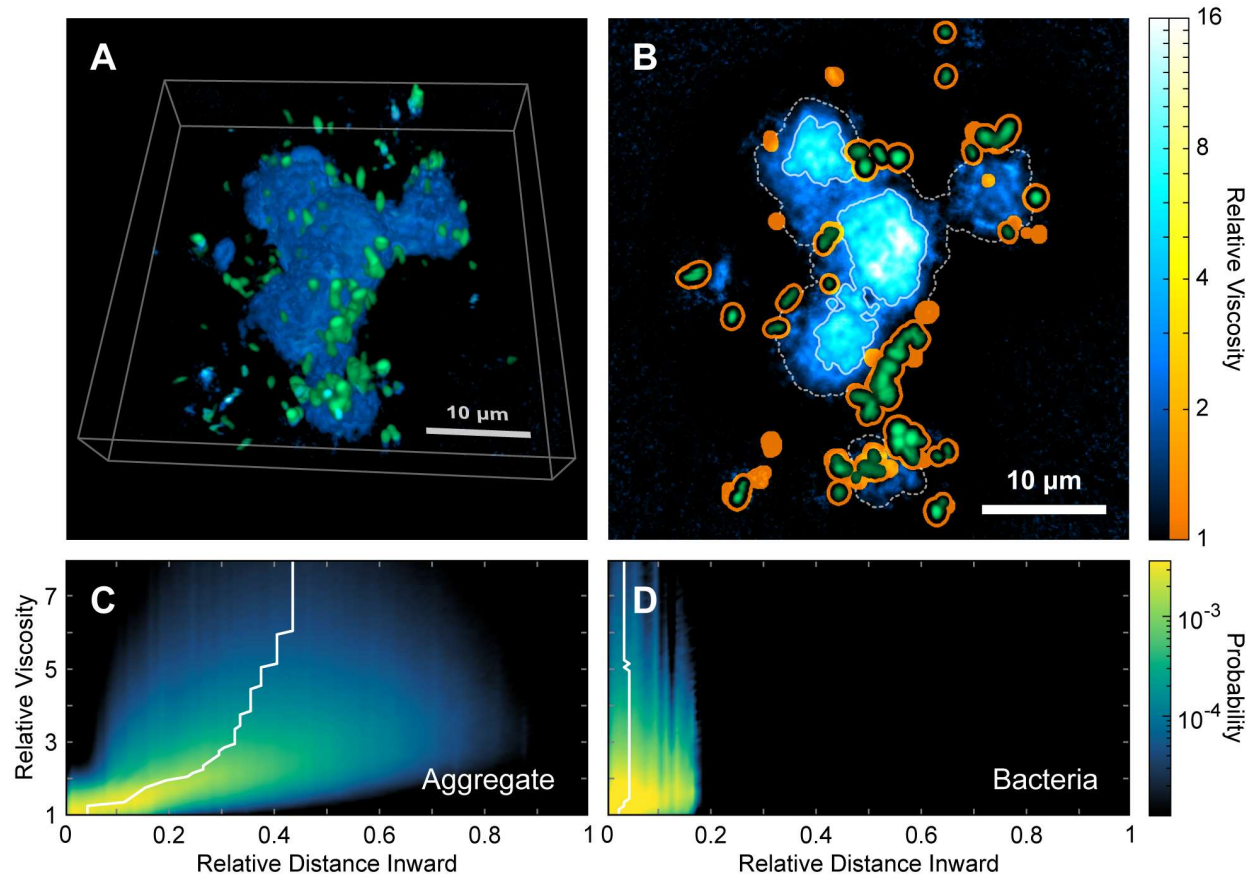


Fig. 1. The viscous ‘mucoscope’ of an aggregate colonized by bacteria. (A) A composite 3D reconstruction of mucus viscosity relative to seawater (blue color scale) and bacteria identified with a nucleic acid stain (green). Bacteria can colonize the surface of the aggregate, which displays substantial nanoscale viscous heterogeneity. (B) A thin slice through the middle of the same aggregate shows internal complexity and viscosity increasing toward the center. Viscosities within $0.3\ \mu\text{m}$ of bacterial cells are highlighted with the orange color scale. Bacteria colonize lower-viscosity edge regions (between the dotted and solid white lines) but are not found in regions with viscosities >4 (inside the solid white line). (C) The mean probability of a relative viscosity occurring at a given distance inward from the aggregate edges, normalized by the maximum distance ($N = 30$ aggregates). The white line indicates the most probable distance for each viscosity. (D) The same as (C) but for viscosities in close proximity to bacteria (orange color scale in (B)). Bacteria are rarely located more than 20% inward from the edge of the aggregate ($N = 30$ aggregates).

Bacteria were rarely found inside regions with relative viscosities >4 (Fig. 1B, solid white contour). Even in areas where bacteria appear to have infiltrated inside the aggregate, local viscosities were generally <4 . This suggests that bacteria must reduce the viscosity of inner aggregate material through enzymatic hydrolysis in order to break through and proliferate. The percentage of aggregate volume inaccessible to bacteria (contiguous internal regions of viscosity >4) ranged from 0.43 to 71%, with a mean of $27 \pm 3.3\%$. Thus, there was substantial variability among aggregates in the volume that is directly accessible to bacteria, even though these aggregates were sampled from the same laboratory diatom culture.

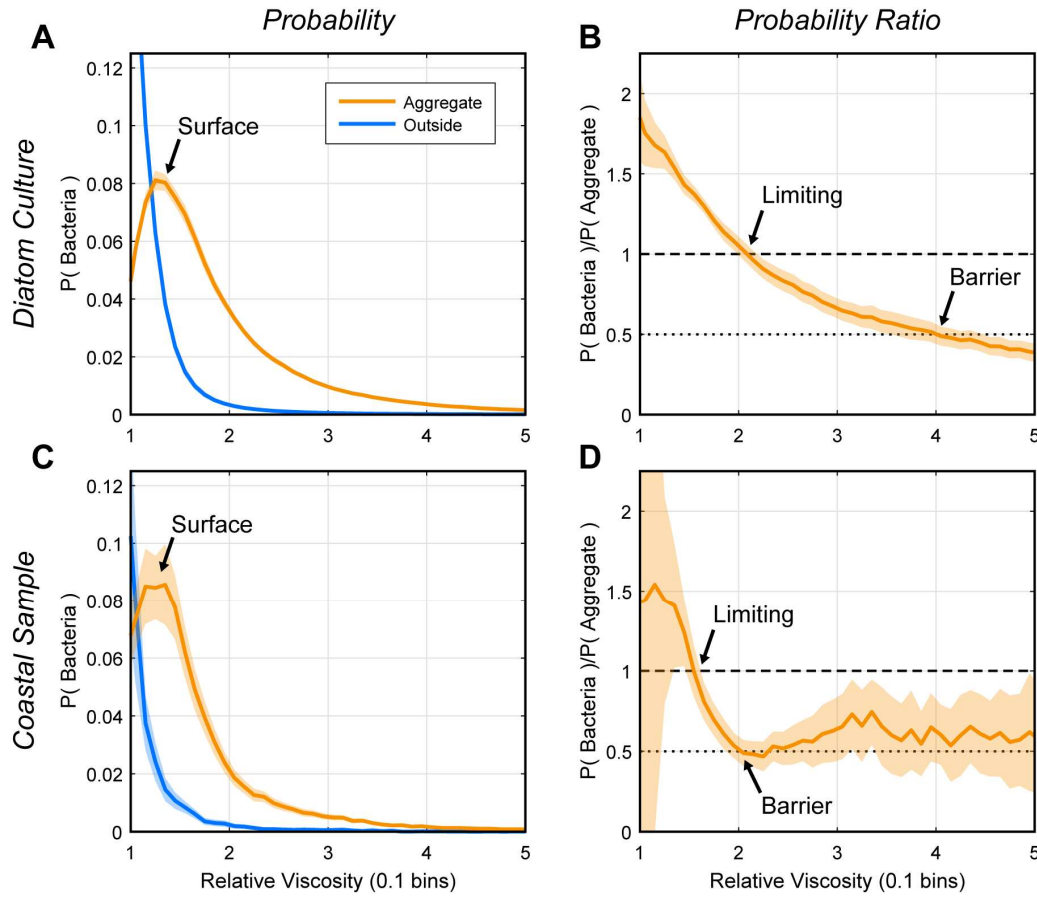


Fig. 2. Bacterial associations with mucus aggregate viscosities. (A) The probability (P) of a viscosity near a bacterial cell (orange, Fig. 1B) in 0.1 relative viscosity bins for aggregates from diatom cultures. Bacteria colonizing the aggregate (orange line) are most associated with a viscosity of 1.25, which represents a colonizable surface for bacterial activity. The most probable viscosity for free-living bacteria outside the aggregate (blue line) is 1, i.e. seawater. (B) The ratio of the probability of a viscosity occurring in the proximity of bacteria versus the rest of the aggregate volume. Bacteria are less associated with aggregate viscosities >2 (dashed line crossing) and half as likely to encounter viscosities >4 (dotted line crossing), indicative of a physical mucus barrier. More than 6450 bacteria were analyzed across N = 30 aggregates. (C and D) The same analyses as (A) and (B), respectively, but for aggregates sampled from the coastal environment. More than 1060 bacteria were analyzed across N = 11 environmental marine snow samples. Error bars represent the standard error.

Aggregates from coastal environmental samples collected off of the Scripps Institution of Oceanography pier exhibited similar patterns of bacterial associations (Fig. 2, C and D; see sampling conditions in table S1). These aggregates were somewhat less viscous than laboratory samples, with a median and 95th percentile viscosity of 1.6 and 10.5, respectively (N = 11 aggregates). Bacteria are mostly associated with relative viscosities of ~1.25 (Fig. 2C). Relative viscosities >2 appear to represent a barrier to bacterial infiltration of these aggregates (Fig. 2D), which is lower than the barrier viscosity found in laboratory aggregates owing to the relatively lower aggregate viscosities in coastal samples in the denominator of the ratio. Although the barrier viscosity threshold differed between laboratory and environmental samples, both support our definition of a physical niche space for bacteria in marine snow: Lower-viscosity regions are

accessible for colonization, whereas higher-viscosity regions may be impenetrable until the viscous material is broken down. The accessible surface and inaccessible barrier viscosity thresholds may vary depending on the source and chemical composition of the marine snow and the enzymatic capabilities of the colonizing bacteria in other parts of the ocean. Nonetheless, this niche space definition represents a useful framework for interpreting those differences and their significance for the biological carbon pump.

The viscosity degradation rate of individual aggregates

Marine bacteria, particularly those associated with marine snow, produce a suite of hydrolytic enzymes that break down high-molecular weight polymers such as polysaccharides, proteins, lipids, and nucleic acids (37, 43–45). Some polymers (e.g. laminarin) are easily hydrolyzed by bacteria, whereas others (e.g. fucose-containing sulphated polysaccharides) are more resistant to enzymatic degradation (46, 47). The ultimate remineralization of aggregates into dissolved organic matter is attributed to a combination of bacterial enzyme activity and physical dissolution, but this breakdown (and associated reductions in viscosity) has never been directly observed in individual aggregates (48, 49). Unlike bulk assays of specific enzyme activities (e.g., glucosidase and protease), our molecular rotor method tracks the physical degradation of mucus by various enzymes through decreases in viscosity. We observed reductions in viscosity over time within single aggregates colonized by bacteria (Fig. 3A). Over the course of 7 hours, the probabilities of higher viscosities decreased, and the probabilities of lower viscosities increased (Fig. 3B). This is consistent with a conversion of higher viscosities to lower viscosities throughout the aggregate. The average change in the relative viscosity of laboratory-generated diatom aggregates was $-0.017 \pm 0.0033 \text{ hours}^{-1}$ ($N = 7$ aggregates at three time points). At the same time, the aggregate volumes shrank at a rate of $-0.024 \pm 0.011 \text{ hours}^{-1}$, corresponding to 34% in one day (Fig. 3C). Based on simulated particle fluxes fit to ocean observations, the volume shrinkage rate of marine snow ranged from -0.0017 to $-0.045 \text{ hours}^{-1}$ (50–53). In these studies, the magnitude of the shrinkage rate increased primarily with the bacterial remineralization rate. Here, both the high degree of bacterial colonization (mean of 95 ± 16 per aggregate) and high shrinkage rate of aggregates here suggest that the observed degradation was driven by enzymatic activity rather than physical dissolution.

Viscosity degradation occurs throughout the aggregate rather than just near surface-embedded bacteria, which suggests that exoenzyme activity is responsible for the observed breakdown of mucus structure. At an advanced stage of degradation, aggregates appear to break apart into low-viscosity fragments that are highly infiltrated by bacteria (fig. S11). Because bacteria are not found in higher-viscosity regions, viscosity degradation may allow bacteria to infiltrate aggregates at an average rate of $-0.012 \pm 0.0053 \text{ hours}^{-1}$ (normalized by the maximum aggregate radial distance) and expose their membrane-bound enzymes to new, nondiffusing aggregate material (Fig. 3C). Subsequent breakdown of polymers near the bacterial membrane, transport of smaller substrates into the cells, and internal metabolism result in the ultimate decomposition of organic matter into inorganic constituents (54–56). Thus, microscale degradation of mucus viscosity – breakdown of the physical structure of mucus and subsequent exposure of new material to bacterial surfaces – is a rate-limiting step in oceanic cycling of particulate organic matter. Our measurement of the viscosity degradation rate provides a first glimpse into the microscale decomposition of aggregates that may vary with different strains of bacteria and different marine snow sources across the world's oceans. Quantifying the variability of this rate in other ocean regimes is an important next step for understanding particle breakdown and its influence on the ocean carbon pump.

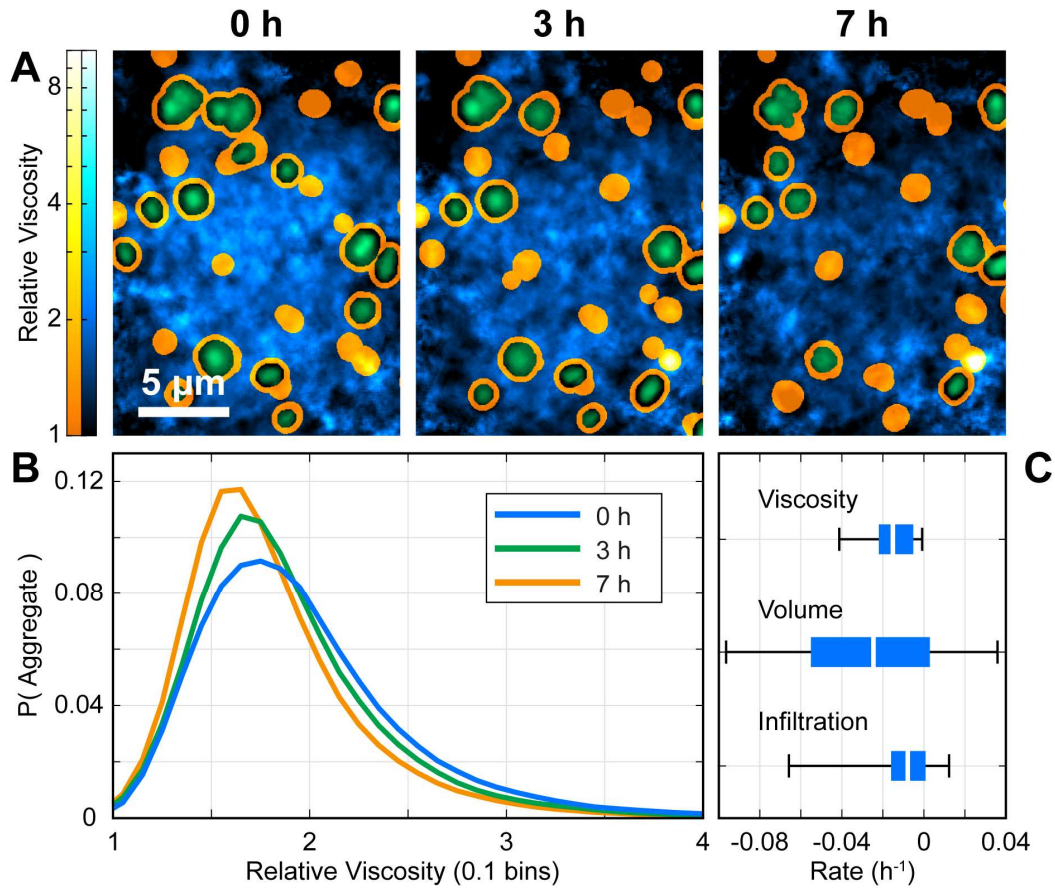


Fig. 3. Degradation and transformation of the viscous structure within a mucus aggregate. (A) A representative thin slice of the relative viscosity near the edge of an aggregate at 0, 3, and 7 hours. Internal aggregate viscosities (blue color scale) reduce over time, holes appear, and the aggregate ultimately fragments. Viscosities also decrease near the walls (orange color scale) of bacterial cells (green nucleic acid stain). (B) The probability distribution of viscosities in a single aggregate over time, corresponding to the time points in (A). The leftward shift of the probability distributions indicates that higher viscosities are converted to lower viscosities throughout the aggregate. (C) The viscosity degradation, volume shrinkage, and bacterial infiltration rates for $N = 7$ aggregates at three time points. Viscosity degradation may allow bacteria to infiltrate inside the aggregates, reducing their distance to the aggregate centroid over time.

Marine snow viscosity and the ocean carbon sink

Marine snow forms from a diversity of biological sources in the upper ocean, including zooplankton fecal pellets and carcasses, phytoplankton exudates and aggregates, viral cell lysis, discarded appendicularian mucus houses, ballast biominerals, and other detritus (4, 57). These sources vary substantially in their molecular composition and density (32, 33) and may display a high degree of viscosity variability across different sources and oceanic ecosystems. Our data shows that even mucus particles from the same source can exhibit appreciable differences in viscosity: the median relative viscosity per aggregate sampled from laboratory diatom cultures ranged from 1.6 to 7.9 ($N = 30$ aggregates). Because the viscous structure of mucus degrades over time according to the measured rate of $-0.017 \text{ hours}^{-1}$, aggregates with higher median viscosities take longer to degrade than lower viscosity aggregates. At equivalent sinking speeds, higher-

viscosity aggregates will sink deeper than lower-viscosity aggregates before they fully decompose and remineralize.

Particle sinking is also influenced by morphological properties, such as material density or drag, and a variety of external environmental factors, such as density stratification, turbulence, or zooplankton grazing (10, 18, 36, 58–63). To explore the effect of viscosity degradation on marine snow sinking, we formulated an exponential decay model that depends primarily on the viscosity degradation rate, volume shrinkage rate, and degree of bacterial colonization (Fig. 4; see materials and methods). Converting particle viscosity to a density difference above seawater, diminishing density and size slowed the descent of the particle until it stopped sinking (Fig. 4A, white line, and eq. S2). A particle with an initial median viscosity of 1.25, representing the lower end of coastal environmental samples studied, would descend 530 m. A marine snow particle with an initial median viscosity of 2, typical of the relatively fresh diatom-derived aggregates from laboratory cultures, would reach 1015 m, roughly twice the distance. These sinking speeds and maximum depth values are consistent with mucilaginous marine snow attenuation observed in various ocean regions (20, 24, 64–66). Note that varying the initial particle size, drag coefficient, and reference density in eq. S2 changes the absolute values of the maximum depth but not the factor increase in sinking distance in the example above. This means that higher-viscosity particles always sink farther than lower-viscosity particles, all else being equal.

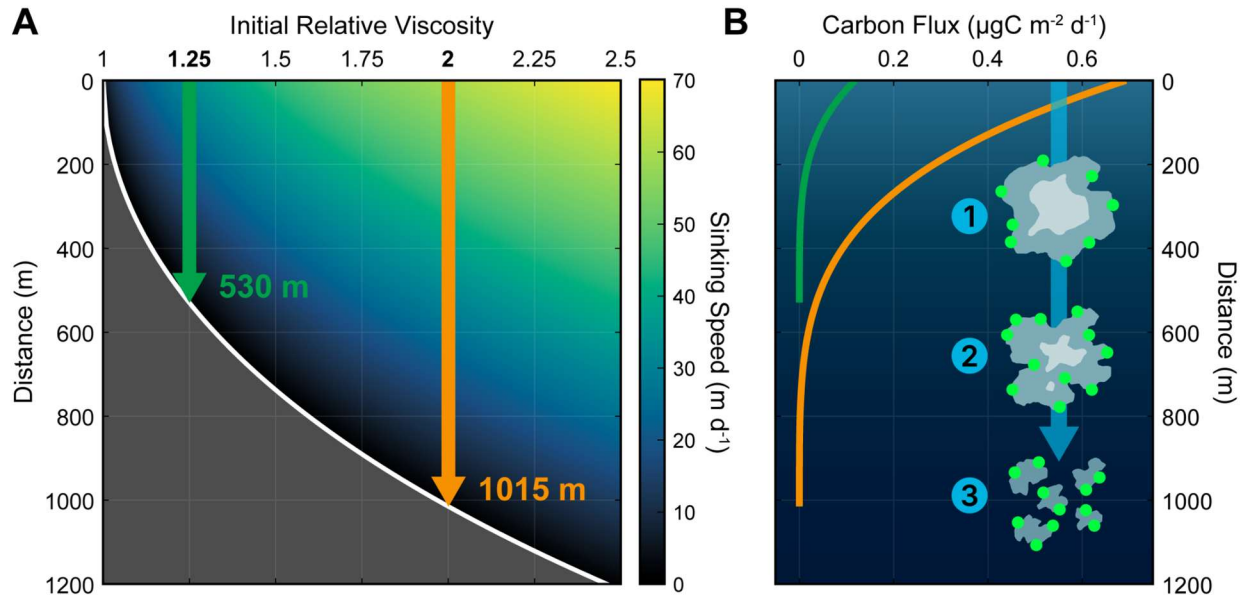


Fig. 4. Higher-viscosity aggregates take longer to degrade, sink deeper, and contribute more to the ocean carbon sink. (A) Modeled decay of relative viscosity and sinking speed with depth for marine snow given an initial median viscosity (top axis) and an equivalent spherical radius of 0.25 mm. The viscosity degradation rate reduces the density of the particle and the volume shrinks, both slowing the descent until the particle stops sinking (white line). An aggregate with an initial viscosity of 2 (orange arrow) sinks roughly twice as far as an aggregate with an initial viscosity of 1.25 (green arrow). (B) (Left) The single-particle carbon flux attenuates with depth for aggregates with an initial viscosity 1.25 (green line) and 2 (orange line). (Right) A conceptual illustration of the physical degradation of marine snow: (1) Bacteria (green) colonize the surface of an aggregate as it sinks in the upper ocean. (2) As the internal viscous structure degrades, bacteria gain access to inner regions. (3) The infiltrated aggregate shrinks and may eventually fragment.

The depth at which sinking particles may contribute to carbon sequestration can vary depending on the physics and ecology of the water column (67). When defined as “the depth below which carbon is stored for 100 years or more,” the sequestration depth can be located between 100 and 1000 m (68). Based on the functional shape of the maximum depth curve (Fig. 4, white line), small variations in particle viscosity at the lower end of initial viscosities lead to relatively large changes in sinking distance. Because higher-viscosity particles contain a greater concentration of polymers and thus more carbon (69, 70), particles with an initial viscosity of 2 contribute more than a factor of six increase in carbon flux at any given depth compared with particles with an initial viscosity of 1.25 (Fig. 4B). This suggests that the ultimate fate of a particle (recycling in the upper ocean or sinking to depth) is strongly influenced by the viscosity degradation rate. As such, variability in the starting viscosity of particles and the degradation rate may mechanistically account for some of the observed variation in carbon export from the upper ocean described by the classic Martin curve (71). This analysis demonstrates that higher-viscosity aggregates take longer to degrade, tend to sink farther, and are more likely to contribute to carbon sequestration than low-viscosity aggregates.

Conclusions

Bacteria-mucus interactions are important drivers of carbon cycling and food web structure in most aquatic and terrestrial ecosystems (72–74). Using molecular rotors and confocal microscopy to reveal the viscous structure of undisturbed mucus aggregates, we show that viscosity correlates to a physical barrier, separating aggregates into regions that are accessible or impenetrable to bacteria. This represents the first quantitative description of mucus as a complex spatial habitat and physical niche space occupied by bacteria. Our methodology and conceptual framework highlight previously unrecognized controls of marine snow remineralization and present new opportunities for quantifying bacterial colonization and infiltration of mucus in marine snow and other biological systems. These include phytoplankton exudates (phycospheres), fish skin, kelp forests, coral reefs, land plant root systems (rhizospheres), and animal mucus membranes. This approach can also provide new insights into the physical regulation of bacterial colonization of the human gut and infection of nasal, throat, and lung mucosa.

Imaging of qualitative, visual features of marine snow morphology is considered an important determinant of sinking and carbon sequestration (24). Indeed, “hidden,” transparent mucus trails associated with visible aggregates impact sinking rates, yet it is unclear how common this is in marine snow from different oceanic regimes (36). Our method provides a means to visually and physically quantify both the external and internal structure of transparent marine snow and associated bacteria, which have previously evaded simultaneous imaging. It is important to note that these relationships between bacteria and aggregate viscosities are correlative. Other factors, including binding of surface-expressed lectins, bacterial motility, and the elastic and porous properties of aggregates may also affect bacterial colonization, and additional research is required to establish a causal relationship. Further, microviscosities inferred from molecular rotors reflect the local free volume and crowding of the local environment by nonsolvent molecules. Although molecular rotor measurements correlate with macroviscosities in our calibrations (fig. S1), they should not be interpreted as reporting resistance to flow at the macroscale (hydrodynamic viscosity) or elastic properties of the medium. We quantified the viscosity degradation rate of

mucus aggregates and demonstrated that higher-viscosity aggregates take longer to degrade, potentially sinking farther and contributing more to the ocean carbon sink than lower-viscosity aggregates. Viscosity degradation provides a mechanistic link between bacterial remineralization and physical breakdown of particles, contributing to our understanding of the attenuation of carbon export given by the Martin curve. Marine snow viscosity is thus a physical constraint – a ‘particulate recalcitrance’ – of deep-sea carbon export in the world’s oceans.

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Supplementary Materials

Materials and Methods

Supplementary Text

Figs. S1 to S11

Tables S1 and S2

References (77–94)

Movies S1 and S2