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The sinking of organic particles in the ocean and their degradation by marine microorganisms is one of the main drivers of one of the most conspicuous carbon fluxes on Earth, the biological pump[1–7]. Yet, the mechanisms determining the magnitude of the pump remain poorly understood, limiting our ability to predict this carbon flux in future ocean scenarios. Current ocean models assume that the biological pump is governed by the competition between sinking speed and degradation rate, with the two processes independent from one another[8–11]. Contrary to this paradigm, we show that sinking itself is a primary determinant of the rate at which bacteria degrade particles. Heterotrophic bacterial degradation rates were obtained from a laboratory study on model surface-colonized particles at atmospheric pressure under a range of flow speeds to mimic different sinking velocities. We find that even modest sinking speeds of 8 m/day enhance degradation rates more than 10-fold compared to degradation rates of non-sinking particles. We discovered that the molecular mechanism underlying this sinking-enhanced degradation is the flow-induced removal of the oligomeric breakdown products from the particles, which otherwise compete for enzymatic activity. This mechanism applies across several substrates and bacterial strains, suggesting it could potentially occur more broadly under natural marine conditions. Integrating our findings into a mathematical model of vertical particulate carbon flux, we show that the coupling of sinking and degradation may contribute, in conjunction with other processes, to determine the magnitude of the vertical carbon flux in the ocean.

The biological pump is the process by which CO_2 from the atmosphere is converted by marine photosynthetic organisms into biomass and inorganic carbonate shells, which undergo aggregation when those cells die to form 'marine snow' particles that sink to the ocean depth[3–5]. Several processes that vary in magnitude with site, depth and season concurrently affect the sinking of particles and the vertical export of the carbon present in marine snow. These processes

include zooplankton particle consumption and excretion[1,2,12], zooplankton vertical migration[1,2], particle aggregation and fragmentation[13] and degradation by marine bacteria[14]. An often important role is played by bacteria residing on sinking particles, which convert the particles' organic carbon into biomass or recycle it back into the dissolved phase[6,7]. From the perspective of bacteria, the phases of particle decomposition proceed through colonization[15–17], enzymatic degradation and the associated consumption of breakdown products to fuel cell growth[16], and finally detachment in pursuit of new particles[17–19]. Particles are hotspots of enzymatic hydrolysis, where hydrolysis rates greatly exceed those in the surrounding seawater[6,20]. As a result, most particulate organic carbon (POC) that escapes consumption and modification by higher trophic levels[21] is remineralized to CO_2 by microbial respiration in the upper water column[9,22,23], so that only 5–25% of the fixed carbon leaves the euphotic zone and only about 1% reaches the sediments, where it remains buried for thousands of years[9,24,25]. Thus, the degradation of organic particles by bacteria governs a major component of the global carbon cycle[6], and its understanding is essential to predicting the role of the oceans in regulating atmospheric carbon dioxide.

At the heart of the carbon pump lay two opposing processes: sinking and degradation. Higher sinking speeds enhance the vertical carbon flux by accelerating the descent of particles, whereas degradation reduces the vertical carbon flux by removing carbon from sinking particles. This competition is captured in some models of the Martin curve, the empirical relation describing the decrease in vertical POC flux with depth[8,9]. In such models, the vertical POC flux $F(Z)$ at depth Z is described either by Martin's classic power-law equation, $F(Z) = F(Z_0)(Z/Z_0)^{-b}$, or by its exponential variant, $F(Z) = F(Z_0)e^{-\lambda (Z-Z_0)/W}$, where Z_0 is the depth of the euphotic layer[8–10]. In the first equation, b is the coefficient of flux attenuation (the higher the value of b, the less carbon reaches the ocean depth). In the second equation, λ is the rate of POC degradation and W is the sinking speed: their ratio $Z^* = W/\lambda$ is the remineralization length scale[8,9,11]. Studies that modelled the flux decay, for example by taking into account the contribution of the oceanic food-web, the role of mineral ballast in particles or the dependence of bacterial degradation rates on the size of individual particles, have greatly expanded our understanding of the processes driving the biological pump[2,8,26,27]. Notably, a paradigm underlying all these models is that sinking speed and degradation rate are considered to be independent of each other.

Here we show that sinking speed and degradation rate of particles can in fact be coupled. We demonstrate and quantify this coupling with a series of experiments in which we track the degradation of individual particles. We find that degradation rate increases with increasing sinking speed up to a speed of 8 m/day, and saturates for larger sinking speeds at a value that is 12- to 15-fold higher than the degradation rate in the absence of sinking. Using a mathematical model of the vertical carbon flux that accounts for the observed sinking-enhanced degradation, we predict that the enhancement of particle degradation due to sinking can reduce the transport efficiency of the carbon pump by up to two-fold compared to a null model that ignores this enhancement.

Sinking enhances the bacterial degradation of particles

To quantify the degradation of sinking particles, we imaged individual alginate particles (diameter 0.88 ± 0.03 mm) pre-colonized by the GFP-labelled marine gammaproteobacterium

Vibrio cyclitrophicus ZF270 in a custom microfluidic channel and measured by image analysis their size over time upon exposure to a constant rate of flow (Fig. 1a-c, Movie S1, and Extended Data Tables 1 and 2 for bacterial characterization). Alginate is a polysaccharide produced by brown macroalgae, particularly in coastal oceans and the Sargasso Sea[28], and serves as a carbon source for *V. cyclitrophicus* ZF270 as well as for many other copiotrophic bacteria[29]. *V. cyclitrophicus* ZF270 is a copiotrophic marine bacterium isolated from large organic particles[30], which in our experiments resided on the outer surface of the alginate particles and degraded these using a non-secreted form of alginate lyases (Extended Data Text). Flow with a constant speed toward a fixed particle is equivalent to a particle sinking at that speed in otherwise quiescent fluid. Results from a mathematical model of the transport within our microfluidic device show that the concentration around the particle of leaching nutrient produced by degradation is similar to that occurring around a freely sinking particle[31], indicating that our model system captures the fundamental role of sinking on transport (Fig. 1d; Methods).

Particle degradation in the presence of flow differed dramatically from degradation without flow (compare Movies S1A and S1B). For flow speeds corresponding to natural sinking speeds of marine snow[32], the volume of individual particles exhibited sigmoidal dynamics over time, with a lag time of 10–20 h followed by rapid shrinking lasting 15–40 h (Fig. 1a,b). Particles remained nearly round while shrinking and bacteria were confined to the particle surface, without infiltrating it (Fig. 1a, Movie S1), so that the reduction in particle volume is a good proxy for particle degradation (Extended Data Text, Extended Data Fig. 3). Particle degradation was accompanied by exponential cell growth fuelled by the breakdown products, as revealed by the dynamics of bacterial GFP fluorescence on the particle (Fig. 1c, Movie S2). The maximum degradation rate occurred after 30–40 h (depending on the flow rate), after the particle surface became entirely covered by bacteria (Fig. 1b, Movie S1). The process ended with the detachment of a majority of the bacteria, leaving a fraction (32–37% by volume) of the particle unconsumed, even after 70 h (Movie S2, Fig. 1a,b, Extended Data Fig. 1).

In contrast, the experiments without flow showed much slower degradation dynamics and a linear rather than sigmoidal decrease in particle volume, accompanied by bacterial growth that had a short lag and was linear with time (Fig. 1b,c, Movie S1A, Movie S2). Fluid flow was previously shown to counteract O_2 limitation within marine particles[33]. However, the difference we observed between degradation rates under flow and no-flow conditions was not a consequence of O_2 limitation under no-flow conditions, for even without flow, the diffusive flux of O_2 into the device was sufficient to support the bacterial population on the particle (Extended Data Text, Movies S1, S2, Extended Data Fig. 2).

Controlling sinking speed by imposing a given flow rate in our experiments allowed us to isolate the effect of flow on the dynamics of particle degradation and bacterial growth. With increasing flow rate, the maximum degradation rate increased as a power law with exponent 0.21 (Fig. 2a). Bacterial growth dynamics were also flow-dependent: higher flow rates caused longer lag times in growth, yielding a power-law dependence of lag time on flow rate with exponent 0.18 (Fig. 2b). Both maximum degradation rate and lag time showed a linear correlation (R^2 = 0.49 and 0.66, respectively) with the Sherwood number, *Sh*, the dimensionless parameter quantifying the ratio of total (*i.e.*, advective plus diffusive) mass transfer to/from the particle, to diffusive mass

transfer alone (Fig. 2c,d)[34]. This signifies that transport of nutrients by fluid flow plays an important role in setting the degradation rate.

The role of flow is also evidenced by the inverse relationship of both the maximum degradation rate and the bacterial lag time (R^2 = 0.58 and 0.61, respectively) with the concentration on the surface of the particle of oligo-alginate, the by-product of the enzymatic degradation of alginate, predicted from our transport model (Figs. 1d, 2e,f). These negative correlations suggest that the rate of particle degradation is regulated by the concentration of the by-product oligo-alginate within the boundary layer, which in turn is directly affected by fluid flow (Fig. 1d). This hypothesis is also supported by measurements of the immediate microenvironment around the particle surface by Raman microspectroscopy, which revealed an accumulation of oligo-alginate on the surface of the particle even at intermediate flow rates during bacterial degradation, consumption and growth (Extended Data Fig. 4, Methods).

Oligomers inhibit the enzymatic degradation of particles

We hypothesized that the bacterial alginate-lyase enzymes responsible for particle degradation are inhibited by high concentrations of dissolved oligo-alginate. This hypothesis was supported by the results of three experiments. First, we quantified the degradation of particles in the presence of flow of solutions containing different concentrations of oligo-alginate. The addition of oligo-alginate reduced the rate of particle degradation by bacteria by up to 11-fold, in a concentration-dependent manner (Fig. 3a,b, Movie S3). This effect arose independently of effects on bacterial population growth on the particle, which in fact increased at high oligo-alginate concentration (Extended Data Fig. 5, Movie S3). Second, we quantified the degradation of particles in the presence of rich medium in the flow (1% Marine broth), instead of oligo-alginate. The addition of rich medium also increased bacterial growth on the particles, but did not reduce the particle degradation rate, indicating that the reduction of the degradation rate is specifically caused by oligo-alginate and not by nutrient availability at the particle surface (Fig. 3, Extended Data Fig. 5). Third, we directly confirmed that high concentrations of oligo-alginate are sufficient to inhibit the degradation of particles by alginate lyase. Using sterile particles, in which degradation was driven solely by pure alginate-lyase enzyme added to the bacteria-free flowing solution, revealed that here, too, degradation was inhibited by the addition of oligo-alginate (Extended Data Fig. 6a, Movie S4).

Remarkably, the inhibition of the alginate lyase during bacterial degradation did not arise by classical product inhibition, whereby the products of the reaction inhibit the specific activity of the enzyme, as the enzymatic activity (measured with enzymes in solution by a plate reader) was unaffected by the addition of oligo-alginate (Extended Data Fig. 6b). Instead, the new mechanism we propose is that enzymatic depolymerization, and thus particle degradation, is reduced by the encounter of the bacterial alginate-lyase enzymes with the oligo-alginate molecules that are the initial product of degradation. As they diffuse from the particle on account of being small and dissolved, the degradation products compete for enzymatic activity with the larger polymer molecules that constitute the particle itself. The enhanced degradation in flow thus arises because the otherwise competing oligo-alginate is swept away (Fig. 3c).

Predicted impact of sinking–degradation coupling on vertical POC flux

To predict the implications of this enhancement of particle degradation by flow and thus the potential impact of coupling between sinking speed and degradation rate on the vertical flux of POC in the ocean, we developed a mathematical model that accounts for the observed coupling (Methods). We consider an initial particle size distribution (PSD) $P(R_0)$ of particles of radius R_0, with a range of sizes $R_l < R_0 < R_g$ and total concentration of particles C at the euphotic depth Z_0. Size distributions are chosen based on observed particle distributions in the ocean and account for suspended and sinking POC[35]. The model evolves the depth $Z(t)$ and radius $R(t)$ of each particle, based on classic assumptions (including the decreasing sinking speed and increasing density as particle size gets smaller, both based on empirical power laws[36]) and on our observed dependence of degradation rate on sinking speed (Methods). Whereas in general, multiple processes affect particle degradation and thus vertical carbon flux, including for example fragmentation, coagulation or consumption by zooplankton, the model focuses on the contribution of bacterial degradation (it does, however, account for variations in PSD, and thereby indirectly for the results of particle fragmentation and coagulation; see below). This model, therefore, does not intend to replace large-scale biogeochemical models, but only to provide a measure of the relative importance of including versus neglecting the new mechanism we report. For this reason, we do not attempt to predict the absolute carbon flux at a given location or time. Instead, we predict the vertical carbon flux over depth relative to the flux at the bottom of the euphotic zone, $F(Z)/F(Z_0)$, and compare this with the reference case (null model) in which the effect of flow on degradation is ignored.

Accounting for the observed effect of sinking resulted in a much stronger attenuation of carbon flux with depth, as sinking causes more carbon to be remineralized by bacteria in the upper water column. This was reflected in a 2.8-fold higher coefficient of carbon attenuation b in the best-fit Martin curve and in a much shallower half-decay depth of 150 m below Z_0, compared to ~1450 m in the case without coupling between sinking and degradation (Fig. 4, Methods). In line with this result, the relative POC transfer efficiency 100 m below the euphotic zone[2,37], denoted T_{100}, was 56%, compared to 94% in the case without coupling (Fig. 4, Methods). Our model thus predicts a large effect, overlooked in current biogeochemical models, of the coupling between sinking and bacterial degradation, which in several regions of the ocean can represent an important contribution to the vertical flux of carbon (further analysis in Methods, Extended Data Figs. 7-10).

The impact of the coupling between sinking and degradation is predicted to vary by oceanic province (see also Extended Data Discussion). To study the potential contribution of the coupling in different oceanic regions and in the context of additional processes affecting the biological pump, we quantified the transfer efficiency T_{100} for different initial particle size distributions (PSD) in the surface ocean. Steeper PSDs are typical of oligotrophic waters; shallower PSDs are typical of more eutrophic waters[38,39]. Model results indicate that the coupling of particle degradation and sinking speed strongly enhances particle degradation in eutrophic waters (compared to a model that ignores the coupling), where the relative abundance of larger and thus typically faster sinking particles is greater (T_{100} = 43% for the coupled case vs T_{100} = 92% for the uncoupled case, for a PSD with exponent of -2, corresponding to a 2.14-fold decrease; Methods, Extended Data Discussion and Extended Data Fig. 9). We expect this scenario to apply in eutrophic waters, under bloom conditions with strong coagulation of

particles, and for example in the subtropical ocean during winter, where fast sinking particles (>10 m/day) contribute considerably to the carbon flux[2,38,40–42]. A weaker but still considerable effect is observed in oligotrophic waters (T_{100} = 60% for the coupled case vs. T_{100} = 95% for the uncoupled case, for a PSD with exponent of -5, corresponding to a 1.58-fold decrease), where the relative abundance of smaller and thus typically slower sinking particles is greater[2,38,41–43]. We expect this scenario to apply in waters rich with fragmented particles[13], and for example in the subtropical oligotrophic Atlantic and Pacific oceans, the Subarctic Ocean, the North Pacific Ocean and the northwest Mediterranean Sea in the summer, where slow sinking particles (<10 m/day) contribute substantially to the carbon flux[40,41].

Model results show that the effect of the sinking-degradation coupling is robust to the incorporation of other characteristics of the particle transport process. Accounting for the decrease of enzymatic activity with decreasing temperature, and thus with increasing depth (with a Q_{10} of 2.5; Methods), generally increases the transfer efficiency of POC, yet the difference between the coupled and uncoupled cases is preserved (T_{100} = 74% and T_{100} = 98%, respectively; Methods, Extended Data Fig. 10). Moreover, the effect of the coupling between sinking and degradation in decreasing the transfer efficiency T_{100} is greater than the effect of temperature on the degradation rate (see Extended Data Discussion). Finally, the temperature-dependence of seawater viscosity has a negligible effect on our predictions of T_{100} (Methods, Extended Data Fig. 11). In summary, even when taking into account further aspects of the complexity of the natural process, the sinking-enhanced degradation mechanism is predicted to play an important role in setting the bacterial degradation rate of particles in the ocean (Extended Data Discussion).

Although our model results demonstrate that sinking-enhanced degradation can impose, if validated in the environment, an important control on carbon flux, the actual carbon flux at a given location will be further affected by several other factors, including particle consumption by zooplankton[21], particle fragmentation[13], and local temperature[44]. Indeed, a limitation of our model is that aggregation and disaggregation and the incorporation of ballast in particles[8], known to affect the carbon flux in the ocean, are not accounted for. Unlike in our model system, in the environment particles of a given size can have different sinking speeds, permeabilities and porosities. For example, the inclusion of ballast material, which is dense and non-permeable, may cause the sinking speed to increase as the (often less dense) labile material is degraded: by sinking faster, the particle can thus escape the inhibited degradation experienced at low sinking speeds. Additionally, aggregation and disaggregation may respectively accelerate or slow down the sinking of particles and thus alter their degradation via the coupling to flow; the actual quantitative importance of these factors will be best quantified using global POC models. These limitations notwithstanding, our work suggests that global models should account for the dependence of degradation rate on sinking speed, provides a quantitative formulation for this dependence, and cautions against parameterizing models using degradation rates obtained from quiescent, *in vitro* experiments, which will considerably underestimate particle degradation rates.

The fundamental transport-based nature of the role of flow suggests that the coupling between sinking and degradation that we reported is not specific to our particular experimental system (Extended Data Discussion). The proposed sinking-enhanced degradation mechanism is likely to be independent of the specific bacterial strain causing degradation, for it is apparent when degradation is produced purely by enzymes in solution (Extended Data Fig. 6a, Movie S4).

Support for this generality comes also from our additional observations that the same mechanism applies for other polymers found on marine particles: a sinking speed of 7.25 m/day enhanced degradation by 4.5-fold for chitin particles and by 2.5-fold for short-chain chitosan particles compared to no-flow conditions, for a co-culture of *Vibrio splendidus* 1A01 and *Psychromonas* (Extended Data Fig. 12, Movie S5 and Methods).

While polymeric carbohydrates such as alginate account for a major fraction of labile carbon in several oceanic regions[45,46], often serving as the glue that holds particles together[47], natural particles harbour greater complexity than our model particles. Thus, further analysis will be required to assess the contributions to particle degradation of chemical composition, as well as other factors such as porosity (which adds degradation from within the particles) and microbial community composition (see Extended Data Discussion). The flow due to sinking will also have additional effects that can further affect degradation, such as increasing particle encounters with bacteria[17], decreasing the competitive advantage of non-degrading microbes on particles[48], and enhancing the flux of oxygen to particles' interior[33] and of secreted enzymes and signalling molecules away from particles. The formation of a thick biofilm could also change the transport and degradation dynamics[48]. These additional effects notwithstanding, our observations establish the coupling between sinking and degradation as a new, fundamental mechanism that — together and possibly in synergy with other processes — can impact the vertical flux of carbon in the ocean. Ultimately, our work shows that not only the ecological interactions on particles[49], but also the microscale transport dynamics play a fundamental role in determining the degradation rate of particles by bacteria, and can contribute to the global-scale carbon flux to the oceans' depths.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information, details of author contributions and competing interests, and statements of data and code availability are available on line.

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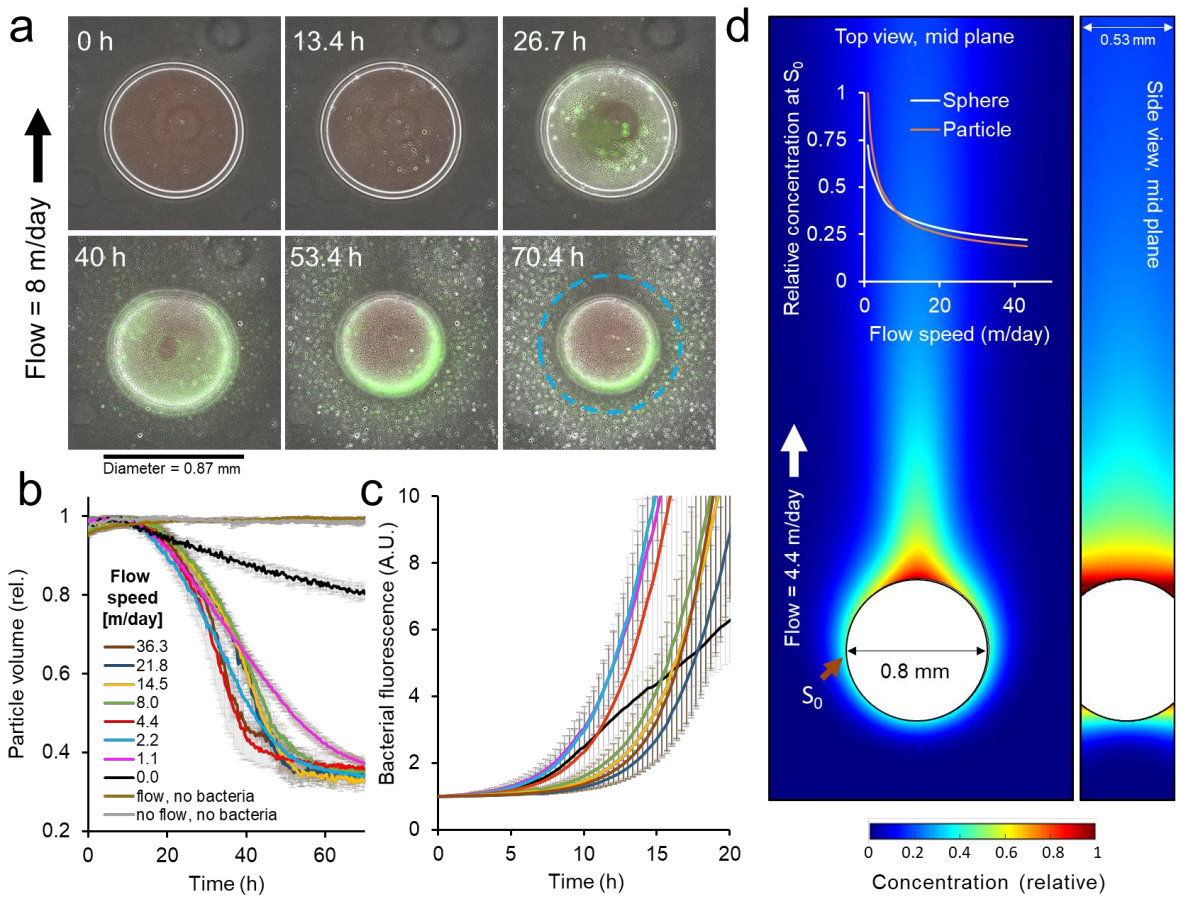

Fig. 1. Marine particle degradation is flow-dependent. (**a**) Time-lapse images of alginate particles degraded by *Vibrio cyclitrophicus* ZF270 in flow. Phase images (greyscale) shown with overlaid GFP signal from the bacteria (green). Initial particle diameter (here, 0.87 mm) highlighted in blue in the final image. (**b**) Time series of particle volume during bacterial degradation, relative to initial volume, for different flow speeds (mean and SD; $n = 3$ replicate experiments for each flow speed, except for 4.4 m/day for which $n = 6$). The flow speed in the absence of bacteria (grey line) was 7.25 m/day. (**c**) Time series of bacterial abundance on particles up to 20 h, relative to initial value, for different flow speeds, measured as the average GFP fluorescence intensity at the interface between the particle and the glass slide (Movie S2). For full 70-h time series, see Extended Data Fig. 1. Colours and n as in panel b. A.U. = arbitrary units. (**d**) Nutrient concentration around a particle within the microfluidic channel, as predicted by a mathematical model (top and side views). Nutrient flux from the particle was assumed steady and uniform over the particle surface. ***Inset:*** nutrient concentration at the particle's equator (position S_0) as a function of flow speed (orange curve). Results from a model for a freely sinking, 0.8-mm-diameter spherical particle are shown for comparison (white curve).

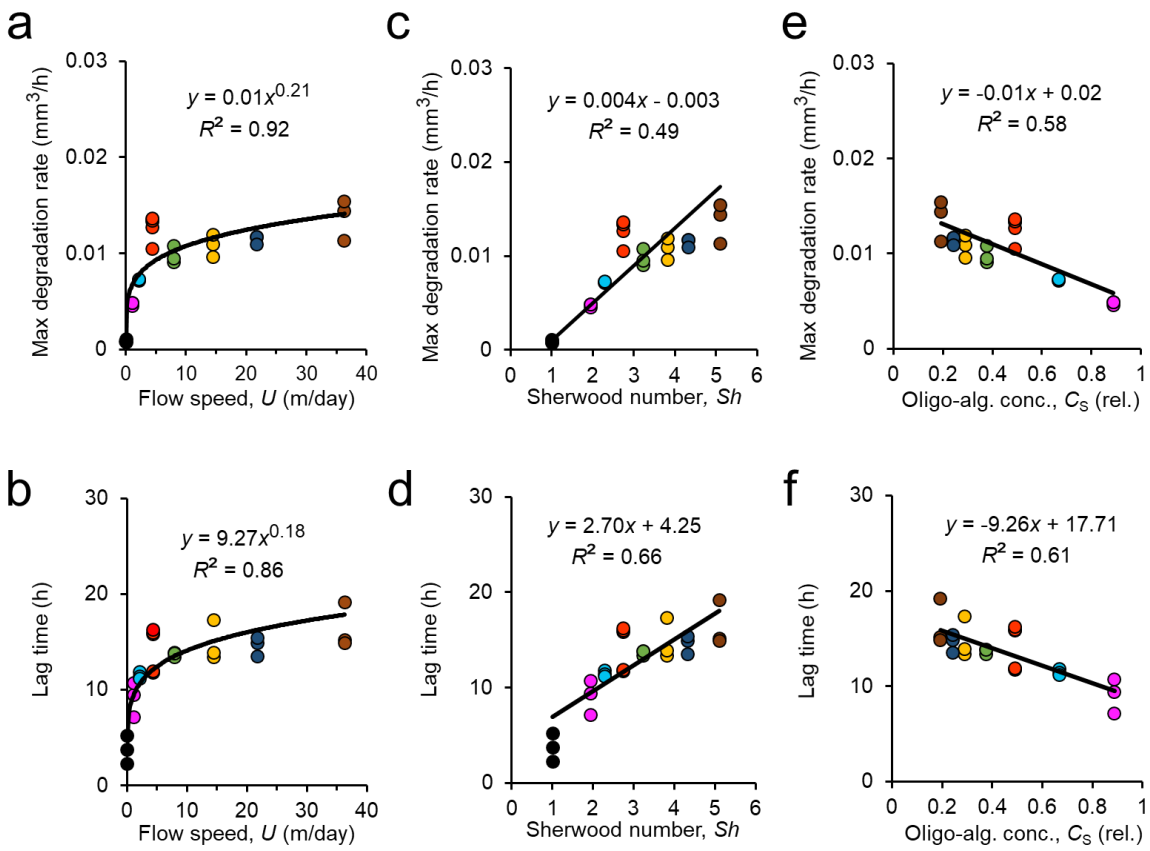

Fig. 2. Flow plays a key role in determining bacterial growth on, and degradation of, model marine particles. Maximum degradation rate of alginate particles (**a,c,e**) and lag time of bacteria growing on particles (**b,d,f**), as a function of flow speed, *U* (**a,b**), Sherwood number, *Sh* (**c,d**), and oligo-alginate concentration on the particle surface, C_S (**E,F**) (see *COMSOL transport model* in Methods). Curves show power-law (**a,b**) or linear least-squares (**c–f**) fits to the data (R^2 shown in panels, $p < 0.0001$ in all cases). The linear fit in panel C was constrained to intersect with the rate of degradation (1×10^{-3} mm^3/h) obtained at no-flow (*Sh* = 1). In all panels, colour-code for flow speeds as in Fig. 1b.

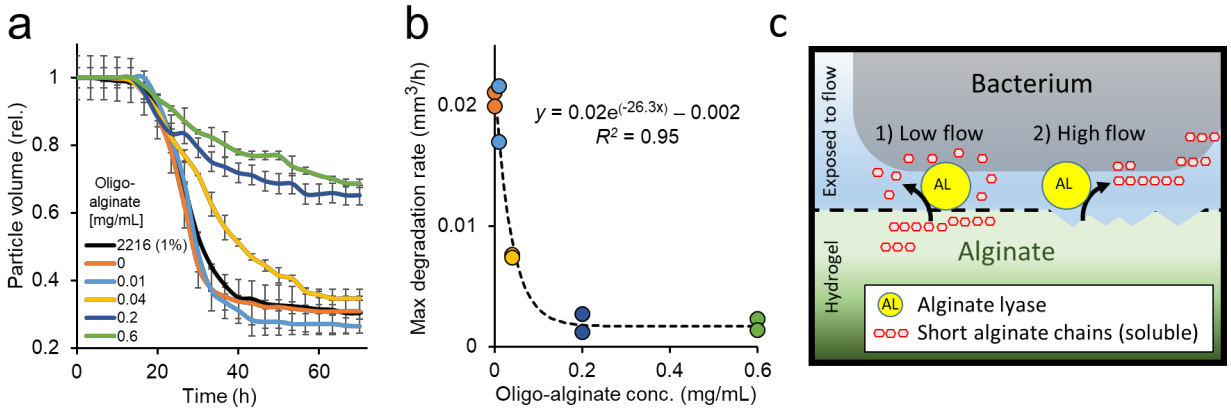

Fig. 3. High concentrations of oligo-alginate inhibit the degradation of alginate particles. (**a**) Time series of particle volume, normalized by initial value, during bacterial degradation under a flow of 7.25 m/day of medium supplemented with different concentrations of oligo-alginate (in mg/mL; colours) or with 1% 2216 marine broth (black; complementary control, see main text). Shown are mean and SD (n = 2). **(b)** Maximum particle degradation rate as a function of oligo-alginate concentration in the medium (colours as in panel A; n = 2). A first-order decay model (dashed) was fitted to the data. Maximum degradation rate for medium supplemented with 1% 2216 marine broth was 0.017 ± 0.001 mm^3/h. **(c)** Schematic model of alginate degradation and how it is influenced by flow. Upon colonization, *Vibrio cyclitrophicus* ZF270 expresses alginate lyase (AL) in order to solubilize, transport and feed on the polysaccharide particle. Under low flow rates (left), the degradation and dissolution of the alginate polysaccharide is inhibited because a high concentration of oligo-alginate accumulates around the particle. The alginate lyase can react with any of the available forms of alginate, but preferentially encounters the dissolved short polymers, oligo-alginate, which have higher concentration and larger diffusivity. High flow removes the short oligo-alginate, removing the competition for enzymatic activity and thereby accelerating depolymerisation of the particle (right).