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## Supplementary information

# Sinking enhances the degradation of organic particles by marine bacteria

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## Supplementary data

# Sinking enhances the degradation of organic particles by marine bacteria

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## 1. Modelling the potential effect of sinking-enhanced degradation on the efficiency of the ocean's carbon pump.

In order to investigate how the coupling of the flow caused by sinking and the rate of degradation, revealed in our experiments, can affect the vertical flux of carbon in the ocean, we develop a model of marine particle degradation and sinking which incorporates the observed effects of flow (hereafter referred to as coupled). Code for the model can be obtained from GitHub: (https://github.com/fpeaudecerf/marine_snow_model).

### *1.1 General principles.*

We consider a reference depth $Z_0$, typically the bottom of the euphotic zone, where we assume a known total abundance of particles $C$ (particles per litre) in a defined range of particle sizes. Here we assume spherical particles characterized by their radius $R_0$, so that the initial range of radii is defined by $R_l < R_0 < R_g$, with $R_l$ the minimum particle radius at $Z_0$ and $R_g$ the maximum particle radius at $Z_0$. We assume a probability distribution of particle radii $P(R_0)$ so that the number of particles of radius comprised between $R_0$ and $R_0 + \mathrm{d}R_0$ at depth $Z_0$ is given by $C\,P(R_0)\,dR_0$. We then assume that through the water column, the sinking speed $U$ of a particle is only a function of its radius $R$, given by a law $U(R)$ (see below for details). Furthermore, we assume that the dry mass of a particle is only a function of its radius $R$, given by a law $m(R)$ (see below for details). With these elements, the expression for the vertical flux $D$ of dry mass at depth $Z_0$ is

$$D(Z_0) = \int_{R_l}^{R_g} C\,P(R_0)U(R_0)m(R_0)dR_0. \qquad (1)$$

The vertical flux of dry mass associated with sinking particles is proportional to the vertical flux of particulate organic carbon. We consider here a conversion factor $\sigma = 35\%$ POC per total dry mass [1], so that the vertical flux of POC at depth $Z_0$ can be written as

$$F(Z_0) = \int_{R_l}^{R_g} C\,P(R_0)U(R_0)\,\sigma\,m(R_0)dR_0.$$

We investigate how the vertical flux $F(Z)$ changes with depth $Z$ as particles are degraded while sinking. First, we implement in the model the dynamics of degradation of a particle. These dynamics, which capture the coupling of degradation rate with flow, are described in detail below. They permit the computation of the radius $R(R_0,Z)$ of a particle of initial radius $R_0$ at initial depth $Z_0$ when the particle reaches the depth $Z$. To determine the vertical flux at depth $Z$ associated with all particles initially present at $Z_0$, we integrate with respect to the initial radius $R_0$. We thus calculate how many particles that were initially of radius between $R_0$ and $R_0 + \mathrm{d}R_0$ are present per unit volume at depth $Z$. Assuming a steady-state problem, the conservation of the

flux and of the number of particles with depth imposes this number to be $C\,P(R_0)\,U_0\,dR_0 / U(R(R_0,Z))$. Therefore, the expression for the vertical flux of POC at any depth $Z$ is

$$F(Z) = \int_{R_l}^{R_g} C\,P(R_0)U(R_0)\;\sigma\, m[R(R_0,Z)]dR_0. \qquad (2)$$

Through this general formulation, we compare the evolution of *F(Z)* with depth *Z* for degradation dynamics including or excluding the observed coupling of degradation with flow.

In the following sections we provide detailed descriptions of the formulation of the different elements of the model.

### *1.2 Initial size distribution $P(R_0)$.*

We assume a probability distribution of particle radii that follows a power law, so that

$$P(R_0) = A\,R_0^{\beta} \text{ for } R_l < R_0 < R_g, \qquad (3)$$

with $A = (\beta - 1)\left[\frac{R_l^{\beta-1}R_g^{\beta-1}}{R_l^{\beta-1} - R_g^{\beta-1}}\right]$ being a normalization constant. Radius distributions of marine particles in the environment[2] typically show a PSD slope between $\beta = -2$ and $\beta = -5$. Here we assume $\beta = -4$ for the baseline case, and additionally performed simulations with a range of values of $\beta$ from -2 to -5 (see section 1.5). Furthermore, we take the minimum and maximum radii of particles at depth $Z_0$ to be $R_l$ = 125 µm and $R_g$ = 750 µm, a typical range of sizes covered in sampling campaigns[3].

### *1.2 Sinking speed U(R) and dry mass content m(R).*

We assume the sinking speed *U* of a particle to follow a power law with respect to its radius *R*, so that

$$U(R) = B\,R^{\omega}. \qquad (4)$$

The values of the parameters *B* and $\omega$ are set to empirical values obtained by experimental characterization of sinking aggregates[4], that is

$$B = 4.18 \times 10^{-3}\ \mathrm{m}^{1-\omega}\,\mathrm{s}^{-1} \qquad \text{and} \qquad \omega = 0.26. \qquad (5)$$

The power law in equation (4) reflects the fact that larger particles sink faster, but with a weaker scaling than expected from Stokes' sedimentation law (where sinking speed varies with the square of the radius), due to the lower density and higher porosity of larger particles.

The dry mass content of a particle $m$ is also assumed to follow a power law with respect to its radius $R$, so that

$$m(R) = E\ R^{\chi}\ . \qquad (6)$$

The values of the parameters $E$ and $\chi$ are set to empirical values obtained by experimental characterization of sinking aggregates[4], that is

$$E = 4.55\ \times 10^{-5}\ \text{kg m}^{-\chi} \qquad \text{and} \qquad \chi = 1.125. \qquad (7)$$

Here, again, the power law in equation (6) corresponds to a dry mass that scales with an exponent lower than that expected for particles having a fixed density across sizes (for which mass would scale with volume, that is $R^3$). This scaling accounts for the fact that large particles tend to be more porous and less dense than small particles.

### *1.3 Degradation dynamics.*

To represent the dynamics of particle degradation in the model and account for the observed coupling of degradation with sinking speed, we make some simplifying assumptions, while still capturing the fundamental features of particle degradation observed in our experiments.

First, while the experiments show a lag-time in the start of measurable degradation linked to the progressive coverage of the particle surface by bacteria, we will here assume that the particles considered at depth $Z_0$ are already entirely covered in bacteria, and that the surface of the particle remains covered during sinking. Therefore, we do not consider explicitly the bacterial dynamics of colonization and growth. While these dynamics are crucial in the environment to explain natural bacterial community assemblage, this simplification can be justified here by the fact that we consider the initial distribution of particles at the bottom of the euphotic zone (depth $Z_0$), where we expect colonization to have already occurred.

With this assumption of complete coverage of the surface, we next assume that the rate of mass loss of a particle of radius $R$ is proportional to its surface area, $4\pi R^2$. This assumption stems from the localization of bacteria at the surface only, and from considering membrane-bound enzymes that constrain polymer degradation to the external surface only. Therefore, we can assume that for a particle of radius $R$, the loss of mass follows the differential equation

$$\frac{dm}{dt} = -\ 4\ \pi\ R^2\ \theta(R, U), \qquad (8)$$

with $\theta$ a function of particle radius $R$ and sinking speed $U$ capturing how the presence of flow around the particle modifies its degradation dynamics, and corresponding physically to a mass loss rate per unit surface area of particle.

To determine the function $\theta(R, U)$, we model the rate of mass loss of particles based on the mass loss observed in our experiments. We use the observed dependency of the maximum degradation rate (*i.e.*, the maximum volume loss rate; Fig. 2c) on the Sherwood number, *Sh*, which characterizes the relative importance of advection and diffusion in the transport of chemicals

away from (or towards) the particle (Fig. 2c). We fit the experimentally measured maximum volume loss rate $\alpha$ as

$$\alpha = 4\,\pi R_{\text{exp}}^2\,[\gamma_0 + \gamma_1(Sh - 1)], \tag{9}$$

with $R_{\text{exp}}$ = 0.44 mm the radius of particles in experiments, $\gamma_0$ the mean radius shrinking rate observed in experiments without flow, and $\gamma_1$ the fitting parameter. We note that this expression enables recovery of the reference case of no flow, in which transport of chemicals by advection away from the particle is neglected, by setting $Sh$ = 1 (diffusion only), in which case $\alpha = 4\,\pi R_{\text{exp}}^2 \gamma_0$, equal to the observed maximum volume loss rate in experiments in no flow conditions. The fit of experimental data following equation (9) (Fig. 2c) results in the values used in the model

$$\gamma_0 = 1.06\ \times 10^{-10}\ \text{m s}^{-1} \quad \text{and} \quad \gamma_1 = 4.35\ \times 10^{-10}\ \text{m s}^{-1}\,. \tag{10}$$

Using the density of alginate $\rho_{\text{alginate}}$ = 15 kg m$^{-3}$, we can convert the maximum volume loss rate $\alpha$ into a maximum mass loss rate per unit surface area, which reads

$$\frac{\rho_{\text{alginate}}\alpha}{4\,\pi R_{\text{exp}}^2} = \rho_{\text{alginate}}[\gamma_0 + \gamma_1(Sh - 1)]. \tag{11}$$

A key assumption of our model is to set the theoretical mass loss rate per unit surface area $\theta$ to this experimental maximum mass loss rate, that is

$$\theta(R, U) = \rho_{\text{alginate}}[\gamma_0 + \gamma_1(Sh - 1)]. \tag{12}$$

By considering the Sherwood number $Sh$ as the non-dimensional variable that captures the effects of flow on degradation, we are thus able to account for the mass loss rate for particles of any radius $R$, extending the effects of flow to particles having radii that are different from the experimental radius $R_{\text{exp}}$. We can then express the mass loss rate per unit surface area $\theta$ explicitly as a function of the variables of particle radius $R$ and sinking speed $U$ by using established semi-analytical expressions for the Sherwood number $Sh$ for a sinking spherical particle[5],

$$Sh = 1 + 0.619\ Re^{0.412}\ \left(\frac{\nu}{D}\right)^{\frac{1}{3}}, \tag{13}$$

with $Re = 2\,R\,U/\nu$ the Reynolds number, $\nu$ the kinematic viscosity of seawater, and $D$ the diffusivity of oligomers. This expression is a good approximation across all values of Reynolds number. We use a diffusivity of oligomers of $D = 10^{-9}$ m$^2$ s$^{-1}$ and a kinematic viscosity of $\nu = 1.20 \times 10^{-6}$ m$^2$ s$^{-1}$ for seawater at 15 ˚C. We thus can write the expression of the mass loss rate per unit surface $\theta$ from equation (12), using equation (13), as

$$\theta(R, U) = \rho_{\text{alginate}}\left[\gamma_0 + \gamma_2\ (R\,U)^{\delta}\right], \tag{14}$$

with $\delta$ = 0.412 (the exponent acting on $Re$ in equation (13)) and $\gamma_2 = 0.619\ \gamma_1\ (\nu/D)^{1/3}\ (2/\nu)^{\delta}$.

By using the expression for the sinking speed in equation (4) together with equation (8) and equation (14), we obtain a differential equation for the rate of dry mass loss as a function only of the particle radius *R*, namely

$$\frac{dm}{dt} = -4\,\pi\,R^2\,\rho_{\text{alginate}}\left[\gamma_0 + \gamma_2\,B^{\delta}R^{(1+\omega)\delta}\right]. \qquad (15)$$

Using the expression of the mass content as a function of radius in (6), we finally obtain a closed differential equation for the temporal dynamics of the particle radius *R*, which reads

$$\frac{dR}{dt} = -\frac{4\pi\,\rho_{\text{alginate}}}{E\chi}\,R^{3-\chi}\left[\gamma_0 + \gamma_2\,B^{\delta}R^{(1+\omega)\delta}\right]. \qquad (16)$$

We solve this equation numerically with the initial condition $R(t = 0) = R_0$ to obtain the dynamics of the radius $R(t)$ with time for a particle of initial radius $R_0$ at depth $Z_0$. The instantaneous radius $R(t)$ then determines the instantaneous sinking speed $U(t)$ through (4), which allows us to solve for the particle's depth $Z(t)$ with time. Thus, for any initial radius $R_0$ of a particle, we can solve for its radius at depth *Z*, which we denote as $R(R_0,Z)$.

As described above under *General Principles*, knowing $R(R_0,Z)$, together with the initial size distribution equation (3), sinking law equation (4), mass law equation (5) and the conversion factor σ, provides the vertical flux of POC $F(Z)$ as a function of depth *Z*. To obtain the 'no-flow' reference case scenario (hereafter referred to as uncoupled), in which degradation rate is independent of sinking speed, we solve (16) with $\gamma_2 = 0$ (this is equivalent to setting $Sh = 1$). In this scenario, all particles have the same mass loss rate per unit surface area, corresponding to the experimental value observed without flow (*i.e.*, the minimal value). Using this model, we predicted the vertical flux of POC as a function of depth using a custom script in Python, both with (coupled) and without the sinking-enhanced degradation (uncoupled), (Fig. 4.).

### *1.4 Sensitivity of results to the characteristics of the initial size distribution $P(R_0)$.*

Particle size distributions (PSDs) in the ocean can vary with the oceanic regime. While the PSD slope $\beta = -4$ chosen in this study is representative of observed particle size distributions[2], typical oligotrophic waters have a stronger contribution of small particle sizes to POC, which translates into PSD slopes closer to -5, whereas for rich, eutrophic waters, the stronger contribution of larger particle sizes to the flux[6] results in flatter PSDs with slopes that can reach values of -2. We ran further simulations with our model through the whole range of PSD slopes between -5 and -2, in intervals of 0.5. Additionally, we also considered the effect of changing the range of particle sizes included in the model, by performing simulations with an extended range of particle sizes ($R_0$ = 22.5 to 2500 µm), such as those captured by recent methods with more advanced sampling capabilities, e.g., Underwater Video Profilers[7]. From the model's results, we computed the POC transfer efficiency 100 m below the euphotic zone, $T_{100} = F(Z_0 + 100)/F(Z_0)$, for both the cases with and without sinking-enhanced degradation (Extended Data Fig. 7).

The steeper the slope of the PSD (*i.e.*, the more oligotrophic the conditions), the smaller is the difference in transfer efficiency between our coupled model including sinking-enhanced

degradation and our reference model omitting this effect. This stems mostly from a higher transfer efficiency for our coupled model when the PSD is steep (PSD slopes of -5 to -4), due to the larger contribution of smaller particles to the POC flux in these oligotrophic conditions. As smaller particles typically have a lower sinking speed, they will have weaker enhancement of degradation by flow than larger particles. The consequences of a larger range of initial sizes follows the same logic: for oligotrophic conditions (PSD slopes of -5 to -4), including a broader range of sizes in the model mostly impacts the POC flux via the smallest particles of the range, which are only weakly sensitive to the sinking-enhanced degradation mechanism. This results in a transfer efficiency that increases considerably in the coupled case (for $\beta = -5$, $T_{100}$ changes from ~60% for the narrower size range to ~90% for the wider size range, Extended Data Fig. 7), and reduces the difference between the model predictions with and without coupling for $T_{100}$ (for $\beta = -5$, this difference changes from ~35% to ~10% when extending the range of particle sizes, Extended Data Fig. 7). In contrast, for typical eutrophic conditions (PSD slopes of -3 to -2), including a broader range of particle sizes has a weaker effect, because even if a large number of small particles (which are less sensitive to the coupling) is considered, their impact on the flux is outweighed by the dominating larger particles (which are affected strongly by the coupling). This results in a $T_{100}$ which does not change substantially when considering a broader range of particle sizes (for $\beta = -2$, $T_{100}$ changes from 43% for the narrower size range to 37% for the wider size range, Extended Data Fig. 7), and a difference in the value of $T_{100}$ between the coupled and non-coupled cases that remains large (for $\beta = -2$, this difference is 49% for the narrower size range and 52% for the wider size range, Extended Data Fig. 7).

### *1.5 Comparison with the scenario in which bacterial enzymatic activity is dampened over depth by the reduction in temperature ($Q_{10}$).*

In our general model approach described above, the degradation rate of the particles is based on a parametrization obtained from experiments performed at 25 °C, via the parameters $\gamma_0$ and $\gamma_1$ in equation (10). To further test the robustness of our results showing an important deviation between a POC flux including the coupling between sinking and degradation, and one omitting it, we explore the consequences of a reduction of bacterial enzymatic activity (and thus a reduction in the bacterial degradation rate of the particles) with decreasing temperature.

We focus on a temperature profile with strong temperature variations, corresponding to a fit to experimental data from subtropical waters[8], given by

$$T(Z) = 2 + 12\, e^{-Z/150} + 12e^{-Z/500}, \qquad (17)$$

with $T$ the temperature in degrees Celsius and the depth $Z$ in metres. This temperature profile is chosen to test the sensitivity of our results to temperature-driven changes in degradation rate because it will yield a particularly strong modulation of the degradation rate in view of its strong variations in temperature. Using this formulation, we performed simulations based on the model described in (16), but for which the instantaneous degradation rate of a particle is set by modified parameters $\gamma_0$ and $\gamma_1$ modulated by the local temperature $T$ at the particle's current depth $Z$, that is

$$\gamma_0' = \gamma_0 Q_{10}^{\frac{T(Z)-T_{\mathrm{ex}}}{10}} \text{ and } \gamma_1' = \gamma_1 Q_{10}^{\frac{T(Z)-T_{\mathrm{ex}}}{10}}. \quad (18)$$

$Q_{10}$ is the temperature coefficient for this degradation mechanism, yielding the factor by which the degradation rate is dampened for each loss of 10 °C. $T_{\mathrm{ex}} = 25$ °C is the temperature in our experiments. For most biological systems, the $Q_{10}$ value is between 2 and 3, and direct evidence in marine particles points to the same range[9]. Therefore, we use $Q_{10} = 2.5$ in the following.

The resulting POC flux profiles with temperature dampening of degradation rate show a reduction of attenuation with respect to the general approach above (Extended Data Fig. 8), with a transfer efficiency changing from $T_{100} = 56\%$ to $T_{100} = 74\%$ for the coupled regime, and from $T_{100} = 94\%$ to $T_{100} = 98\%$ in the uncoupled regime. These increases in transfer efficiency result directly from the fact that the chosen temperature profile includes temperatures below the experimental reference temperature for the entire depth below the euphotic zone. Along the whole path of each particle, the degradation rate is thus always lower than the degradation rate used in our general model, which directly reduces the attenuation of the POC flux. However, the difference between a model including the coupling between flow and degradation and one omitting it remains large when incorporating this $Q_{10}$ effect, with a difference of more than 20% in transfer efficiency between the coupled and uncoupled cases. This result indicates that the coupling between flow and degradation has a strong impact on the carbon flux regardless of whether the effect of temperature on enzymatic activity is accounted for.

We additionally performed simulations with a theoretical degradation rate corresponding to a constant temperature of 15 °C over the entire water column, a temperature chosen to match the temperature at which the parameters used for the sinking law were obtained[4] (equations (4) and (5); Extended Data Fig. 8). The resulting flux curves fall between our default model and the model accounting for the $Q_{10}$ effect with a complex temperature profile (equation (17)), and again exhibit a large difference in transfer efficiency between the case coupling sinking with degradation and the reference case omitting it.

### *1.6 Comparison with the scenario in which the increase of seawater viscosity with decreasing temperature is accounted for.*

In our general model approach, for simplicity we did not account for changes of seawater viscosity with temperature. To test if the sinking-enhanced degradation mechanism is robust to the temperature-driven increase of viscosity with depth, we performed additional simulations in which we included this effect in the model, namely in two locations. First, the kinematic viscosity $\nu$ enters explicitly in the coefficient $\gamma_2$ of equation (14), stemming from the expression of the Sherwood number as a function of physical parameters. Second, the sinking law given in equation (4) was obtained at $T$ = 15 °C. Since particles sink slowly, we expect the flow around them to be in the creeping flow regime, and thus, their sinking speed to scale inversely with the dynamic viscosity $\mu$. Therefore, we account for changes in dynamic viscosity by considering a varying pre-factor $B$ in equation (4) (and ultimately equations (15) and (16)), that is

$$\boldsymbol{B} = \frac{\boldsymbol{B'}}{\boldsymbol{\mu(T)}} \quad (19)$$

where the value of $B'$ is temperature-independent and obtained from the known dynamic viscosity at 15 °C, and $\mu(T)$ is the value of the dynamic viscosity[10] at temperature $T$. With $\mu(15\,°\mathrm{C}) = 1.22 \times 10^{-3}\ \mathrm{kg\,m^{-1}s^{-1}}$, we obtain $B' = 5.08 \times 10^{-6}\ \mathrm{kg\,m^{-\omega}\,s^{-2}}$.
We focus on the temperature profile given in equation (17) to test the impact of temperature-induced viscosity changes, as it accounts for strong variations in temperature with depth. For each depth to which a particle sinks, the local values of the kinematic and dynamic viscosity corresponding to the temperature at that depth are obtained from established fits[10] for a salinity of 33.6 g/L (corresponding to the salinity at the location where the parameters of our sinking law were measured[4]). We do not consider the effect of pressure in this sensitivity analysis, since increasing pressure with depth will only very slightly decrease viscosity and thus would only reduce the impact of temperature investigated here.

Despite considering a strongly varying temperature profile, the effect of changes in viscosity with temperature is very small (Extended Data Fig. 9), with a negligible change to the transfer efficiencies $T_{100}$, which remain close to 56% for the coupled case and to 94% for the uncoupled case. The small reduction in flux with depth occurring when one accounts for temperature-driven viscosity changes stems from the slightly reduced sinking speed associated with more viscous seawater. Overall, the effect of changes of viscosity on carbon flux is of much smaller magnitude than the effect of the sinking-degradation coupling.

### *1.7 Alternative choice for the integration of the vertical flux.*

In the approach described above, the range of particle radii considered for the integration of the vertical flux decreases with depth and reaches a value that is smaller than the initial value $R_l$. Thus, as the particles of initial radius $R_0$ in the range $[R_l, R_g]$ at depth $Z_0$ sink and get degraded as described by equation (16), the range of radii contributing to the vertical flux at a given depth $Z$ becomes $[R(R_l, Z), R(R_g,Z)]$, with $R(R_l,Z) < R_l$ and $R(R_g,Z) < R_g$. We argue that this change in the range of particle sizes bears similarity with the actual particle dynamics in the ocean. In shallow waters initially, the freshly formed aggregates of organic carbon that contribute to the flux are of the order of 125 µm or larger, while the smaller particles present are suspended micro-gels and live cells (<20 µm), which typically do not participate in the carbon flux without coagulation[11,12]. Then, as the aggregates sink, they shrink in size as they are degraded, which populates the lower end of the particle size range. Nevertheless, some experimental techniques for measuring the POC flux, such as underwater vision profilers and others[3,7], have a fixed lower resolution, which imposes a lower limit on the size of particles detected. We thus ask whether the observed effect of the coupling of sinking and degradation on carbon flux, predicted by our model, is of similar magnitude if one were to consider a fixed range of particle radii for integration of the vertical flux of particulate matter at every depth.

In this second approach, we therefore fix a minimum particle radius contributing to the vertical flux at any depth, $R_{min}$ (note that a fixed maximum radius is not necessary, since in our model size always decreases with depth). The initial particle radius $R_0$ of a particle at depth $Z_0$, which after degradation has reached the size $R_{min}$ at depth $Z$, is denoted as $R_{0,min}(R_{min},Z)$. The vertical flux at any depth $Z$ can then be obtained from equation (1) by integrating over the range of initial radii $[R_{0,min}(R_{min},Z), R_g]$ instead of $[R_l, R_g]$. The result, when considering a lower bound of

particle radius $R_{min}$ = 20 µm, shows a very similar impact of the feedback of flow on degradation as in the approach without a lower bound, with the vertical flux being reduced by 50% at approximately 400 m, compared to approximately 1750 m in the case without coupling of sinking and degradation (Extended Data Fig. 5).

Our model considers a degradation rate that is coupled to and increases with sinking speed, following our experimental results (Fig. 4). To demonstrate that our model is indeed shaped by this complex coupling between flow and degradation, and is not simply a result of the higher degradation rate on all particles that arises because we consider flow, we also computed the POC flux obtained in the reference case when imposing a constant high degradation rate $\gamma_0'$ on all particle sizes, independent of sinking speed (Extended Data Fig. 6). This alternative approach considers no coupling. For this case we used the radius shrinking rate $\gamma_0'$ obtained from the largest particle considered ($R_0^{max}$ = 750 µm) in the coupled model, that is

$$\gamma_0' = \left[\gamma_0 + \gamma_2 B^{\delta} R_0^{\max(1+\omega)\delta}\right], \quad (20)$$

which gives a numerical value of $\gamma_0' = 2.72 \times 10^{-9}$ m s$^{-1}$. We then compute the degradation dynamics using equation (14) with $\gamma_2 = 0$ and $\gamma_0 = \gamma_0'$. This approach ignores the reduction in degradation expected when particles get smaller and sink more slowly. As a result, it shows an overshot attenuation of the POC flux with depth compared to the coupled case (Extended Data Fig. 6). The difference between the two scenarios ('coupled' and 'uncoupled-high' in Extended Data Fig. 6) demonstrates the specific impact of coupling between flow and degradation and its sizeable effect on the shape of the POC flux with depth.

## 2. Supplementary Text

To verify that the enhanced degradation in flow was not simply a consequence of release from oxygen limitation that might occur under no-flow conditions, we measured respiration rates of fully colonized particles using an oxygen-sensitive optode sensor (Methods; Extended Data Fig. 1b). The estimated oxygen requirement per particle (8.9 ± 0.7 pmol min$^{-1}$ particle$^{-1}$; at peak growth, 40 h post-inoculation, $n$ = 3) is far below the predicted diffusive flux of oxygen into the chamber (151 pmol min$^{-1}$, see calculation in Methods), indicating that oxygen limitation cannot be the reason for the reduced rate of degradation under no-flow conditions in our device. Furthermore, the YFP proteins that are expressed by the bacteria on the particle require oxygen for their production[13,14], and so would not mature to fluoresce in anaerobic conditions. Note that unlike oxygen, which can freely diffuse into the chamber through the parafilm, under conditions without flow other nutrients would not be replenished and eventually could limit growth. Nevertheless, even with no flow, growth of bacteria on and around the particle is observed up until the end of the experiment (Movie S1, Movie S2 and Extended Data Fig. 1a).

It was also necessary to verify that the observed reduction in the volume of the particles indeed serves as a good proxy for net particle degradation, to rule out, for example, the possibility that bacteria secrete enzymes and degrade the particle also from within. When grown on an alginate-containing agar plate, colonies of *V. cyclitrophicus* ZF270 did not form a hollow ring of lysed

alginate, indicating that bacteria consumed alginate without secreting alginate lyase into the medium (Extended Data Fig. 1c). On a particle, degradation would thus occur only from the surface inwards. Indeed, *V. cyclitrophicus* ZF270 lacks the highly secreted alginate lyase homologue (PL7G) responsible for the secreted enzymatic activity in the related species *Vibrio splendidus*[15] (Table S2). The reduction in the volume of the particle by bacterial degradation in our experimental system therefore corresponds to an equivalent reduction in the mass of the particle.

## 3. Supplementary Discussion

A common assumption in global biogeochemical models of the ocean is that sinking speed and bacterial degradation rate of organic particles are independent from each other. Contrary to this paradigm, we find that particle degradation rate is strongly coupled to sinking speed. Moreover, measurements of carbon consumption and enzymatic degradation of marine particles are often performed in quiescent conditions (e.g., Smith et al. 1992[16]). Our results imply that, when one does not account for sinking, measurements of the degradation rate can underestimate actual degradation rate by up to an order of magnitude. Measurements of degradation that account for sinking are not subject to this underestimation. Our study demonstrates that the degradation of polymeric substances, such as the polysaccharides alginate, chitosan or chitin, is inhibited when flow is absent or very weak. We uncovered the fundamental mechanism by which sinking accelerates degradation: the flow that is generated by sinking carries away the oligomers resulting from enzymatic hydrolysis that would otherwise compete for enzymatic activity. The high abundance of polymeric substrates in the marine environment and the flow regime characteristic of sinking marine particles makes our finding relevant in particular to the marine carbon pump.

Polysaccharides and other polymeric substrates are key elements of marine snow in the ocean. For example, marine particles isolated from the southern ocean were found to have as much as 40–60% of their mass in the form of carbohydrates[17]. Similarly, a recent study revealed that the polysaccharide laminarin accounts for up to 50% of organic carbon in sinking, diatom-containing particles[18]. The sources of the polysaccharides incorporated in particulate organic matter (POM) can be diverse. For example chitin, which is considered the most abundant polysaccharide in the ocean, is produced in the marine environment by fungi, yeast, green algae, zooplankton and other crustaceans, all organisms whose remains are known to contribute to marine particles[19]. Another important example are the polysaccharide-based larvacean houses that form a conspicuous source of cellulose-based POM[20]. In general, polysaccharides are the ‘glue’ that holds the components of particles together, and materials such as transparent exopolymer particles (TEP), extracellular polymeric substances (EPS) and other microgels, key structural components of marine snow[21,22], are introduced to particles already at their coagulation stages. Degradation of those polymeric components may thus induce physical solubilization and loosening of the rest of the structure[21,22]. Interestingly, copepod faecal pellets, which are another large source of POM in the ocean, are also held together by a peritrophic polymeric membrane, in many species consisting of multilayered chitinous microfibrils[23]. In light of their complex composition, it is perhaps unsurprising that particles have been found to be hotspots for hydrolytic activity, and in particular for enzymes with polysaccharide substrates[16,24]. Overall, the key role of polymeric substrates in marine particles, both as major components of the organic carbon in particles, and

as structural elements of these particles, indicate that our findings are relevant beyond our model particles, also for marine particles with complex structure and composition.

Although not capturing the full complexity of real marine snow, our experimental system reliably captures the interplay between flow and degradation. Unlike real particles[25], our model particles do not allow the colonization of the particle interior, and degradation occurs only on the particle surface. Nevertheless, although porous, most marine snow particles are not very permeable[26,27], meaning that flow moves around the particle and not through the pores of the particle. As a consequence, transport in the particle interior is diffusion-limited, so to a first approximation the degradation in the interior occurs at a very low rate, similar to the values measured by our experiments without flow (Fig. 1b). This slower degradation rate at the core of particles is also evident in previous studies, which highlighted for example the role of the lack of oxygen at low flow rates[27,28]. We thus expect that degradation from the interior will make only a small contribution to overall degradation, justifying our model system in which no interior degradation occurs. Ultimately, of course, the interior of the particle is not decoupled from what happens on the surface: by promoting enhanced elimination of oligo-alginate from the particle surface, the flow due to sinking will also contribute to decreasing the concentration of oligo-alginate in the particle interior, so that even the small amount of interior degradation will be enhanced by sinking. Therefore, although learning more about the spatial distribution of bacteria on particles is an important and intriguing research question, the sinking-enhanced degradation mechanism will hold largely independently of the spatial distribution of bacteria on the particle, making our experimental system not only convenient (because it is easier to measure degradation over time through video microscopy), but also realistic.

Understanding the mechanistic controls on the biological carbon pump still represents an open challenge[29]. Our results contribute to this understanding by identifying one of these controls, namely the acceleration of bacterial degradation rate with increasing particle sinking speed. We argue that this mechanism, being purely physical, might be one of the factors leading to varying transfer efficiencies around the globe. Although ‘marine snow’ was historically defined as particles larger than 0.5 mm[30], POM in most oceanic regions is actually smaller. The particle size distribution (PSD) in most oceanic regimes and depths has a slope that varies between -2 and -5, meaning that there are 2 to 5 orders of magnitude higher concentrations of small particles in the ocean for each order of magnitude reduction in particle size[6]. Considering the abundance of micrometre-sized particles and the high degradation rate of larger particles, most particles are expected to either start small or eventually become small[6,31] and therefore their degradation will be inhibited by the low flow associated with slow sinking at some point. Moreover, active particle fragmentation has been suggested to explain up to 50% of the carbon attenuation in the ocean, and this process by definition results in small and slowly sinking particles[32]. Inhibited degradation thus tends to reduce attenuation of the carbon flux, while fragmentation (that forms slowly sinking particles) tends to increase this attenuation. Ultimately, the balance between the two processes is expected to result in higher fluxes than those originally predicted by fragmentation alone[32]. Based on our observations, we hypothesize that the coupling between sinking speed and degradation rate may thus underlie the counterintuitively high contribution to the carbon flux of slow sinking particles in different oceanic regimes[33–40].

Two typical environments allow us to explore opposite limits of this coupling between flow and degradation: eutrophic waters, characterized by greater numbers of large, fast-sinking particles, and oligotrophic waters, dominated by small particles with low sinking speeds.

We first consider eutrophic waters, where large particles strongly contribute to the carbon flux. For eutrophic waters we find that the sinking-enhanced degradation results in faster remineralisation of particles and consequently in a strong attenuation of the POC flux ($T_{100}$ = 43% for the coupled case vs. $T_{100}$ = 92% for the uncoupled case, for a PSD with slope of -2; Extended Data Fig. 7). Therefore, in the coupled model most of the POC flux attenuation within the 100 m layer below the euphotic zone (100% - $T_{100}$) derives from the sinking-enhanced degradation. Although ours is a highly simplified model of the biological carbon pump, as it assumes purely polymeric particles and omits other carbon pump mechanisms such as zooplankton grazing[41], our results show that the sinking-enhanced degradation clearly results in a considerable attenuation of POC flux in eutrophic regions. Our findings are also in line with the low transfer efficiencies measured in eutrophic regions[42].

We next consider oligotrophic waters, such as the vast subtropical and tropical open ocean. These areas are dominated by smaller phytoplankton and as such are characterized by slowly sinking, small particles that are primarily degraded by heterotrophic bacteria in the mesopelagic[31]. Our observations suggest that the slow flow associated with the low sinking speeds will inhibit particle degradation, due to the accumulation of breakdown products. Due to the resulting slower degradation, our model predicts higher transfer efficiencies, as commonly observed in oligotrophic regions[31]. However, even under very oligotrophic conditions (e.g., at PSD slope of -5), we find that sinking-enhanced degradation still makes a strong contribution to the total POC flux attenuation in our model (which yields $T_{100}$ = 60% in the coupled case vs. $T_{100}$ = 95% in the uncoupled case; Extended Data Fig. 7). When extending the range of particle sizes considered, to include even more of the very small particles ($R_0$ = 22.5 to 2500 μm), the transfer efficiencies increase, but the importance of the sinking–degradation coupling compared to the reference case omitting the coupling is preserved (with $T_{100}$ = 90% in the coupled case vs. $T_{100}$ = 98% in the uncoupled case; Extended Data Fig. 7). Explicitly considering flow is thus important across both eutrophic and oligotrophic marine environments.

The modulation of the microbial degradation rate by temperature tends to oppose the flow–degradation coupling, across different oceanic regions. Cold, productive waters will see a degradation rate that is decreased by the low temperatures, but enhanced via the sinking–degradation coupling. In contrast, warm, oligotrophic waters will see a degradation rate that is enhanced by the high temperatures, but reduced by the sinking–degradation coupling in view of the low sinking speeds. Because our model considers idealized particles, the outcome of the two opposing effects in the ocean remains difficult to predict quantitatively. However, a set of simulations taking into account these two opposing effects supports the idea that the sinking–degradation coupling will dominate in magnitude the effect of temperature: whereas including the coupling between sinking and degradation decreases the transfer efficiency by 38% with respect to the uncoupled reference case, including the effect of temperature on degradation rate increases the transfer efficiency by only 3% in the uncoupled case (19% in the coupled case) (Methods, Extended Data Fig. 8).

In summary, by revealing a key mechanism contributing to determining the efficiency of the carbon pump, our work also paves the way to a deeper understanding of other factors modulating

microbial degradation in the ocean. Future work investigating, for example, the role of natural community composition or natural chemical composition of particles, can now be performed with a proper control of confounding factors, by taking into account the effect of flow on particle degradation.

## 4. Supplementary Captions of Movies

**Movie S1. Alginate degradation dynamics are flow dependent.** Degradation dynamics of alginate particles, observed in a microfluidic channel, under different rates of flow. Images of the mid plane of each particle were acquired in phase and fluorescence microscopy every 20 min for 70 h (Methods). Brightness and contrast in the green channel (bacterial fluorescence) were adjusted in each panel to better visualize bacterial growth. (A) No flow. (B) 1.1 m/day. (C) 4.4 m/day. (D) 21.8 m/day. Presented are representative movies of the degradation dynamics.

**Movie S2. Growth dynamics on alginate particles are flow dependent.** Representative movie of bacterial growth on an alginate particle. Images acquired as in Movie S1, but at the interface between the glass slide and the alginate particle. Growth dynamics (A) without flow and (B) with a slow flow rate of 1.1 m/day.

**Movie S3. High concentrations of oligo-alginate promote bacterial biofilm formation and inhibit the degradation of alginate particles.** Representative movie of the degradation dynamics of particles exposed to different concentrations of oligo-alginate (<10 kda) or marine broth 2216 medium (1%). Images acquired as in Movie S1. Brightness and contrast are comparable between panels. Flow of oligo-alginate or 1% 2216 medium in the channel was started 17 h after the beginning of the experiment (Methods). All experiments were performed at a flow rate of 7.25 m/day.

**Movie S4. High concentrations of oligo-alginate inhibit the enzymatic degradation of alginate particles.** Enzymatic degradation of alginate particles in the presence of oligo-alginate. Images were acquired every minute for 127 min for the control and for 180 min for the experiments (Methods). (A) Control (oligo-alginate only, 1 mg/mL). (B) Alginate lyase (10 µg/mL). (C) Oligo-alginate (1 mg/mL) and alginate lyase (10 µg/mL). All experiments were performed at a flow rate of 7.25 m/day.

**Movie S5. Degradation dynamics of chitin particles is flow dependent.** Degradation dynamics of chitin particles by *Vibrio splendidus* (1A01) and *Psychromonas* (6CO6), observed in a microfluidic channel, under a flow rate of 7.25 m/day or with no flow. Images of the mid plane of each particle were acquired in phase microscopy every 20 min for 240 h (Methods). (A) No flow. (B) 7.25 m/day. Presented are representative movies of the degradation dynamics.

## 5. Supplementary References

1. Alldredge, A. The carbon, nitrogen and mass content of marine snow as a function of aggregate size. *Deep Sea Res. Part I Oceanogr. Res. Pap.* **45**, 529–541 (1998).

2. Stemmann, L. *et al.* Volume distribution for particles between 3.5 to 2000μm in the upper 200m region of the South Pacific Gyre. *Biogeosciences* **5**, 299–310 (2008).
3. Guidi, L. *et al.* Plankton networks driving carbon export in the oligotrophic ocean. *Nature* **532**, 465–470 (2016).
4. Alldredge, A. L. & Gotschalk, C. In situ settling behavior of marine snow. *Limnol. Ocean.* **33**, 339–35 (1988).
5. Karp-Boss, L., Boss, E. & Jumars, P. A. Nutrient fluxes to planktonic osmotrophs in the presence of fluid motion. *Oceanogr. Mar. Biol. an Annu. Rev.* **34**, 71–107 (1996).
6. Guidi, L. *et al.* Effects of Phytoplankton Community on Production , Size and Export of Large Aggregates : A World-Ocean Analysis. *Limnol. Oceanogr.* **54**, 1951–1963 (2009).
7. McDonnell, A. M. P. & Buesseler, K. O. Variability in the average sinking velocity of marine particles. *Limnol. Oceanogr.* **55**, 2085–2096 (2010).
8. Zakem, E. J. *et al.* Ecological control of nitrite in the upper ocean. *Nat. Commun.* **9**, (2018).
9. Wohlers, J. *et al.* Changes in biogenic carbon flow in response to sea surface warming. *Proc. Natl. Acad. Sci. U. S. A.* **106**, 7067–7072 (2009).
10. Sharqawy, M. H., Lienhard V, J. H. & Zubair, S. M. Erratum to Thermophysical properties of seawater: A review of existing correlations and data. *Desalin. Water Treat.* **29**, 355–355 (2011).
11. Jackson, G. A. & Lochmann, S. E. Effect of coagulation on nutrient and light limitation of an algal bloom. *Limnol. Oceanogr.* **37**, 77–89 (1992).
12. Jackson, G. A. A model of the formation of marine algal flocs by physical coagulation processes. *Deep Sea Res. Part A. Oceanogr. Res. Pap.* **37**, 1197–1211 (1990).
13. Potzkei, J. *et al.* Real-time determination of intracellular oxygen in bacteria using a genetically encoded FRET-based biosensor. *BMC Biol.* **10**, 28 (2012).
14. Heim, R., Prasher, D. C. & Tsien, R. Y. Wavelength mutations and posttranslational autoxidation of green fluorescent protein. *Proc. Natl. Acad. Sci. U. S. A.* **91**, 12501–12504 (1994).
15. Badur, A. H. *et al.* Exploiting fine-scale genetic and physiological variation of closely related microbes to reveal unknown enzyme functions. *J. Biol. Chem.* **292**, 13056–13067 (2017).
16. Smith, D. C., Simon, M., Alldredge, A. L. & Azam, F. Intense hydrolytic enzyme activity on marine aggregates and implications for rapid particle dissolution. *Nature* **359**, 139–142 (1992).
17. Kim, B. K. *et al.* Vertical distributions of macromolecular composition of particulate organic matter in the water column of the amundsen sea polynya during the summer in 2014. *J. Geophys. Res. Ocean.* **123**, 1393–1405 (2018).
18. Becker, S. *et al.* Laminarin is a major molecule in the marine carbon cycle. *Proc. Natl. Acad. Sci.* **117**, 6599–6607 (2020).
19. Souza, C. P., Almeida, B. C., Colwell, R. R. & Rivera, I. N. G. The Importance of Chitin in the Marine Environment. *Mar. Biotechnol.* **13**, 823–830 (2011).
20. Katija, K. *et al.* Revealing enigmatic mucus structures in the deep sea using DeepPIV. *Nature* **583**, (2020).
21. Passow, U., Alldredge, A. L. & Logan, B. E. The role of particulate carbohydrate exudates in the flocculation of diatom blooms. *Deep. Res. Part I* **41**, 335–357 (1994).
22. Alldredge, A. L., Passow, U. & Logan, B. E. The abundance and significance of a class of

large, transparent organic particles in the ocean. *Deep Sea Res. Part I Oceanogr. Res. Pap.* **40**, 1131–1140 (1993).
23. Köster, M., Sietmann, R., Meuche, A. & Paffenhöfer, G. A. The ultrastructure of a doliolid and a copepod fecal pellet. *J. Plankton Res.* **33**, 1538–1549 (2011).
24. Arnosti, C. Microbial Extracellular Enzymes and the Marine Carbon Cycle. *Ann. Rev. Mar. Sci.* **3**, 401–425 (2011).
25. Lampitt, R. S., Wishner, K. F., Turley, C. M. & Angel, M. V. Marine snow studies in the Northeast Atlantic Ocean: distribution, composition and role as a food source for migrating plankton. *Mar. Biol.* **116**, 689–702 (1993).
26. Ploug, H. & Passow, U. Direct measurement of diffusivity within diatom aggregates containing transparent exopolymer particles. *Limnol. Oceanogr.* **52**, 1–6 (2007).
27. Zetsche, E., Larsson, A. I., Iversen, M. H. & Ploug, H. Flow and diffusion around and within diatom aggregates: Effects of aggregate composition and shape. *Limnol. Oceanogr.* lno.11420 (2020) doi:10.1002/lno.11420.
28. Ploug, H. Small-scale oxygen fluxes and remineralization in sinking aggregates. *Limnol. Oceanogr.* **46**, 1624–1631 (2001).
29. Buesseler, K. O., Boyd, P. W., Black, E. E. & Siegel, D. A. Metrics that matter for assessing the ocean biological carbon pump. *Proc. Natl. Acad. Sci. U. S. A.* **117**, 9679–9687 (2020).
30. Alldredge, A. L. & Silver, M. W. Characteristics, dynamics and significance of marine snow. *Prog. Oceanogr.* **20**, 41–82 (1988).
31. Herndl, G. J. & Reinthaler, T. Microbial control of the dark end of the biological pump. *Nat. Geosci.* **6**, 718–724 (2013).
32. Briggs, N., Dall'Olmo, G. & Claustre, H. Major role of particle fragmentation in regulating biological sequestration of $CO_2$ by the oceans. *Science (80-. ).* **367**, 791–793 (2020).
33. Durkin, C. A., Estapa, M. L. & Buesseler, K. O. Observations of carbon export by small sinking particles in the upper mesopelagic. *Mar. Chem.* **175**, 72–81 (2015).
34. Bol, R., Henson, S. A., Rumyantseva, A. & Briggs, N. High-Frequency Variability of Small-Particle Carbon Export Flux in the Northeast Atlantic. *Global Biogeochem. Cycles* **32**, 1803–1814 (2018).
35. DeVries, T. & Weber, T. The export and fate of organic matter in the ocean: New constraints from combining satellite and oceanographic tracer observations. *Global Biogeochem. Cycles* **31**, 535–555 (2017).
36. Henson, S. A., Sanders, R. & Madsen, E. Global patterns in efficiency of particulate organic carbon export and transfer to the deep ocean. *Global Biogeochem. Cycles* **26**, 1–14 (2012).
37. Marsay, C. M. *et al.* Attenuation of sinking particulate organic carbon flux through the mesopelagic ocean. *Proc. Natl. Acad. Sci. U. S. A.* **112**, 1089–94 (2015).
38. Weber, T., Cram, J. A., Leung, S. W., DeVries, T. & Deutsch, C. Deep ocean nutrients imply large latitudinal variation in particle transfer efficiency. *Proc. Natl. Acad. Sci. U. S. A.* **113**, 8606–8611 (2016).
39. Richardson, T. L. Mechanisms and Pathways of Small-Phytoplankton Export from the Surface Ocean. *Ann. Rev. Mar. Sci.* **11**, 57–74 (2019).
40. Giering, S. L. C. *et al.* High export via small particles before the onset of the North Atlantic spring bloom. *J. Geophys. Res. Ocean.* **121**, 6929–6945 (2016).

41. Buesseler, K. O. & Boyd, P. W. Shedding light on processes that control particle export and flux attenuation in the twilight zone of the open ocean. *Limnol. Oceanogr.* **54**, 1210–1232 (2009).
42. Henson, S. A., Sanders, R. & Madsen, E. Global patterns in efficiency of particulate organic carbon export and transfer to the deep ocean. *Global Biogeochem. Cycles* **26**, 1–14 (2012).
43. Enke, T. N., Leventhal, G. E., Metzger, M., Saavedra, J. T. & Cordero, O. X. Microscale ecology regulates particulate organic matter turnover in model marine microbial communities. *Nat. Commun.* **9**, 2743 (2018).
44. Ebrahimi, A., Schwartzman, J. & Cordero, O. X. Cooperation and spatial self-organization determine rate and efficiency of particulate organic matter degradation in marine bacteria. *Proc. Natl. Acad. Sci. U. S. A.* **116**, 23309–23316 (2019).