Self-similarity, density-size dynamics and the sinking speed of marine aggregates

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Abstract

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Self-similarity, density-size dynamics and the sinking speed of marine aggregates.

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Key Points:
• Poor estimates of the sinking speed of marine aggregates stem primarily high vari-
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• Self-similarity of aggregation facilitates efficiently modelling of aggregate size and
excess density, and hence sinking speed.

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13 Abstract

We propose self-similarity of aggregation provides a tractable framework for estimating 14 the sinking speed of natural marine particle aggregates for ocean biogeochemical mod-15 els. It does so by providing a means to tracking both size and excess density of aggre-16 gates as they are formed and transformed by aggregation, degradation and fragmenta-17 tion processes. A self-similarity parameter a in the range 1.8 to 2.1 is well supported by 18 direct observations drawn from an extensive database of aggregate size and sinking speed. 19 This provides a mechanistic description of how spatial and temporal variations in plank-20 tonic communities impact size and density characteristic of aggregate assemblages and 21 their subsequent export from the surface ocean. We provide a simple model for which 22 we conduct sensitivity analyses for the self-similarity parameter, stickiness, and turbu-23 lent dissipation rate. While incomplete in several aspects, the model compares well with 24 observations of aggregate size spectra covering the global ocean. 25

²⁶ Plain Language Summary

How fast dead stuff sinks is perhaps the biggest uncertainty in estimating how the 27 world's oceans cycle elements, and in particular, how they sequester carbon. We present 28 a model that links surface plankton communities with the density and size character-29 istics of the aggregates of dead material they produce, and are thus able to estimate the 30 sinking speeds of all aggregates that emerge. A key assumption that allows for efficient 31 32 simulation is self-similarity of aggregation; that the underlying process of how aggregates form is well described by a set of global rules, even though this is often hidden by dif-33 ferences in what they are made of, and how they are degraded and fragmented. Although 34 really quite simple, our model compares well with macroscopic properties of aggregates 35 assemblages seen in nature. 36

37 1 Introduction

Perhaps the greatest hurdle to attaining a mechanistic understanding of the oceans' 38 biogeochemical cycles is the incomplete description of the sinking speeds of particulate 39 matter. This issue is central to key questions such as how much organic material is ex-40 ported from the sunlit surface ocean (Ducklow et al., 2001; Mouw et al., 2016), its de-41 pendence on the ever changing structure of the surface plankton community (Boyd & 42 Newton, 1995; Henson et al., 2012), the depth to which detrital material sinks before be-43 ing solubilized (Cavan et al., 2017; Marsay et al., 2015), what this means for carbon se-44 questration (Kwon et al., 2009), consumption of oxygen (Suess, 1980; Bopp et al., 2002) 45 nutrient recycling (Tréguer & Jacques, 1992; Buesseler et al., 2007), and how much reaches 46 the seabed to be buried in sediments or feed benchic communities (Gooday, 2002; Cael, 47 Bisson, et al., 2021). Despite years of observations from laboratory and field, sinking speeds 48 of natural aggregate particles remain as enigmatic as ever; aggregates of any size from 49 microns to centimeters seemingly sink at any speeds from practically zero to several 1000s 50 of meters per day (Iversen & Lampitt, 2020; Laurenceau-Cornec et al., 2020; Cael, Ca-51 van, & Britten, 2021). Yet the physics of sinking speed is unequivocal. Sinking speed 52 is set by a balance between buoyancy forces and drag (Stokes, 1851; Clift et al., 1978), 53 and while the precise formulation may not be as neat as Stokes' law (Oseen, 1910; White, 54 1991; Loth, 2008), the following principle must hold: sinking speed is a monotonically 55 increasing function of aggregate size and excess density *ceteris paribus*. 56

The key concept we explore here is that aggregation is a geometrically self-similar process, such that the linear dimension r_{ioj} of an aggregate formed by the combination of two parent aggregates of linear dimension r_i and r_j respectively is given by:

$$r_{i \circ j} = (r_i^a + r_j^a)^{(1/a)} \tag{1}$$

That is, for the binary process of aggregation, r^a is an additive conservative property. 60 This is not a new idea (Jackson, 1998; Wiesner, 1992) and arises from the general ob-61 servation that aggregates are fractal objects (Alldredge & Gotschalk, 1988; Meakin, 1987; 62 Logan & Wilkinson, 1990). We term a the self-similarity parameter, and note a < 363 in compliance with the observed increase in porosity under aggregation. We stress that 64 a is not the fractal dimension of the aggregate. Neither is it an inherent property of ag-65 gregates and we will not attempt to use a to produce scaling laws as is the usual trajec-66 tory of these considerations. At this point we simply want to treat a as a parameter gov-67 erning the binary process of aggregation. 68

⁶⁹ Under geometric self-similarity, the total mass of an aggregate produced by the com-⁷⁰ bination of 2 aggregates of mass m_i and m_j can be deduced to be the sum of these two ⁷¹ masses, plus a bit extra due to the inclusion of some fluid (density ρ_w) that occupies the ⁷² expanded aggregate volume (i.e. increase in porosity). Specifically,

$$m_{ioj} = m_i + m_j + (v_{ioj} - v_i - v_j)\rho_w$$
(2)

⁷³ where v_i , v_j and v_{ioj} are the volumes of the two parent aggregates and the daughter ag-⁷⁴ gregate respectively. Note that m is the total mass, not just the dry mass of the aggre-⁷⁵ gate. It is convenient to recast this in terms of density of the aggregates, ρ_i , ρ_j , ρ_{ioj} . It ⁷⁶ follows that excess density

$$\rho_{ioj} - \rho_w = \frac{r_i^3}{r_{ioj}^3} (\rho_i - \rho_w) + \frac{r_j^3}{r_{ioj}^3} (\rho_j - \rho_w)$$
(3)

Equations (1) and (3) provide a construct by which the size and excess density, and 77 hence sinking speed, of particle aggregates can be estimated. However, processes other 78 than aggregation also effect size and density; chief amongst these are degradation, dis-79 solution and fragmentation. This is illustrated in Figure 1 for a single primary particle 80 (a diatom for instance) where aggregation produces larger and less dense aggregates, degra-81 dation and /or dissolution removes mass but has no immediate impact on aggregate size, 82 and fragmentation, particularly on large porous aggregates produces smaller aggregates 83 which can be reincorporated into the aggregation process. Though out, sinking speed 84 can be estimated. At the system scale (e.g. the surface mixed layer), a dynamic can be 85 established between the supply of primary particles (e.g. from primary production, de-86 position of dust, faecal pellets) and the loss of aggregates by sinking. While still rela-87 tively complex, each of the sub-processes can in principle be constrained from observa-88 tions, parameterized and mechanistically formulated. What makes this framework par-89 ticularly attractive is the development of size-based and trait-based models of plankton 90 communities (Banas, 2011; Serra-Pompei et al., 2020; Serra-Pompei et al., 2022) which 91 provide precisely the type of information (size and trait resolved primary productivity 92 and zooplankton grazers) that can serve as input. Indeed a resolved particle aggrega-93 tion model can provide a mechanistic link between emerging plankton community struc-94 ture and export flux; one of the key unresolved issues of the biological carbon pump (Boyd 95 & Newton, 1995; Bach et al., 2019). 96

⁹⁷ 2 Analysis of self-similarity from observations.

A large literature exists reporting observations of the sinking speed and size of marine aggregates. These were recently collated and published in a database (Laurenceau-Cornec et al., 2015; Cael, Cavan, & Britten, 2021), and, together with additional observations (Gärdes et al., 2011; Bach et al., 2019; Iversen & Lampitt, 2020) provide the basis for this analysis. While aggregate density in itself is a difficult parameter to measure, it can be estimated from observed sinking speeds (Engel et al., 2009; Iversen & Ploug, 2010). In particular,

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$$\rho - \rho_w = \frac{3}{8} \frac{Cw^2}{gr} \tag{4}$$



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Figure 1. Aggregate dynamics depicted in 2 dimensional state space. Dynamics are driven by 3 processes; aggregation producing larger less dense aggregates, degradation/dissolution which reduces the solid mass (and hence excess density) of aggregates, and fragmentation. Primary particles (e.g. diatoms) are produce in a specific size and density range. The production of other material such as dust and TEP can also be specified. The distribution of aggregates in this state space eventually reaches steady state when the rate of supply is balanced by the sinking losses particularly of large dense aggregates.

where w is sinking speed, r the estimated spherical radius, g the gravitational acceleration, and C is an empirically derived drag coefficient. While there are several formulations, generally expressed as a function of Reynolds number $(R = 2rw/\eta, \text{ with } \eta \text{ be$ $ing the kinematic viscosity of seawater})$, the most commonly used is

$$C = \frac{24}{R} + \frac{6}{1 + \sqrt{R}} + 0.4\tag{5}$$

(White, 1991). This, and similar formulas are robust for R up to about 10^5 . Estimates 111 of excess density and observed sinking speed for aggregates are plotted in Figure 2 and 112 summarized in Table 1. The preponderance of observations correspond to R < 100 and 113 thus lie well within the range where (5) is valid. The general features of Figure 2 nearly 114 illustrate some of the properties of aggregation already mentioned. For instance, that 115 large aggregates tend to sink faster and have a lower excess density than small aggre-116 gates. Further, while there is considerable variance of sinking speed with size, this ap-117 pears to be reduced for excess density. Indeed, the ensemble of excess density observa-118 tions appears to collapse roughly to a power law r^b with b around -1.4. 119

¹²⁰ Under special conditions, self-similarity makes quite strong predictions on how ag-¹²¹ gregate properties (e.g. mass, density, porosity) scale with size. Specifically, for a mono-¹²² culture of primary particles of size r_0 and density ρ_0 , and in the absence of degradation, ¹²³ dissolution, and fragmentation, then aggregates' excess density follows a power law:

$$\rho(r) - \rho_w = \left(\rho_o - \rho_w\right) \left(\frac{r}{r_0}\right)^{a-3} \tag{6}$$

¹²⁴ Under these conditions, the aggregation vector in the Figure 1, would have an expected ¹²⁵ slope a - 3.

Within the set of field and laboratory observations reported in Table 1, a subset meet suitable criteria that can reveal such a relationship. For instance, (Iversen & Ploug, 2010) conducted laboratory studies of aggregates from relatively fresh monocultures of the chain forming diatom *Skeletonema costatum* and the coccolithophore *Emiliania huxleyi*, and mixtures of the two. Log-log regressions on these indicate b in the range -1.2



Figure 2. (a) Aggregate sinking speed (w) observed in a large number of studies (cf. Table 1) as a function of estimated spherical radius (r) and (b) the excess density $(\rho - \rho_w)$ calculated from observed sinking speeds using a modified Stokes law. Colors represent different studies. The lines in panel (a) are contours of Reynolds number ranging from 100 to 0.001. The grey lines in panel (b) indicate a log-log slope of -1.4.

to -1.0 i.e. a in the range 1.8 to 2.0. Other laboratory observations that have avoided 131 degradation and extraneous manipulations with TEP and dust indicate similar relation-132 ships with b in the range [-1.2, -0.9] (Engel & Schartau, 1999; Engel et al., 2009; Laurenceau-133 Cornec et al., 2015). These values are consistent with laboratory experiments for non-134 biological particle aggregation (Lin et al., 1989) for which a ranges between 1.8 and 2.1. 135 The lower value corresponds to a relatively porous structure that arises when aggregates 136 are built-up of very sticky, similarly sized particles that combine immediately on con-137 tact. The value a = 2 corresponds to a random walk arrangement in 3 dimensions, and 138 has been used in previous model settings (Jackson & Burd, 1998; Jokulsdottir & Archer, 139 2016). From these considerations, it appears that a in the ranges 1.8 to 2.1 is a reason-140 able choice. 141

It is also clear that a large number, indeed the majority, of studies listed in Table 142 1, exhibit slopes b that are spread across a much broader range. These studies all fol-143 low quite different experimental (e.g. natural aggregates, lab cultures, manipulations with 144 ballast material) and observational procedures (e.g. in situ cameras, roller tanks, ver-145 tical flow systems). In some instances it can be argued that the observation method is 146 poorly designed to capture the characteristics of the full aggregate community. Roller 147 tanks for instance preferentially generate large, fast-sinking aggregates (Jackson, 2015) 148 producing particle size spectra that are not representative of natural aggregate commu-149 nities. Perhaps more important is the heterogeneity of the primary particles. In some 150 experimental setups, ballasting material of considerably different excess densities are present 151 or introduced. Further, natural plankton communities are seldom mono-cultures, and 152 are generally composed of unicellular organisms covering a range of sizes and densities; 153 some with shells and spines, some vacuolated, some chain-forming. In any given size range, 154 the aggregate community will be an ad-mixture derived from different primary particles. 155 Furthermore, as aggregates degrade and fragment, smaller, less dense aggregates come 156 into the mix – grist to the mill – so that aggregate density, and hence sinking speed, will 157 exhibit a relatively broad distribution at any given aggregate size. We must therefore 158 conclude that while the majority of observations plotted in Figure 2 are perfectly fine 159 in relating the sinking speed to the size of an aggregate, methodological issues mean that 160

they remain mute on any self-similarity in the underlying aggregation process. Seen in this light, it appears that the variance of excess density (Figure 2 (b)) is composed of two elements; a general negative slope being due to increased aggregate porosity with size, and an inherent variability due to the excess density of primary aggregate material.

¹⁶⁶ **3** Dynamic Aggregate Model

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Here we provide a brief description of a simplified model . The physical setting we consider is a surface mixed layer of depth h where aggregates are produced from a range of primary particles, transformed and sink out according to the dynamics described in Figure 1. The model simulates the number and mass of aggregates in a two dimensional state space (size and excess density). We supply the code for the model in the supplementary material, and encourage readers to perform their own simulations.

173 It is convenient right from the outset to introduce two transformed variable (x, z)174 that map to $(r, \rho - \rho_w)$ as

$$r = r_o \delta^x, \quad \rho - \rho_w = \rho_o z \delta^{(a-3)x} \tag{7}$$

x is a logarithmic scaling of aggregate size, and z a stretched linear scaling of excess den-176 sity. The factor $\delta^{(a-3)x}$ takes advantage of the reduction of density by aggregation and 177 expands the density resolution for large aggregates. Key variables in the model are the 178 matrices N and M representing the number of aggregates and their total mass respec-179 tively within 1×1 bins in discretized (x, z) state space. Suitable range choices for x and 180 z, scaling factors r_o [µm] and ρ_o [kg m⁻¹], and logarithmic interval δ allow for a rela-181 tively complete representation of the aggregate community within computationally con-182 venient dimensions of N and M. These are related by $M = m \circ N$ where \circ represents 183 piece-wise matrix product and \mathbf{m} is the mean mass of an aggregate within each bin. 184

The model determines the rate of change of M due to five processes: production, 185 aggregation, degradation, fragmentation and sinking losses. Several of these processes 186 are relatively simple to implement. For instance production is prescribed and sinking losses 187 $Q = -M \circ w/h$, where w is the mean aggregate sinking speed in discretized state space. 188 Aggregation is computationally the most complex aspect of the model as it involves a 189 binary convolution of N (Smoluchowski, 1916). It is governed by encounter kernels β ; 190 the rate at which aggregates collide, and stickiness α ; the probability that collision will 191 lead to aggregation (Burd & Jackson, 2009; Jokulsdottir & Archer, 2016). Performing 192 binary convolution calculations is greatly facilitated by self-similarity. Specifically, the 193 ordinates of an aggregate produced from the combination of (x_i, z_i) and (x_i, z_i) is given 194 by: 195

$$\begin{aligned} x_{i\circ j} &= x_i + \log_{\delta}((1 + \delta^{(x_j - x_i)a}))/a \\ &= x_j + \log_{\delta}((1 + \delta^{(x_i - x_j)a}))/a \\ z_{i\circ j} &= \frac{z_i}{1 + \delta^{(x_j - x_i)a}} + \frac{z_j}{1 + \delta^{(x_i - x_j)a}}. \end{aligned}$$

$$(8)$$

It follows that the combination of aggregates from any two 1×1 bins in state space will be confined to a third 1×1 bin, albeit offset from the matrix grid spacing. The model utilizes this in optimizing the algorithm architecture.

We implement degradation as a drift of particle numbers to lower density bins. Specifically, if γ is the degradation rate, then it can be shown that the z ordinate of an aggregate follows $dz/dt = -\gamma z$. In this, degradation acts only on excess density. We set $\gamma =$ 0.1 day⁻¹ consistent with a range of studies (Kiørboe, 2001; Cavan & Boyd, 2018; Bach et al., 2019) although it should be noted that there is considerable variation. Finally fragmentation is simulated simply as a rate at which aggregate mass is transported to smaller sizes classes. We implement this as an increasing function of aggregate size. Of the processes considered, fragmentation remains the least well constrained; aggregates appear
resistant to mechanical shear (Alldredge et al., 1990), and fragmented appears to be chiefly
mediated by metazooans through handling and feeding appears to be important (Dilling
& Alldredge, 2000) and by microbial "mining" and dissolution of adhesive material. We
set the maximum fragmentation rate at 0.5 day⁻¹ for large porous aggregates, a value
consistent with observations (Briggs et al., 2020).

²¹² 4 Results and sensitivity

We present a series of simulations for a fixed rate of primary particle production 213 (size range 1 to 30 μ m in radius, excess density range 10 to 100 kg m⁻³) that corresponds 214 to a mixed community of unicellular auto- and heterotrophic plankton ranging from cyanobac-215 teria to diatoms. Simulations were run to quasi-steady state (i.e. relative differences be-216 tween successive daily estimates (normalized root-mean-square deviation) were $< 10^{-6}$) 217 using a MATLAB ode solver. Three sets of parameters (self-similarity, stickiness and tur-218 bulent dissipation rate) were varied between runs and the emerging aggregate commu-219 nity was characterized by its size spectrum and size resolved export flux. All simulations 220 assumed a mixed layer depth of h = 50 m, and a production rate of $P_{\text{total}} = 0.1 \text{ gC m}^{-2}$ 221 day^{-1} of primary detrictal particles. Results are presented in Figure 3, and the numer-222 ical code that produced it can be found in the supplementary material. 223

Particle size spectra $n(r(x)) = \sum_{z} N(x,z)/dr(x)$ were estimated in the normal 224 manner (Burd & Jackson, 2009) as per size bin width and provide a macroscopic mea-225 sure of the underlying dynamics of production, transformation and sinking. Measure-226 ments of such spectra are routinely made and often conform to a power law of the form 227 $n(r) \sim r^p$. Observations (Stemmann et al., 2008; Guidi et al., 2009; Reynolds & Stram-228 ski, 2021) from different oceanic regions and spanning aggregate sizes from microns to 229 centimeters, show that p ranges from -2 to -6 and cluster around -3 to -4 in the sur-230 face ocean. For our model simulations (Figure 3:b,d,f), all runs exhibited particle size 231 spectra slopes of about -4 for aggregates from 1 to several 100s of μm in size. 232

The flux distributions $f(r(x)) = \sum_{z} \mathsf{M}(x, z) \circ \mathsf{w}(x, z) / (hP_{\text{total}})$ are the flux con-233 tributions summed over different excess density bins, reported within aggregate size bins 234 and normalized with regards total primary particle production P_{total} . The net sum is 235 a little less than unity; difference being due to the net loss of mass due to degradation. 236 The shape of f(r) is universally dome-shaped with very little flux at either small (low 237 sinking speed) or large (low total mass) aggregate sizes. The peak of the flux distribu-238 tion, and to some extent its width, varies with self-similarity, stickiness and turbulent 239 dissipation rate. Low self-similarity indices for instance, push the flux distribution to-240 wards larger aggregate sizes, as do high turbulent dissipation rates. Stickiness by con-241 trast has a relatively minor influence on the flux distribution. Maximum flux appears 242 to be associated with a steepening of the particle size spectrum n(r). 243

While we have argued that a universal self-similarity index, if it exists, is relatively 244 well constrained within the range [1.8, 2.1], this range still presents a large variation in 245 the characteristics of the export flux. For instance, the peak of the flux distribution (Fig-246 ure 3 a) ranges over an order of magnitude in aggregate size, from 300 to 3000 μm. Fur-247 ther, the flux distribution range is much narrower for high self-similarity indices, a fea-248 ture that is exacerbated given the logarithmic scaling of the size bins. The total export 249 flux however, remains virtually the same across all these self similarity values (within 250 99% of each other). Indeed, the self similarity parameter has counteracting effects on sink-251 ing speed in terms of aggregate size and excess density (large a produce small but low 252 porous aggregates and vice versa). The sinking speeds for aggregates in flux maxima (Fig-253 ure 3 a) vary only modestly, from 10 to 20 m day⁻¹ across all values of the self-similarity 254 parameter. It should be noted that the export flux distribution in terms of aggregate size, 255



Figure 3. Aggregate community structure at steady state; f(r) size resolved normalized export flux (a,c,b) and n(r) particle size spectra (b,d,f) for a range of different *a* self-similarity parameters (a,b), α stickiness coefficients (c,d) and turbulent dissipation rates $[m^2 s^{-3}]$ (e,f). Dissipation rates are related to encounter rate β as given in (Burd & Jackson, 2009). Dashed lines in (b,d,f) indicate log-log slopes of -4.

excess density and sinking speed sets many of the key characteristics of the subsequent flux attenuation curve within the mesopelagic (e.g. remineralization length scale (Cavan et al., 2017) and subsequent sequestration time scales (Boyd et al., 2019)). While we cannot at this time provide argumentation to further constrain the self-similarity parameter, we have put in place a mechanistic model that can guide empirical studies to improve resolution.

²⁶² 5 Conclusions

Much of the literature concerning the fractal dimensions of aggregates has been built 263 on the restrictive assumptions of irreversibity and uniform primary particles (Meakin, 264 1987; Lin et al., 1989) which leads to the rather handy definition that the fractal dimen-265 sion of aggregates a' can be found from their mass-size relationship $m \sim r^{a'}$ (Meakin, 266 1987; Burd & Jackson, 2009). At the same time, aggregates found in the marine envi-267 ronment have been deemed to be fractal objects in that they display fractal type prop-268 erties (Alldredge & Gotschalk, 1989; Logan & Wilkinson, 1990); an increase in poros-269 ity and a decrease in excess density as a function of size for instance. There is however 270 a disconnect between these two concepts, namely that aggregation in the marine envi-271 ronment is not irreversible; aggregates degrade and fragment, and they are not composed 272 of identical primary particles. All manner of primary particles are introduced into the 273 surface ocean by primary producers, sloppy feeding, fecal matter and aeolian dust de-274 posits. Further, the constituent components of detritus vary significantly in excess den-275 sity (relative to seawater $\rho_w = 1027$ kg m⁻³) ranging from positively buoyant e.g. TEP 276 in the range -200 to -300 kg m⁻³ (Azetsu-Scott & Passow, 2004) and lipids around -100277 kg m⁻³ (Visser & Jónasdóttir, 1999) to near neutrally buoyant e.g. cytoplasm 3 to 70 278 kg m⁻³ (Tappan & Loeblich Jr, 1973), to very much negatively buoyant, e.g. coccol-279 iths 1700 to 1900 kg m⁻³ (Toktamis et al., 2016), diatom frustules 1600 kg m⁻³ (Miklasz 280 & Denny, 2010) and atmospheric dust (quartz, feldspar, calcite) approximately 1700 kg 281 m^{-3} . It is no surprise that neither a well constrained fractal dimension nor a size depen-282 dent sinking speed for marine aggregates has been found. 283

More than anything, the poor ability to estimate the sinking speed of marine ag-284 gregates stems from the high variability of their excess density. Other factors, like shape, 285 surface roughness and the through flow of interstitial fluid have been suggested, but at 286 most, contribute a factor 2 to sinking speed corrections. This is negligible compared to 287 the orders of magnitude variance (yet alone a potential change in sign) exhibited in the 288 excess density. The modelling framework we propose is designed specifically to track both 289 size and excess density throughout an emerging aggregate community. We purposefully 290 present the model itself in its simplest form. In this we are mindful that overly complex 291 models become increasingly inscrutable, and unattractive for integration into higher level 292 computational products. There are clearly aspects that can be expanded. For instance 293 resolving aggregate porosity would allow a distinction between dry mass and total mass 294 and provide a more robust implementation of degradation and fragmentation processes. 295 Stickiness is also a parameter that shows large variability in primary material (from TEP 296 to dust). Further, temporal aspects such as annual cycles of productivity, turbulence and 297 mixed layer depth are yet to be explored. Finally, our concept of self-similarity of ag-298 gregation, and a governing parameter a constrained to the range 1.8 to 2.1 is certainly 299 open to scrutiny, particularly given its impact on the emerging flux-size distribution. That 300 there is some systematic control on aggregate size and density is evident in figure 2.b. 301 How this is manifest in particular setting is however highly variable. We argue that in 302 part, this variability can be accounted for through the aggregation process for which we 303 provide a mechanistic description. A large part of the variance remains however, and re-304 flects the vastly different excess densities of the primary material from which the aggre-305 gates derive. Failure to recognize the variability in the density of primary material and 306

how this propagates through an aggregate community confounds efforts to estimate fluxes
 and attenuation length scales of particulate matter in the oceans.

³⁰⁹ 6 Open Research

The model code and associated documentation for the simulations presented here is open source, and freely available on GitHub github.com/AndyWVisser/Aggregation and zenodo.org/record/6731544#.Yra-0HZBxPY. Data sets used in the analysis are available in the supplementary material and accessible at zenodo.org/record/6731670#.Yra9i3ZBxPY.

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319 References

- Alldredge, A. L., & Gotschalk, C. (1988). In situ settling behavior of marine snow.
 Limnology and Oceanography, 33(3), 339–351. doi: 10.4319/lo.1988.33.3.0339
- Alldredge, A. L., & Gotschalk, C. C. (1989). Direct observations of the mass floc culation of diatom blooms: characteristics, settling velocities and formation of
 diatom aggregates. Deep Sea Research Part Ii: Topical Studies in Oceanogra phy, 36, 159–171. doi: 10.1016/0198-0149(89)90131-3
- Alldredge, A. L., Granata, T. C., Gotschalk, C. C., & Dickey, T. D. (1990). The physical strength of marine snow and its implications for particle disaggregation in the ocean. *Limnology and Oceanography*, 35(7), 1415–1428.
- Azetsu-Scott, K., & Johnson, B. D. (1992). Measuring physical characteristics of particles: A new method of simultaneous measurement for size, settling velocity and density of constituent matter. *Deep Sea Research Part A. Oceanographic Research Papers*, 39(6), 1057–1066. doi: 10.1016/ 0198-0149(92)90039-v
- Azetsu-Scott, K., & Passow, U. (2004). Ascending marine particles: Significance of transparent exopolymer particles (TEP) in the upper ocean. *Limnology and oceanography*, 49(3), 741–748.
- Bach, L. T., Stange, P., Taucher, J., Achterberg, E. P., Algueró-Muñiz, M., Horn,
 H., ... Riebesell, U. (2019). The influence of plankton community structure
 on sinking velocity and remineralization rate of marine aggregates. *Global Biogeochemical Cycles*, 33(8), 971–994. doi: 10.1029/2019gb006256
- Banas, N. S. (2011). Adding complex trophic interactions to a size-spectral plank ton model: Emergent diversity patterns and limits on predictability. *Ecological Modelling*, 222(15), 2663-2675. doi: 10.1016/j.ecolmodel.2011.05.018
- Belcher, A., Iversen, M., Giering, S., Riou, V., Henson, S. A., Berline, L., ...
 Sanders, R. (2016). Depth-resolved particle-associated microbial respiration in the northeast Atlantic. *Biogeosciences*, 13(17), 4927–4943. doi:
 10.5194/bg-13-4927-2016
- 348Bopp, L., Le Quéré, C., Heimann, M., Manning, A. C., & Monfray, P.(2002).349Climate-induced oceanic oxygen fluxes: Implications for the contempo-350rary carbon budget.Global Biogeochemical Cycles, 16(2), 6–1.35110.1029/2001gb001445
- Boyd, P. W., Claustre, H., Levy, M., Siegel, D. A., & Weber, T. (2019).
 Multi

 assa
 faceted particle pumps drive carbon sequestration in the ocean.
 Nature,

 assa
 568 (7752), 327. doi: 10.1038/s41586-019-1098-2
 Nature,
- Boyd, P. W., & Newton, P. (1995). Evidence of the potential influence of planktonic

356	community structure on the interannual variability of particulate organic car-							
357	bon flux. Deep Sea Research Part I: Oceanographic Research Papers, $42(5)$,							
358	619–639. doi: 10.1016/0967-0637(95)00017-Z							
359	Briggs, N., Dall'Olmo, G., & Claustre, H. (2020). Major role of particle fragmen-							
360	tation in regulating biological sequestration of CO2 by the oceans. Science,							
361	367(6479),791-793.							
362	Buesseler, K. O., Lamborg, C. H., Boyd, P. W., Lam, P. J., Trull, T. W., Bidigare,							
363	R. R., Wilson, S. (2007). Revisiting carbon flux through the ocean's							
364	twilight zone. Science, 316(5824), 567–70. doi: 10.1126/science.1137959							
365	Burd, A. B., & Jackson, G. A. (2009). Particle aggregation. Annual Review of Ma-							
366	rine Science, 1, 65–90. doi: 10.1146/annurev.marine.010908.163904							
367	Cael, B. B., Bisson, K., Conte, M., Duret, M. T., Follett, C. L., Henson, S. A.,							
368	Lampitt, R. S. (2021). Open ocean particle flux variability from sur-							
369	face to seafloor. Geophysical Research Letters, 48(9), e2021GL092895. doi:							
370	10.1029/2021gl092895							
371	Cael, B. B., Cavan, E. L., & Britten, G. L. (2021). Reconciling the size-dependence							
372	of marine particle sinking speed. <i>Geophysical Research Letters</i> , 48(5),							
373	e2020GL091771. doi: 10.1029/2020gl091771							
374	Carder, K. L., Steward, R. G., & Betzer, P. R. (1982). In situ holographic measure-							
375	ments of the sizes and settling rates of oceanic particulates. Journal of Geo-							
376	physical Research: Oceans, 87(C8), 5681–5685. doi: 10.1029/jc087ic08p05681							
377	Cavan, E. L., & Boyd, P. W. (2018). Effect of anthropogenic warming on microbial							
378	respiration and particulate organic carbon export rates in the sub-Antarctic							
379	Southern Ocean. Aquatic Microbial Ecology, 82(2), 111–127.							
380	Cavan, E. L., Trimmer, M., Shelley, F., & Sanders, R. (2017). Remineralization of							
381	particulate organic carbon in an ocean oxygen minimum zone. Nature Commu-							
382	nications, 8(1), 1-9.							
383	Clift, R., Grace, J. R., & Webber, M. E. (1978). Bubbles, Drops and Particles. San							
384	Diego: Academic Press.							
385	Diercks, AR., & Asper, V. L. (1997). In situ settling speeds of marine snow ag-							
386	gregates below the mixed layer: Black Sea and Gulf of Mexico. Deep Sea Re-							
387	search Part I: Oceanographic Research Papers, 44(3), 385–398. doi: 10.1016/							
388	s0967-0637(96)00104-5							
389	Dilling, L., & Alldredge, A. L. (2000). Fragmentation of marine snow by swimming							
390	macrozooplankton: A new process impacting carbon cycling in the sea. Deep							
391	Sea Research Part I: Oceanographic Research Papers, 47(7), 1227–1245.							
392	Ducklow, H. W., Steinberg, D. K., & Buesseler, K. O. (2001). Upper Ocean Carbon							
393	Export and the Biological Pump. Oceanography, 14(4), 50–58. doi: 10.5670/							
394	oceanog.2001.06							
395	Engel, A., Abramson, L., Szlosek, J., Liu, Z., Stewart, G., Hirschberg, D., & Lee,							
396	C. (2009). Investigating the effect of ballasting by CaCO3 in Emiliania							
397	huxleyi, II: Decomposition of particulate organic matter. Deep Sea Re-							
398	search Part Ii: Topical Studies in Oceanography, 56(18), 1408–1419. doi:							
399	10.1016 / j.dsr 2.2008.11.028							
400	Engel, A., & Schartau, M. (1999). Influence of transparent exopolymer particles							
401	(TEP) on sinking velocity of Nitzschia closterium aggregates. Marine Ecology							
402	Progress Series, 182, 69–76. doi: 10.3354/meps182069							
403	Gibbs, R. J. (1985). Estuarine flocs: their size, settling velocity and den-							
404	sity. Journal of Geophysical Research: Oceans, $90(C2)$, $3249-3251$. doi:							
405	10.1029/jc090ic02p03249							
406	Gooday, A. J. (2002). Biological responses to seasonally varying fluxes of organic							
407	matter to the ocean floor: a review. Journal of Oceanography, $58(2)$, $305-332$.							
408	doi: 10.1023/A:1015865826379							
409	Guidi, L., Jackson, G. A., Stemmann, L., Miquel, J. C., Picheral, M., & Gorsky,							
410	G. (2008). Relationship between particle size distribution and flux in the							

411 412	mesopelagic zone. Deep Sea Research Part I: Oceanographic Research Papers, 55(10), 1364–1374. doi: 10.1016/i.dsr.2008.05.014
413	Guidi, L., Stemmann, L., Jackson, G. A., Ibanez, F., Claustre, H., Legendre, L.,
414	Gorskya, G. (2009). Effects of phytoplankton community on production.
415	size, and export of large aggregates: A world-ocean analysis. Limnology and
416	Oceanoaraphy, 54(6), 1951-1963.
417	Gärdes, A., Iversen, M. H., Grossart, HP., Passow, U., & Ullrich, M. S. (2011).
418	Diatom-associated bacteria are required for aggregation of Thalassiosira weiss-
419	flogii. ISME Journal, 5(3), 436–445. doi: 10.1038/ismej.2010.145
420	Henson, S., Lampitt, R., & Johns, D. (2012). Variability in phytoplankton commu-
421	nity structure in response to the North Atlantic Oscillation and implications
422	for organic carbon flux. Limnology and Oceanography, 57(6), 1591–1601. doi:
423	10.4319/lo.2012.57.6.1591
424	Hill, P. S., Syvitski, J. P., Cowan, E. A., & Powell, R. D. (1998). In situ observa-
425	tions of floc settling velocities in Glacier Bay, Alaska. Marine Geology, 145(1-
426	2), 85–94. doi: 10.1016/s0025-3227(97)00109-6
427	Iversen, M. H., & Lampitt, R. S. (2020). Size does not matter after all: No evidence
428	for a size-sinking relationship for marine snow. Progress in Oceanography, 189,
429	102445. doi: 10.1016/j.pocean.2020.102445
430	Iversen, M. H., Nowald, N., Ploug, H., Jackson, G. A., & Fischer, G. (2010). High
431	resolution profiles of vertical particulate organic matter export off Cape
432	Blanc, Mauritania: Degradation processes and ballasting effects. Deep
433	Sea Research Part I: Oceanographic Research Papers, 57(6), 771–784. doi:
434	10.1016/j.dsr.2010.03.007
435	Iversen, M. H., & Ploug, H. (2010). Ballast minerals and the sinking carbon flux in
436	the ocean: carbon-specific respiration rates and sinking velocity of marine snow
437	aggregates. Biogeosciences, 7(9), 2613–2624. doi: 10.5194/bg-7-2613-2010
438	Iversen, M. H., & Ploug, H. (2013). Temperature effects on carbon-specific respi-
439	ration rate and sinking velocity of diatom aggregates-potential implications
440	for deep ocean export processes. $Biogeosciences, 10(6), 4073-4085.$ doi:
441	10.5194/bg-10-4073-2013
442	Iversen, M. H., & Robert, M. L. (2015). Ballasting effects of smectite on aggregate
443	formation and export from a natural plankton community. Marine Chemistry,
444	175, 18–27. doi: 10.1016/j.marchem.2015.04.009
445	Jackson, G. A. (1998). Using fractal scaling and two-dimensional particle size spec-
446	tra to calculate coagulation rates for heterogeneous systems. Journal of Colloid
447	and Interface Science, 202(1), 20–29. doi: 10.1006/jcis.1998.5435
448	Jackson, G. A. (2015). Coagulation in a rotating cylinder. Limnology and Oceanog-
449	raphy: Methods, 13(4), 194-201.
450	Jackson, G. A., & Burd, A. B. (1998). Aggregation in the marine environ-
451	ment. Environmental Science & Technology, $32(19)$, $2805-2814$. doi:
452	10.1021/es980251w
453	Jokulsdottir, T., & Archer, D. (2016). A stochastic, Lagrangian model of sinking
454	biogenic aggregates in the ocean (SLAMS 1.0): model formulation, valida-
455	tion and sensitivity. Geoscientific Model Development, $9(4)$, 1455–1476. doi:
456	10.5194/gmd-9-1455-2016
457	Jouandet, MP., Trull, T. W., Guidi, L., Picheral, M., Ebersbach, F., Stem-
458	mann, L., & Blain, S. (2011). Optical imaging of mesopelagic particles
459	indicates deep carbon flux beneath a natural iron-fertilized bloom in the
460	Southern Ocean. Limnology and Oceanography, 56(3), 1130–1140. doi:
461	10.4319/lo.2011.56.3.1130
462	Kajihara, M. (1971). Settling velocity and porosity of large suspended particle.
463	Journal of the Oceanographical Society of Japan, 27(4), 158–162. doi: 10.1007/
464	bf02109135
465	Kiørboe, T. (2001). Formation and fate of marine snow: small-scale processes with

466	large-scale implications. Sci Mar, 65, 57–71.
467	Kwon, E. Y., Primeau, F., & Sarmiento, J. L. (2009). The impact of remineraliza-
468	tion depth on the air-sea carbon balance. Nature Geoscience, $2(9)$, 630–635.
469	doi: 10.1038/ngeo612
470	Laurenceau-Cornec, E. C., Trull, T. W., Davies, D. M., De La Rocha, C. L., &
471	Blain, S. (2015). Phytoplankton morphology controls on marine snow sinking
472	velocity. Marine Ecology Progress Series, 520 (Buesseler 1998), 35–56. doi:
473	$10.3354/{ m meps}11116$
474	Laurenceau-Cornec, E. C., Le Moigne, F. A., Gallinari, M., Moriceau, B., Toullec,
475	J., Iversen, M. H., De La Rocha, C. L. (2020). New guidelines for the
476	application of Stokes' models to the sinking velocity of marine aggregates.
477	Limnology and Oceanography, 65(6), 1264–1285. doi: 10.1002/lno.11388
478	Lin, M., Lindsay, H., Weitz, D., Ball, R., Klein, R., & Meakin, P. (1989).
479	Universality in colloid aggregation. Nature, $339(6223)$, $360-362$. doi:
480	10.1038/339360a0
481	Logan, B. E., & Wilkinson, D. B. (1990). Fractal geometry of marine snow and
482	other biological aggregates. Limnology and Oceanography, $35(1)$, 130–136. doi:
483	10.4319/lo.1990.35.1.0130
484	Loth, E. (2008). Drag of non-spherical solid particles of regular and irregular shape.
485	<i>Powder Technology</i> , 182(3), 342–353. doi: 10.1016/j.powtec.2007.06.001
486	Marsay, C. M., Sanders, R. J., Henson, S. A., Pabortsava, K., Achterberg, E. P.,
487	& Lampitt, R. S. (2015). Attenuation of sinking particulate organic carbon
488	flux through the mesopelagic ocean. Proceedings of the National Academy of
489	Sciences, $112(4)$, $1089-1094$. doi: $10.1073/\text{pnas.}1415311112$
490	McDonnell, A. M., & Buesseler, K. O. (2010). Variability in the average sinking ve-
491	focity of marine particles. Limitology and Oceanography, $55(5)$, $2085-2090$. doi: 10.4310/lo.2010.55.5.2085
492	Moslin P (1087) Fractal aggregates Advances in Colloid and Interface Science
493	28 240-331 doi: 10 1016/0001-8686(87)80016-7
494	Miklasz K A & Denny M W (2010) Diatom sinkings speeds: Improved pre-
496	dictions and insight from a modified Stokes' law. Limnology and Oceanography.
497	55(6), 2513-2525.
498	Mouw, C. B., Barnett, A., McKinley, G. A., Gloege, L., & Pilcher, D. (2016). Phyto-
499	plankton size impact on export flux in the global ocean. <i>Global Biogeochemical</i>
500	Cycles, 30(10), 1542-1562. doi: $10.1002/2015$ gb005355
501	Nowald, N., Fischer, G., Ratmeyer, V., Iversen, M., Reuter, C., & Wefer, G. (2009).
502	In-situ sinking speed measurements of marine snow aggregates acquired with
503	a settling chamber mounted to the Cherokee ROV. In (pp. 1–6). IEEE. doi:
504	10.1109/oceanse.2009.5278186
505	Useen, C. W. (1910). Uber die Stokes' sche Formel und Über eine verwandte Auf-
506	gabe in der Hydrodynamik. Arkiv Mat., Astron. Och Fysik, 0, 1.
507	tributions and estimation of size class contributions using a non parametric
508	approach Lowrnal of Coordination of Size class contributions using a non-parametric
509	Sorra Dompoi C. Soudijn F. Vissor A. W. Kigrhoo T. & Anderson K. H.
510	(2020) (2
511	Progress in Ocean ography 189, 102473, doi: 10.1016/j.pocean.2020.102473
512	Sorra Pompoi C Word B A Pinti I Vissor A W Kigrhoo T & Ander
513	sen K H (2022) Linking plankton size spectra and community com-
515	position to carbon export and its efficiency. Global Bioaeochemical Cucles
516	e2021GB007275.
517	Smoluchowski, M. v. (1916). Drei vortrage uber diffusion. brownsche bewegung und
518	koagulation von kolloidteilchen. Zeitschrift fur Physik, 17, 557–585.
519	Stemmann, L., Eloire, D., Sciandra, A., Jackson, G., Guidi, L., Picheral, M., &
520	Gorsky, G. (2008). Volume distribution for particles between 3.5 to 2000 μm

521	in the upper 200 m region of the South Pacific Gyre. $Biogeosciences, 5(2),$
522	299–310.
523	Stokes, G. G. (1851). On the effect of the internal friction of fluids on the motion of
524	pendulums. Transactions of the Cambridge Philosophical Society, $9(8)$.
525	Suess, E. (1980). Particulate organic carbon flux in the oceans—surface productivity
526	and oxygen utilization. <i>Nature</i> , 288(5788), 260–263. doi: 10.1038/288260a0
527	Syvitski, J. P., Asprey, K., & Leblanc, K. (1995). In-situ characteristics of particles
528	settling within a deep-water estuary. Deep Sea Research Part Ii: Topical Stud-
529	ies in Oceanography, $42(1)$, 223–256. doi: 10.1016/0967-0645(95)00013-g
530	Tappan, H., & Loeblich Jr, A. R. (1973). Evolution of the oceanic plankton. Earth-
531	Science Reviews, $9(3)$, 207–240. (Publisher: Elsevier)
532	Toktamış, D., Toktamış, H., & Yazıcı, A. N. (2016). The effects of thermal treat-
533	ments on the thermoluminescence properties of biogenic minerals present in
534	the seashells. Radiation Effects and Defects in Solids, 171 (11-12), 951–964.
535	Tréguer, P., & Jacques, G. (1992). Review Dynamics of nutrients and phytoplank-
536	ton, and fluxes of carbon, nitrogen and silicon in the Antarctic Ocean. In Wed-
537	dell Sea Ecology (pp. 149–162). Springer. doi: 10.1007/978-3-642-77595-6_17
538	Van der Jagt, H., Friese, C., Stuut, J. W., Fischer, G., & Iversen, M. H. (2018).
539	The ballasting effect of Saharan dust deposition on aggregate dynamics and
540	carbon export: Aggregation, settling, and scavenging potential of marine snow.
541	Limnology and Oceanography, 63(3), 1386–1394. doi: 10.1002/lno.10779
542	Visser, A. W., & Jónasdóttir, S. H. (1999). Lipids, buoyancy and the seasonal verti-
543	cal migration of Calanus finmarchicus. Fisheries Oceanography, 8, 100–106.
544	White, F. M. (1991). Viscous Fluid Flow. New York, NY: McGraw-Hill.
545	Wiesner, M. R. (1992). Kinetics of aggregate formation in rapid mix. Water Re-

search, 26(3), 379–387. doi: 10.1016/0043-1354(92)90035-3

546

Table 1. Estimated exponent $b \pm s$ for excess density vrs aggregate size power law where s is the 95% confidence interval. Δ_r is the $\log_{10} r$ range of aggregate size, and n the number of observations. References as given, and indicate field or lab studies.

b	$\pm s$	Δ_r	n		reference	
-0.38	1.21	0.5	14		(Alldredge & Gotschalk, 1989)	Field
-1.49	0.15	1.9	76		(Alldredge & Gotschalk, 1988)	Field
-2.09	1.22	0.5	13	i	(Azetsu-Scott & Johnson, 1992)	Field
-1.09	1.88	0.4	15	ii	_''_	Lab
-0.72	0.20	0.8	37		(Iversen et al., 2010)	Field
-0.83	0.55	0.9	104		(Belcher et al., 2016)	Field
-1.11	0.94	0.8	10		(Carder et al., 1982)	Field
-2.18	0.28	1.0	332		(Diercks & Asper, 1997)	Field
-1.07	0.09	1.2	294		(Engel & Schartau, 1999)	Lab
-1.21	0.05	1.1	20		(Gibbs, 1985)	Field
-1.46	0.05	1.6	1224		Chase 1979	Field
-1.13	0.14	1.1	63	i	(Iversen & Ploug, 2010)	Lab
-1.20	0.12	0.8	26	ii	_''_	Lab
-1.01	0.20	0.5	97	iii	_''_	Lab
-0.46	0.30	0.5	99		(Hill et al., 1998)	Field
-0.51	0.23	0.9	187		(Iversen & Ploug, 2013)	Lab
-1.34	0.26	1.1	153		(Iversen & Robert, 2015)	Lab
-1.37	0.20	1.4	54		(Kajihara, 1971)	Field
-2.12	0.59	0.8	61	i	(Laurenceau-Cornec et al., 2015)	Field
-1.24	0.21	0.8	59	ii	_''_	Lab
-1.24	0.21	0.8	72	i	(Laurenceau-Cornec et al., 2020)	Lab
-0.35	0.19	0.7	131	ii	_''_	Lab
-1.53	0.12	1.2	274	i	(Engel et al., 2009)	Lab
-1.07	0.09	1.2	249	ii	_''_	Lab
-0.74	0.14	1.2	296	iii	_''_	Field
-1.53	0.70	0.9	49		(Nowald et al., 2009)	Field
-1.22	0.12	1.7	149		(Syvitski et al., 1995)	Field
-0.95	0.37	1.3	57	i	(Van der Jagt et al., 2018)	Field
-2.01	0.30	1.2	85	ii	_''_	Field
-0.88	0.23	1.9	36		(Guidi et al., 2008)	Field
-1.65	0.26	1.7	41		(McDonnell & Buesseler, 2010)	Field
-2.24	0.78	1.0	28		(Jouandet et al., 2011 $)$	Field
-1.59	0.02	1.2	1654		(Bach et al., 2019)	Field
-0.11	0.25	0.7	36		$(G\ddot{a}rdes et al., 2011)$	Lab
-1.74	0.27	1.4	154		(Iversen & Lampitt, 2020)	Field
-1.38	0.02	4.0	6332		All data points	-