In situ Particle Measurements Deemphasize the Role of Size in Governing Particle Sinking Velocity

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Key Points:

- An extensive literature review on particles' sinking velocity and associated particle characteristics was carried out.
- Ex-situ studies typically find size to be a strong predictor of sinking velocity; strong correlations are rarely observed in situ however.
- Results suggest importance of additional factors in predicting particle sinking velocities and fluxes from size-scaling relationships.

Abstract

Sinking particles are important in delivering carbon to the deep ocean where it may be stored out of contact with the atmosphere. Particle sinking velocity strongly influences the amount of carbon reaching the deep ocean, and is thought to be strongly affected by particle size. Here we carried out an extensive literature review (62 datasets) into the size-sinking velocity relationship, and find the relationship is much weaker for studies examining particles in situ (median $R^2 = 0.03$) compared with ex situ studies (median $R^2 = 0.35$). This may be because particles examined in the laboratory have more uniform properties than those studied in situ, and represent only a subset of particles from the natural environment. Our findings suggest a simple relationship between size and sinking velocity may be insufficient when calculating sinking particulate fluxes in the ocean; considering different particle types individually will enable more accurate calculations of particulate fluxes.

1 Introduction

In the ocean, the production, transfer to depth, and remineralization of organic particles provide a major pathway for the export of carbon from the ocean's surface to the ocean interior (Laurenceau-Cornec et al., 2015; Sanders et al., 2016). Collectively termed the Biological Carbon Pump (BCP), these processes act to maintain atmospheric CO_2 approximately 200 ppm lower than they would otherwise be (Maier-Reimer et al., 1996; Parekh et al., 2006). Although several processes contribute to the BCP, the gravitational settling of organic particles are thought to result in ~1000 Pg of ocean carbon storage (Boyd et al., 2019), contributing the majority of carbon sequestered by the BCP (Boyd et al., 2019; Buesseler et al., 2020).

As particulate organic carbon (POC) sinks, proportions of this downward flux are reworked by metazoans, such as zooplankton, and eventually remineralised back into CO_2, predominantly through microbial respiration (Giering et al., 2014). As a result of this particle remineralisation and reworking, sinking POC fluxes are observed to be attenuated with depth. The rate of flux attenuation (and hence the proportion of sinking carbon reaching the deep ocean) is determined by the balance between particle sinking velocities and remineralisation rates (Bach et al., 2019; Marsay et al., 2015). Since particle sinking velocities determine the length of time in which a particle is exposed to metazoan and microbial remineralisation, sinking velocity is a crucial determinant in the degree of attenuation of POC fluxes and BCP efficiency (Laurenceau-Cornec et al., 2015) (Fig. 1).

In recent years, the use of in situ optical methods has emerged as an important tool in the study of the BCP (Giering, Cavan, et al., 2020). Increasingly able to be deployed autonomously (Lombard et al., 2019; Picheral et al., 2022), these methods can provide far greater spatiotemporal resolution and coverage than traditional ship-based sampling methods (Giering, Cavan, et al., 2020; Lombard et al., 2019). Using the particle concentrations obtained by in situ imaging methods, particle fluxes within a given size class can be calculated if sinking velocities of particles within the size class can also be estimated (Guidi et al., 2008; McDonnell & Buesseler, 2010). A robust understanding of the factors that govern particle sinking rate is crucial in the implementation of these cutting-edge methods, for estimating particulate fluxes and studying the BCP.

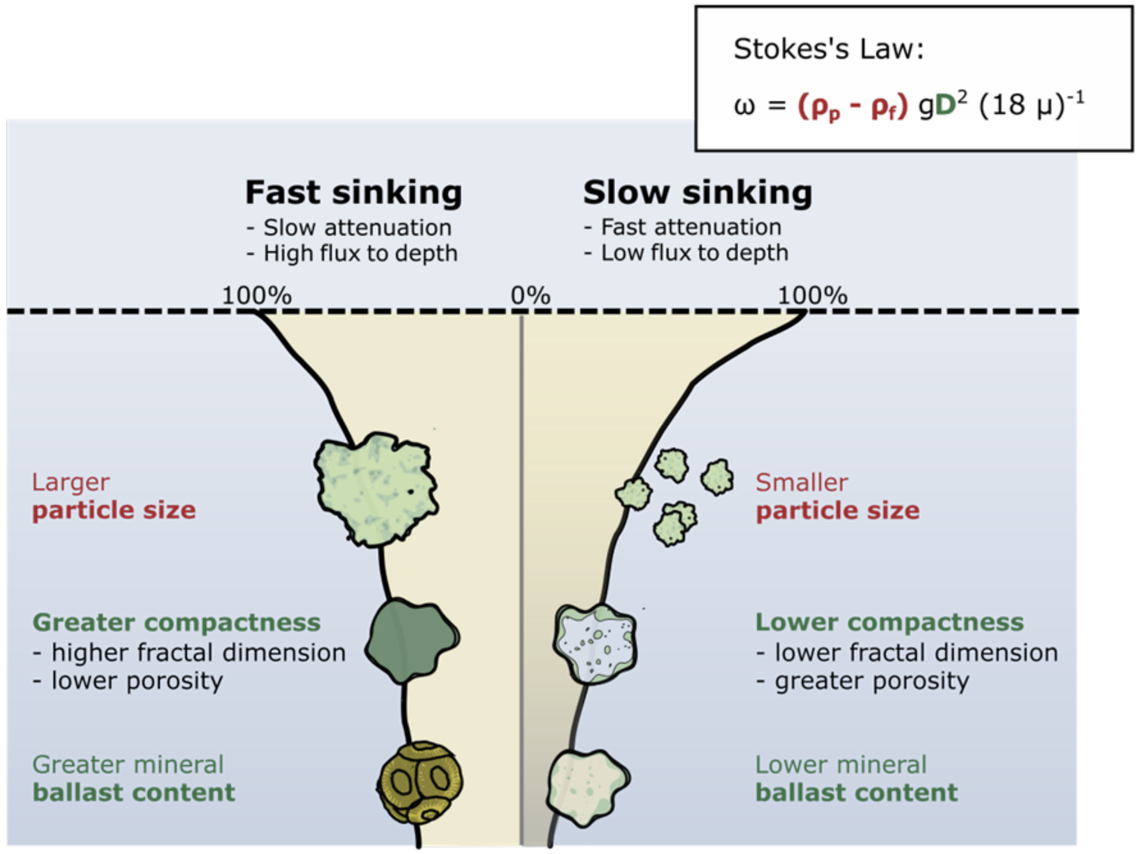


Figure 1: Schematic illustrating factors posed to influence particle sinking velocity, their relation to size (red) or density (green) as described in Stokes's law, and the effect of fast and slow sinking particles on particulate flux attenuation rates and particles fluxes reaching depth. Particles begin sinking from below the mixed layer and are attenuated as they sink. Illustrative flux attenuation curved are shown for fast sinking (left) and slow sinking (right) particles. Fast sinking particles experience slower rates of flux attenuation due to decreased duration of exposure to remineralisation whilst they sink.

To date, particle size has been identified by theory and some empirical studies to be a major determinant of particle sinking velocity (Alldredge & Gotschalk, 1988; Iversen et al., 2010; Laurenceau-Cornec et al., 2015). Considering size as a key predictor of sinking velocity assumes relative constancy of other particle properties such as particle composition, porosity and biomineral content. In recent years, however, empirical studies have called into question this assumption (Iversen & Ploug, 2010; Laurenceau-Cornec et al., 2020; Ploug et al., 2008) and the degree to which size alone constrains sinking velocity (Diercks & Asper, 1997; Iversen & Lampitt, 2020).

Here we review the extent to which empirical evidence supports the hypothesis of size as the main determinant of sinking velocity, and assess the reasons for differences between studies. We recommend avenues for further study that will facilitate improved understanding and modelling of particle sinking velocities and of the BCP.

1. 1.1 A widely held view: size does matter

In recent decades, derivations such as Stokes's law have been widely used to estimate particle sinking velocity (Laurenceau-Cornec et al., 2020; Miklasz & Denny, 2010):

$w = \left(\rho_p - \rho_f\right) \frac{gd^2}{18\mu}$ (2)

where w is the sinking velocity of a sphere (m s^{-1}), $_s$ and $_f$ are the sphere and fluid densities (kg m^{-3}), g is the acceleration due to gravity (9.81 m s^{-2}), d is the sphere diameter (m) ,and is the fluid dynamic viscosity in kg $m^{-1}s^{-1}$. Through balancing the drag and gravitational forces acting on a sinking particle at terminal velocity, these derivations pose size to be a key determinant of sinking velocity. This idea has been represented in various size-dependent parameterizations of particle sinking velocity in biogeochemical models (de La Rocha & Passow, 2007; Kriest & Oschlies, 2008; Laurenceau-Cornec et al., 2015; Tjiputra et al., 2020), and in landmark papers using size spectra to compute particulate fluxes (Guidi et al., 2008; Jouandet et al., 2011; McDonnell & Buesseler, 2010).

When deriving mass fluxes from particle size spectra, total mass flux may be calculated through combining measured number size spectra with estimates of sinking velocity (w) and mass (m) of individual particles. Since both w and m can be expressed as power law functions (of the form ($y = ax^b$), their product is expressed in the same form:

$wm = \ Ad^B$ (3)

where d is particle diameter, and A and B are constants. Hence if A and B are known, size spectra can be used to calculate total mass fluxes. A and B may be estimated through a minimisation procedure (Guidi et al., 2008; Iversen et al., 2010; Nowald et al., 2015) if alternative measurements of particulate fluxes can be made, and assuming that mass and particle size as a function of depth are constant for all depths (Iversen et al., 2010). Alternatively, when additional flux measurements have not been made (such as on autonomous deployments), global estimates of A and B from prior studies can be used (Iversen et al., 2010; Ramondenc et al., 2016). This latter approach assumes that particle mass and sinking velocity as functions of size are universally constant; an assumption which has been called into question by Iversen et al. (2010). Applying global estimates of A and B may lead to flux estimates a factor of 10 out from measured in situ values, on account of variations in particle composition (Iversen et al., 2010). Variability in the composition of particles (Iversen et al., 2010), as well as source, density, and age of particles (Ploug et al., 2008) have all been posed to influence size-dependent scaling relationships of sinking velocity.

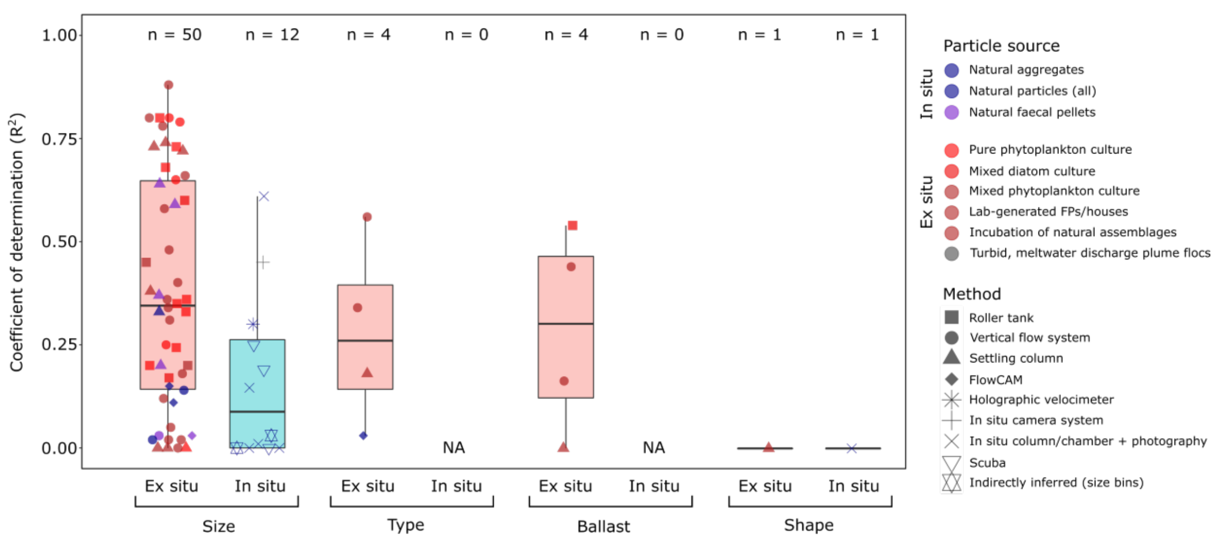
2 Empirical evidence on the size-sinking velocity relationship

To identify the most commonly studied particle characteristics, we carried out a literature search into studies measuring particle sinking velocity and associated particle characteristics. Restricting results to within Earth and Planetary Sciences, we searched for abstracts, titles, and keywords containing the words "Particle" and "Sinking" and "Velocity", as well as a given particle characteristic ("Size", "Ballast", "Morphology", "Composition", "Type", "Shape", "Compactness", "Fractal" [Dimension]). Size returned the greatest number of studies (79), followed by parameters relating to chemical and taxonomic composition (Composition: 37; Type: 22; Ballast: 18). Searches relating to other morphological properties typically returned the fewest results ("Shape": 17; "Fractal" [Dimension]: 5; "Compactness": 1; "Permeability": 1; "Morphology": 1).

2. Using the four most commonly studied particle attributes from our literature search (size, particle type, ballast, and shape) we examined the degree of correlation between sinking velocity and each of the above attributes (Fig. 2). A full description of methods is provided in the *Methods* section. Briefly, to assess the degree of variation in sinking velocity explained by a particle size in each study, a power law function was fitted to the data, and R^2 (proportion of variance in sinking velocity explained by size) of this power law function recorded. For particle type, ballast, and shape, R^2 were recorded from linear regressions for continuous particle characteristics, or from analyses of variance (ANOVAs) for categorical data.

   Despite particle size having received the most interest, our review suggests the dependency of sinking velocity on size is not well constrained (Fig. 2). Size explains between 0-88% in the variation in particle sinking velocity (as determined by the coefficient of determination 'R^2') with a median value of 31%. The strongest correlation between size and sinking velocity was observed for intact salp faecal pellets from the Southern Ocean (Iversen et al., 2017). However, in more than a quarter (16 of 62 datasets), particle size was observed to be a poor predictor of sinking velocity, explaining less than 10% of variation in particle sinking velocity (Fig. 2).
   Particle size did not appear to be a stronger predictor of sinking velocity than particle type or particle ballast content (Wilcoxon rank tests, $p > 0.8$). The median percentage of variance in sinking velocity explained by particle type and ballast content were 26% and 30% respectively. It is noteworthy however that only four ex situ datasets examined the influence of particle type or ballast content. Likewise for particle shape, only one ex situ and one in situ study directly measured a particle shape characteristic (aspect ratio) and sinking velocity, with neither of these studies finding sinking velocity to be explained by particle shape alone.

For the datasets focussing on particle size as a predictor, we found strong differences between measuremends made in situ and ex situ. R^2 values were significantly higher for ex situ studies than in situ studies (Wilcoxon rank test, $p < 0.01$), suggesting that the strength of the size-sinking velocity relationship may be influenced by experimental type. While weak correlations between size and sinking velocity were observed in both situ and ex situ datasets, strong dependencies of sinking velocity on particle size were only observed ex situ. For in situ datsets (n = 12), size explained less than 30% of variability in sinking velocity in all but two studies which respectively examined flocs from meltwater discharge plumes and resuspended near-bottom sediment. For in situ particles, the median percentage of variance in sinking velocity explained by particle size was 3%, contrasting with 35% for particles measured ex situ. Overall these findings suggest that the strong relationships observed ex situ between individual particle characteristics and sinking velocity may not always hold true in situ. As such, the methodological biases outlined below should be taken into consideration before extrapolating relationships observed in ex situ studies to natural marine particles in situ.



5. Figure 2: Boxplot comparing proportion of variance in sinking velocity explained by particle characteristics. Coefficients of determination (R^2) from linear models and analyses of variance (ANOVAs) performed between particle characteristics (size, type, ballast content, shape) and sinking velocities directly measured in previous studies (see text, Supplementary Table S1). Colours of boxplots indicate whether sinking velocity measurements were made in situ (blue) or ex situ (red). Colours of individual points illustrate whether particles were generated ex situ (red colours, cultured or incubated ex situ prior to measurement) or in situ (blue colours, nat-

ural particles observed in situ or measured immediately ex situ without prior incubation). In a small number of cases, natural particles were collected and sinking velocity measured without incubation- these particles are therefore represented as blue points on red boxplots. Shapes indicate method used to measure sinking velocity.

2.1 Ex situ vs in situ: methodological compromises

Most studies into factors constraining sinking velocity involve incubating particles ex situ prior to or during measurements, as this allows the study of a greater number of particle characteristics. By examining particles in a laboratory, detailed measurements of a wide number of particle characteristics can be made, such as fractal dimension, chemical and taxonomic composition, removing the need for estimates of these parameters (Francis & Passow, 2020; Mantovanelli & Ridd, 2006). In addition, studies where particles are generated ex situ also allow for manipulation of particles to test for targeted interactions and effects on sinking velocities (Giering, Cavan et al. 2020).

However, particle dynamics observed ex situ in laboratory studies may not be representative of relationships in the natural environment. Firstly, the highly fragile nature of marine aggregates mean that they are susceptible to damage, alteration, and disaggregation during sampling for ex situ incubations (Giering, Cavan, et al., 2020; Iversen & Lampitt, 2020; Kajihara, 1971). Secondly, particles cultured ex situ are often formed from homogenous particle pools, such as phytoplankton cultures, whilst in the natural environment a heterogenous pool of particles of varied age, composition, density, structure, and porosity exists (Iversen & Lampitt, 2020). As a result, the strong size-sinking velocity relationships observed within homogenous particle pools ex situ (Iversen et al., 2010; Iversen & Ploug, 2010, 2013) is unlikely to be representative of the real ocean. According to a modelling study of Cael *et al.* (2021), uncertainties in the scaling of the size-sinking velocity relationship have also been observed to be greater for in situ than ex situ studies. While this result could be attributed to a larger sample size for particles measured ex situ, this result could also suggest a more homogenous relationship between size and sinking velocity in ex situ studies (Cael, pers. comms). Hence overall, ex situ studies sacrifice some particle realism for the ability to measure and examine particle dynamics in detail (Fig. 3).

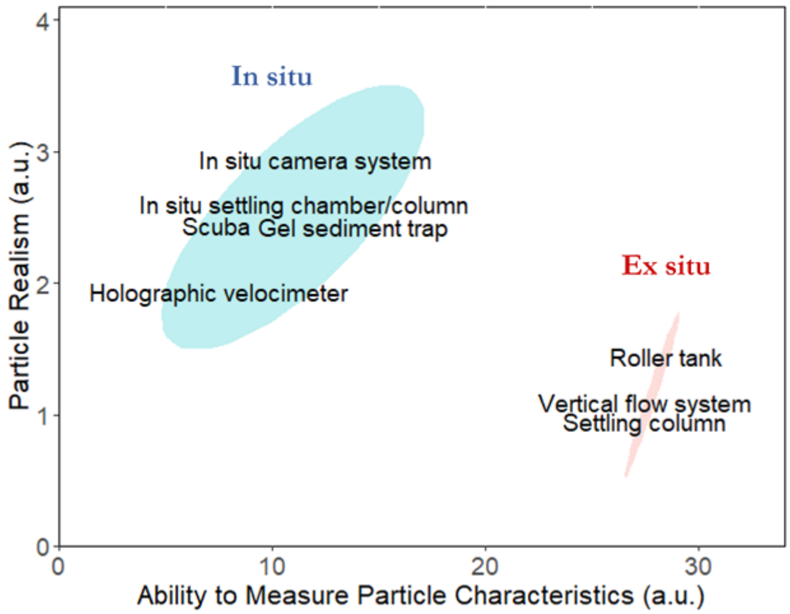


Figure 3: Relative advantages of in situ and ex situ methods (blue and red respectively) in terms of ability to measure particle characteristics and particle realism, when investigating the relationship between particle sinking velocity and particle characteristics. Position of each method relates to an assigned "Particle Realism score" and "Measurement Capability score" as described in *4.3 Methodological Comparisons*; explanations of assertions used for scoring these methods available in Supplementary Table S2.

In situ methods hold the major advantage of observing particles in their natural environment. Any measurements made are therefore acquired without the need for handling particles, decreasing (but not eliminating (Briggs et al., 2011; Cetinić et al., 2012)) the potential alteration and disturbance to particle properties (Giering, Cavan, et al., 2020; Iversen & Lampitt, 2020), and thus maximising the realism of any interactions between sinking velocity and particle characteristics. However, a major drawback of in situ optical devices is that these methods lack the capability to measure provide direct information on a number of particle characteristics, such as particle density and stoichiometry (Giering, Hosking, et al., 2020). These methods must hence rely on additional data or assumptions to estimate particle sinking velocities and calculate particulate fluxes. Given these uncertainties, the expensive nature of in situ camera systems, and a lack of standardization in analysis routines for in situ imge datasets (Giering, Hosking, et al., 2020), in situ studies into particle sinking velocities remain sparse compared with more traditional ex situ methods. In summary, in situ studies thus lack the capacity to study some particle characteristics which may be measured ex situ, but maximise realism when studying particle characteristics and properties.

3 Implications for utilizing novel in situ methods

The lack of agreement in the strength of size-sinking velocity relationships between in situ and ex situ studies has immediate implications for the application of size spectra in generating particulate fluxes. If size is held to be a strong predictor of sinking velocity as a single factor, as suggested by some ex situ studies, relative constancy of additional factors may be assumed. In this case, applying a consistent scaling relationship using previously published global value forms a useful method to calculate particulate fluxes. Such methods have been used previously on cruises and autonomous platforms (Guidi et al., 2008, 2009; Picheral *et al.,* 2022; Ramondenc et al., 2016) and have the advantage of high spatial and vertical resolution.
However, here we have found the strong particle size-sinking velocity relationships often observed ex situ rarely apply to in situ particles, suggesting variability in other particle characteristics in situ may reduce the applicability of size as a sole predictor of sinking velocity. Such heterogeneity of particles in situ would violate the assumption of constancy in other particle characteristics upon which the use of global size-scaling relationships depend. To overcome this uncertainty, one solution can come from improving optical camera system and methods used for in situ studies. Methods that can distinguish between particle types will allow for differential size-sinking scaling between particle types (Iversen & Lampitt, 2020), with machine learning likely to expedite this process (Giering, Cavan, et al., 2020). When considering individual particle types, particles often exhibit clear size-sinking velocity relationships, such as we have have noted here from previous works using salp faecal pellets (Iversen *et al.,* 2017) and pure phytoplankton cultures (Iversen & Ploug, 2010, 2013). Recognising individual size-scaling relationships for varying particle types will enable more accurate sinking velocity and flux estimates for particle groups, allowing a choice of values used in size-scaling relationships. As a result, being able to distinguish between size-scaling relationships for particle types will increase accuracy of flux measurements in a varied ecological and biogeochemical settlings. Focusing scientific effort on developing these methods will not only facilitate improved mechanistic understanding of particle sinking and the BCP, but also promote increased spatio-temporal resolution of methods through the use of autonomous platforms.

4 Methods

4.1 Data compilation

We compiled observations of particle sinking velocity and associated particle characteristics from 62 datasets from 38 studies (see Supplementary Table S1) . These data had previously been compiled by Cael et al. (2021) and Laurenceau-Cornec et al. (2015, 2020); all original datasets were validated and, if needed, redigitized using Plot Digitizer (https://automeris.io/WebPlotDigitizer/). Studies not relating to marine particles were excluded from this analysis. In the small number of cases where size particle size and sinking velocity data had been fitted to a power law function in original studies (n = 10), published R^2 values in the literature were used. Data were assigned to "in situ" and "ex situ" groups for measurement type, based on the method used to measure sinking velocity in each study. The particle types examined in each study were assigned to one of nine particle types (e.g., natural aggregates, mixed diatom culture; for full list Fig. 2, Supplementary Table S1), with method used to measure particle sinking velocities also described through one of nine groups (e.g., Scuba photography, Vertical flow system; for full list see legend of Fig. 2, Supplementary Table S1).

4.2 Sinking velocity/Particle characteristic analyses

To assess the variability in sinking velocity explained by a particle size in each study, a power law function (in form $w = Ad^B$, where w is the sinking velocity, d the diameter, and A and B are scaling coefficients) was fitted to the data. A power law was chosen over a linear regression since sinking velocity is thought to scale with particle diameter according to a power law function according to Stokes's Law and empirically modified version incorporating porosity (Guidi *et al.,* 2008; Laurenceau-Cornec *et al.,* 2020; Xiang *et al.,* 2022).

For particle type, ballast, and shape, R^2 were recorded either from performing linear regressions or analyses of variance (ANOVAs), depending on whether the particle characteristic was described in terms of continuous or categorical data. For example, in some studies particle type was analysed as a categorical variable with discrete groups such as *S. costatum* or *E. huxleyi* aggregates, and sinking velocity was compared between these groups by means of an ANOVA. In another study, particle type was expressed as a percentage of aggregate composition of one diatom morphotype. In this case, a linear regression was performed between percentage of total composition and particle sinking velocity. Lastly, having failed both Levene's and Shapiro Wilk tests, a Wilcoxon rank sum test with continuity correction was performed to assess whether R^2 coefficients differed significantly between in situ and ex situ studies.

4.3 Methodological comparison

To represent the advantages and disadvantages of in situ and ex situ methods for sinking velocity measurement, methods were ranked in terms of their ability to measure particle characteristics, and in terms of particle realism. Although these assertions are subjective rankings, a scoring system was devised to standardise rankings and criteria by which methods were judged. For measurement capability score, particle characteristics (Size, Ballast, Taxonomic composition/Particle type, Chemical composition, Shape, Dry weight, Porosity, Fractal dimension, Density, and Sinking velocity) were assigned a score from 0 to 4, describing the comprehensiveness with which a particle characteristic could be studied with a given method (0 lowest, 4 highest; see Supplementary Table S2). Measurement capability scores of individual characteristics were summed to give an overall score. Where a range of measurement score was given for a particle characteristic, the mean value was used when summing scores to calculate (e.g. 2-3 scored as 2.5).

For the particle realism score, each method was assigned a score from 0 to

4, based on the extent to which the particles measured had been influenced by sampling and measurement procedures, i.e. the extent to which particle communities measured could be expected to reflect natural marine particle communities in situ. A brief explanation for assigned scores and evidence supporting these assertions are outlined in Supplementary Table S2).

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Open Research

All data will be archived on a public repository such as Zenodo and/or Pangaea following revisions and prior to resubmission should this manuscript be accepted for publication. The data are also available via the supporting information.

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