

Respiration rate scales inversely with sinking speed of settling marine aggregates
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Key points

- The average respiration rate for fast-sinking marine particles was 0.12 d^{-1}
- Slow-sinking particles decomposed quicker than fast-sinking particles
- Fast-sinking particles could be more important for transport of carbon to the deep ocean than previously thought

Abstract. Sinking marine particles have been studied for a long time to understand its role in carbon sequestration. Traditionally, sinking speed and respiration rates have been treated as independent variables, but two recent papers suggest a connection albeit in contrasting directions. Alcolombri et al. [2021] demonstrated that slow moving particles are respired faster than motionless particles, whereas García-Martín et al. [2021] found that respiration rate was higher for suspended particles compared with slow- and fast-sinking particles. Here we collected settling aggregates and determined respiration rates of particles sinking at different velocities. The average respiration rate of fast sinking particles ($>100 \text{ m d}^{-1}$) was 0.12 d^{-1} . Slower sinking particles ($<50 \text{ m d}^{-1}$) had on average higher and more variable respiration rates. These findings provide insights into the efficiency of the biological carbon pump and help resolve the apparent discrepancy in the recent studies of the correlation between respiration and sinking speed.

Alcolombri, U., F. J. Peaudecerf, V. I. Fernandez, L. Behrendt, K. S. Lee, and R. Stocker (2021), Sinking enhances the degradation of organic particles by marine bacteria, *Nat Geosci*, 1-6.

García-Martín, E. E., K. Davidson, C. Davis, C. Mahaffey, S. McNeill, D. Purdie, and C. Robinson (2021), Low contribution of the fast-sinking particle fraction to total plankton metabolism in a temperate shelf sea, *Glob Biogeochem Cycles*, 35(9), e2021GB007015.

Plain language summary

Scientists have for a long time tried to quantify the sinking of marine particles because the carbon they contain is removed from the atmosphere if they sink

below 1000-meter depth. The amount of carbon, the sinking speed, how quickly it decomposes and how deep it reaches, all affect this removal of CO₂ from the atmosphere. The sinking speed and decomposition have often been treated as independent variables, but recently two papers suggested there is a connection, but with contradicting results. Our results show that slow sinking particles decompose quicker than fast sinking particles. Consequently, fast sinking particles could be more important for transport of carbon to the deep ocean than previously thought.

Main text

Sinking marine particles have different characteristics, some are compact and sink quickly whereas others consist of more loosely packed material with lower sinking velocity. While sinking, bacteria decompose organic matter, detritivorous zooplankton fragments aggregates and bacterial grazers impose top-down control on remineralization rates [Kjørboe *et al.*, 2003; Mayor *et al.*, 2014]. How much carbon is transported to the deep ocean depends on both the sinking speed and the biological processes connected to the aggregates while sinking.

Traditionally, sinking speed and respiration rates have been treated as independent variables [e.g. Iversen and Ploug, 2010; Omand *et al.*, 2020]. Experimental studies using phytoplankton cultures in roller tanks have indicated that the content of ballasting minerals affects sinking speed whereas respiration rate is approximately 0.1 d⁻¹ [e.g. Iversen and Ploug, 2010]. However, two recent papers demonstrated that sinking speed affects respiration rates – in contrasting directions. On the one hand, Alcolombri *et al.* [2021] demonstrated that slowly moving particles (up to ~40 m d⁻¹) are respired faster than barely moving (1-2 m d⁻¹) or motionless particles, and attributed this to oligomeric breakdown products being more rapidly flushed away at higher flow rates. On the other hand, García-Martín *et al.* [2021] found that respiration rate and bacterial production was higher in the suspended particle fraction (assumed to be non-sinking) than in the slow- and fast-sinking fractions (sinking speeds of <24 and >24 m d⁻¹).

Here we collected material from the sediment traps mounted at the bottom of mesocosm bags during two different mesocosm experiments (2018 and 2021) off the coast of Gran Canaria, Spain. The sediment was divided into slow, medium speed, and fast sinking particles using a settling tube. In 2018, this speed division was <10 m d⁻¹, 10 – 100 m d⁻¹ and >100 m d⁻¹; in 2021, it was changed to <50 m d⁻¹, 50-130 m d⁻¹ and >130 m d⁻¹ for slow, medium speed and fast, respectively. This was done to have a more even distribution of the settling material, as low sediment amounts led to missing respiration data from some sinking fractions in 2018. The different fractions were dark-incubated in glass bottles mounted on a rotating wheel (1 rpm) for 24-36 h, and respiration rate was determined from oxygen measurements using a non-invasive, optical O₂-meter. In 2018, the experimental setup was an artificial upwelling simulation via addition of nutrient-rich deep water [Baumann *et al.*, 2021], whereas in 2021, the mesocosms were not fertilized but had a gradient in alkalinity. More details on the methodology can be found in the supplementary material.

The respiration rate clearly varied with sinking speed (Fig 1). The average (\pm SE) respiration rates for both years were $0.42 \text{ d}^{-1} \pm 0.06 \text{ d}^{-1}$, $0.24 \text{ d}^{-1} \pm 0.04 \text{ d}^{-1}$ and $0.12 \text{ d}^{-1} \pm 0.02 \text{ d}^{-1}$ in the slow, medium speed and fast sinking fraction, respectively, and clearly differed between fractions (Dunn’s test $p < 0.01$; Supplementary Table S1). Dividing up into the individual years, there was no difference between medium speed and fast sinking fractions in 2018 (Dunn $p = 0.29$), whereas in 2021 there was no difference between the slow and medium speed (Dunn $p = 0.79$). The variability in respiration rate was higher in the slow compared with the fast-sinking fraction.

There are different characteristics of sinking particles that make them sink and decompose at different rates. The contrasting results of *García-Martín et al.* [2021] and *Alcolombri et al.* [2021] for slow-sinking particles ($0\text{--}40 \text{ m d}^{-1}$) may depend on the way the measurements were carried out. *Alcolombri et al.* [2021] used uniform particles made from agar placed in a flow cuvette, whereas *García-Martín et al.* [2021] collected natural sinking material with a marine snow catcher, and the collected material was subsequently differentiated into different sinking fractions. Here we took a similar approach as the latter but collected naturally settling particles inside mesocosms.

Our results supported *García-Martín et al.* [2021] in that slow, and in 2021 also medium speed, sinking particles had higher respiration rates than fast sinking particles. The increase in respiration with increasing sinking speed observed by *Alcolombri et al.* [2021] was already saturated at 8 m d^{-1} , which would not have been picked up with our setup as the slow sinking fraction contained particles exceeding this speed. There are *in situ* measurements providing support for the inverse relationship between respiration rate and sinking speed; aggregates in an oligotrophic (Bermuda) location had slower average sinking speed (49 m d^{-1}) but higher respiration rates (0.4 d^{-1}) compared to a mesotrophic site (Western Antarctic Peninsula; average sinking speed 270 m d^{-1} and respiration rate 0.01 d^{-1}) [*McDonnell et al.*, 2015]. The warmer waters in Bermuda compared to Antarctic waters was not sufficient to explain the full magnitude of the difference in respiration between these two sites [*McDonnell et al.*, 2015], and our results suggest that different sinking speed could partly explain the difference in respiration rate between these two sites. It is likely not only sinking speed *per se* that affects respiration of marine aggregates, rather properties that affect sinking speed also affect the respiration rate.

The sinking particles in 2018 were characterized by different particle porosities affecting the sinking speed [*Baumann et al.*, 2021]. Slower sinking particles tended to have a higher porosity, which implies a higher surface to volume ratio and consequently a larger settlement area for bacteria. Hence, the porosity could affect both the sinking speed and the respiration rate. In addition, the slower sinking aggregates in 2018 tended to be smaller. Given a certain porosity, a smaller aggregate diameter also implies a higher surface to volume ratio, consistent with higher respiration rates. The hydrodynamics around a sinking particle, which is affected by speed and shape, controls the initial colonization

by bacteria [Secchi *et al.*, 2020]. A positive correlation between water flow and respiration rate caused by removal of degradation products [Alcolombri *et al.*, 2021] could be overridden by other factors such as surface structure. The higher variability in respiration rate in the slow sinking particles could be due to a more variable particle composition than fast sinking particles, which are likely more compact, but could still vary in composition [Laurenceau-Cornec *et al.*, 2020]. Interestingly, the average respiration rate in the fast-sinking particles was similar to what has been obtained from experimental aggregate formation [Iversen and Ploug, 2010], perhaps an indication that suspended and slow sinking particles are harder to produce in roller tanks.

Here we demonstrated that respiration scales inversely with sinking speed. This suggests that fast sinking particles can be more important for the biological carbon pump than hitherto assumed. There was much higher variability in the respiration rate for slow compared to fast sinking particles. The mechanisms behind this variability should be further resolved to better understand the mechanistic drivers of the biological carbon pump in ocean models. The biological conditions producing the material (e.g. community composition, and biomass) and its porosity regulating sinking speed, likely affected the variability of decomposition rates [Bach *et al.*, 2019]. This information could be used to expand *in situ* imaging technologies to make predictions of carbon fluxes in different ecosystems [Clements *et al.*, 2022].

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Figure caption

Fig 1 Respiration rate measured for the three different sinking fractions in 2018 and 2021. In 2018, this speed division was $<10 \text{ m d}^{-1}$, $10 - 100 \text{ m d}^{-1}$ and $>100 \text{ m d}^{-1}$; in 2021 it was changed to $<50 \text{ m d}^{-1}$, $50-130 \text{ m d}^{-1}$ and $>130 \text{ m d}^{-1}$ for slow, medium speed and fast, respectively. The box outlines the 25-75 percentile, the mid-line is the median, and the whiskers are the 10 and 90 percentiles.

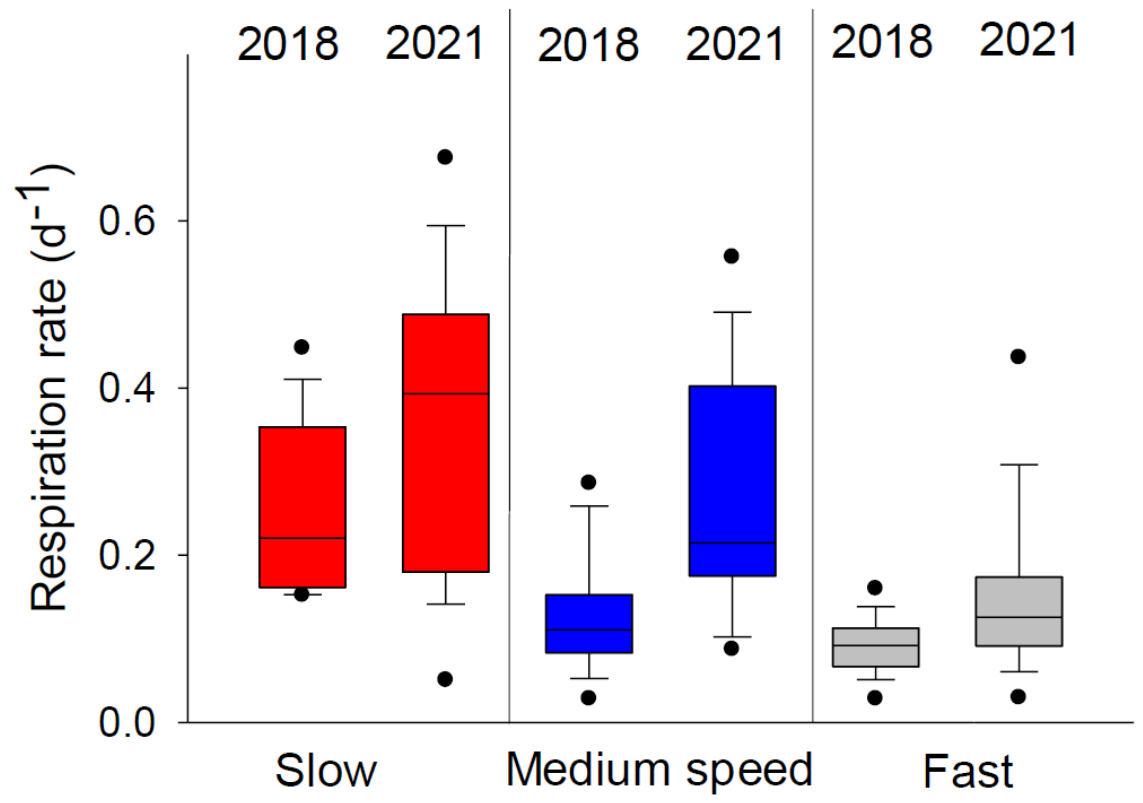


FIG 1