Respiration rate scales inversely with sinking speed of settling marine aggregates

Kristian Spilling[1], Malte Heinemann[2], Mari Vanharanta[3], Moritz Baumann[4], Andrea Noche-Ferreira[5], Philipp Suessle[4], and Ulf Riebesell[4]

[1]Finnish Environment Institute
[2]Kiel University
[3]University of Helsinki
[4]GEOMAR Helmholtz Centre for Ocean Research Kiel
[5]University of Agder

November 24, 2022

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-Martin 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 m d^{-1}) was 0.12 d^{-1}. Slower sinking particles (<50 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.

Garcia-Martin, 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.

Supplementary Table S1. ANOVA on ranks with Dunn's post hoc test of the different sinking fractions plotted in Fig 1.

All data Diff of Ranks Q P

Fast vs Slow 43.817 6.027 <0.001

Slow vs Medium speed 21.698 2.964 0.009

Fast vs Medium speed 22.119 3.089 0.006

2018 data Diff of Ranks Q P

Fast vs Slow 26.328 5.166 <0.001

Slow vs Medium speed 18.104 3.506 0.001

Fast vs Medium speed 8.224 1.668 0.286

2021 data Diff of Ranks Q P

Fast vs Slow 20.667 3.941 <0.001

Slow vs Medium speed 6.000 1.144 0.758

Fast vs Medium speed 14.667 2.797 0.015

Hosted file

`essoar.10512244.1.docx` available at https://authorea.com/users/549755/articles/603716-respiration-rate-scales-inversely-with-sinking-speed-of-settling-marine-aggregates

Hosted file

`supplementary mm.docx` available at https://authorea.com/users/549755/articles/603716-respiration-rate-scales-inversely-with-sinking-speed-of-settling-marine-aggregates

Respiration rate scales inversely with sinking speed of settling marine aggregates

Kristian Spilling[1,2,] Malte Heinemann[3], Mari Vanharanta[4,1], Moritz Baumann[5], Andrea Noche-Ferreira[2], Philipp Suessle[5], Ulf Riebesell[5]

1 Marine Research Centre, Finnish Environment Institute, Finland

2 Centre for Coastal Research, University of Agder, Norway

3 Institute of Geosciences, Kiel University, Germany

4 Tvärminne Zoological Station, University of Helsinki, Finland

5 Biological Oceanography, GEOMAR Helmholtz Centre for Ocean Research Kiel, Germany

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 m d^{-1}) was 0.12 d^{-1}. Slower sinking particles (<50 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 CO_2 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 [*Kiørboe 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 O_2-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 (±SE) respiration rates for both years were 0.42 d^{-1} ± 0.06 d^{-1}, 0.24 d^{-1} ± 0.04 d^{-1} and 0.12 d^{-1} ± 0.02 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 (0–40 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].

Acknowledgments

We would like to thank the Oceanic Platform of the Canary Islands (PLOCAN) and the Marine Science and Technology Park (PCTM), University of Las Palmas for using their facilities. We also thank the whole KOSMOS team from GEOMAR for logistics and technical help. The mesocosm experiment in 2018 were funded by an EU ERC (Grant No. 695094) and in 2021 by EU H2020 (Grant no 869357). Additional funding came from the AQUACOSM project (EU H2020, grant 731065) and Walter and Andree de Nottbeck Foundation to KS and MV. This study utilized research infrastructure part of the Finnish Marine Research Infrastructure consortium (FINMARI).

References

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.Bach, L. T., P. Stange, J. Taucher, E. P. Achterberg, M. Algueró-Muñiz, H. Horn, M. Esposito, and U. Riebesell (2019), The influence of plankton community structure on sinking velocity and remineralization rate of marine aggregates, *Glob Biogeochem Cycles*, *33*(8), 971-994.Baumann, M., J. Taucher, A. J. Paul, M. Heinemann, M. Vanharanta, L. T. Bach, K. Spilling, J. Ortiz-Cortes, J. Arístegui, and N. Hernández-Hernández (2021), Effect of Intensity and Mode of Artificial Upwelling on Particle Flux and Carbon Export, *Front Mar Sci*, 1579.Clements, D., S. Yang, T. Weber, A. McDonnell, R. Kiko, L. Stemmann, and D. Bianchi (2022), Constraining the particle size distribution of large marine particles in the global ocean with in situ optical observations and supervised learning, *Glob Biogeochem Cycles*, e2021GB007276.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.Iversen, M. H., and H. Ploug (2010), Ballast minerals and the sinking carbon flux in the ocean: carbon-specific respiration rates and sinking velocity of marine snow aggregates, *Biogeosciences*, *7*(9), 2613-2624.Kiørboe, T., K. Tang, H.-P. Grossart, and H. Ploug (2003), Dynamics of microbial communities on marine snow aggregates: colonization, growth, detachment, and grazing mortality of attached bacteria, *Appl Env Microbiol*, *69*(6), 3036-3047.Laurenceau-Cornec, E. C., F. A. Le Moigne, M. Gallinari, B. Moriceau, J. Toullec, M. H. Iversen, A. Engel, and C. L. De La Rocha (2020), New guidelines for the application of Stokes' models to the sinking velocity of marine aggregates, *Limnol Oceanogr*, *65*(6), 1264-1285.Mayor, D. J., R. Sanders, S. L. Giering, and T. R. Anderson (2014), Microbial gardening in the ocean's twilight zone: Detritivorous metazoans benefit from fragmenting, rather than ingesting, sinking detritus: Fragmentation of refractory detritus by zooplankton beneath the euphotic zone stimulates the harvestable production of labile and nutritious microbial biomass, *Bioessays*, *36*(12), 1132-1137.McDonnell, A., P. Boyd, and K. Buesseler (2015), Effects of sinking velocities and microbial respiration rates on the attenuation of particulate carbon fluxes through the mesopelagic zone, *Glob Biogeochem Cycles*, *29*(2), 175-193.Omand, M. M., R. Govindarajan, J. He, and A. Mahadevan (2020), Sinking flux of particulate organic matter in the oceans: Sensitivity to particle characteristics, *Scientific reports*, *10*(1), 1-16.Secchi, E., A. Vitale, G. L. Miño, V. Kantsler, L. Eberl, R. Rusconi, and R. Stocker (2020), The effect of flow on swimming bacteria controls the initial colonization of curved surfaces, *Nat Comm*, *11*(1), 1-12.

Figure caption

Fig 1 Respiration rate measured for the three different sinking fractions in 2018 and 2021. 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. The box outlines the 25-75 percentile, the mid-line is the median, and the whiskers are the 10 and 90 percentiles.

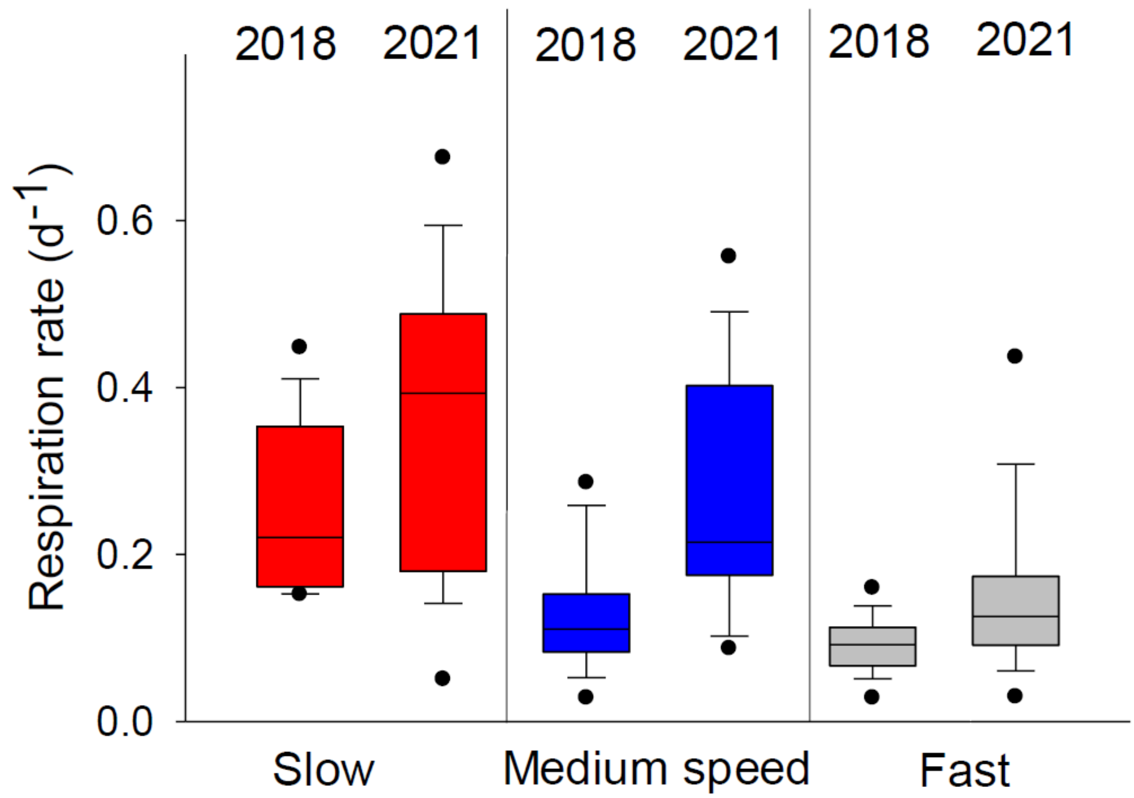
2018
2021
2018
2021
2018
2021
Respiration rate (d-1)
0.6
0.4
0.2
0.0
Slow
Medium speed
Fast

FIG 1