

Role of slowly settling particles in the ocean carbon cycle

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[1] Here we present results from sediment traps that separate particles as a function of their settling velocity, which were moored in the Canary Current region over a 1.5-year period. This study represents the longest time series using "in situ" particle settling velocity traps to date and are unique in providing year-round estimates. We find that, at least during half of the year in subtropical waters (the largest ocean domain), more than 60% of total particulate organic carbon is contained in slowly settling particles $(0.7-11 \text{ m d}^{-1})$. Analyses of organic biomarkers reveal that these particles have the same degradation state, or are even fresher than rapidly sinking particles. Thus, if slowly settling particles dominate the exportable carbon pool, most organic matter would be respired in surface waters, acting as a biological source of CO_2 susceptible to exchange with the atmosphere. In the context of climate change, if the predicted changes in phytoplankton community structure occur, slowly settling particles would be favored, affecting the strength of the biological pump in the ocean. Citation: Alonso-González, I. J., J. Arístegui, C. Lee, A. Sanchez-Vidal, A. Calafat, J. Fabrés, P. Sangrá, P. Masqué, A. Hernández-Guerra, and V. Benítez-Barrios (2010), Role of slowly settling particles in the ocean carbon cycle, Geophys. Res. Lett., 37, L13608, doi:10.1029/2010GL043827.

1. Introduction

[2] Sinking particles have been traditionally considered the most important vehicle by which the biological pump sequesters carbon in the ocean interior [*Buesseler et al.*, 2007a]. This is corroborated by the finding that dissolved organic carbon (DOC) contributes only 10–20%, at a global scale, to the remineralization rates in the dark ocean [*Aristegui et al.*, 2002]. Nevertheless, sinking POC collected with current sediment traps does not explain the remaining 80–90% of oxygen utilization rates in the dark ocean. This apparent imbalance (between carbon supply and consumption) is one of the most exciting unresolved paradoxes in the ocean carbon cycle. It indicates either the existence of unaccounted sources of organic carbon, an overestimation of the metabolic activity

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in the dark ocean, or an underestimation of the vertical particle flux.

[3] Sediment trap collection efficiency depends on the behavior of the traps with respect to hydrodynamic conditions as well as on particle properties [*Buesseler et al.*, 2007b]. Several efforts have been carried out to address the hydrodynamic effects on traps (see reviews by *Gardner* [2000] and *Buesseler et al.* [2007b]). However, intrinsic particle properties have received less attention presumably because of their difficulty in quantifying such characteristics *in situ.* Particle settling velocity is thought to be a key issue influencing vertical fluxes and carbon remineralization, although little is known about its spatio-temporal variability.

[4] Settling velocities are particle size-dependent, and hence are affected by plankton community structure and its physiological state [*Boyd and Newton*, 1995; *Guidi et al.*, 2009]. Additionally, mineral components can play a direct role in regulating the settling velocity of particles via the ballast effect [*Armstrong et al.*, 2001; *Ploug et al.*, 2008]. Recent studies predict a global replacement of diatoms by smaller phytoplankton cells induced by an increase in ocean stratification and nutrient depletion as climate changes [*Bopp et al.*, 2005]. In that scenario, the higher percentages of small versus large particles would result in slower average settling velocities, making determining the regional and temporal variability in the shape of the particle velocity spectrum of great interest.

[5] Here, with the aim of addressing this challenge, we have measured total mass and POC fluxes, amino acid and chloropigment fluxes and compositions, as well as the particle settling velocity spectrum, in the mesopelagic waters of the Canary Current region.

2. Methods

2.1. Sampling

[6] We deployed a mooring south of the Canary Islands during three 6-month periods (from June 2005 to December 2006). In the first two (Periods I and II) the mooring was located at $27^{\circ} 29' 57''$ N; $016^{\circ} 15' 19''$ W, 3600m bottom depth. Rough sea conditions forced the mooring deployment closer to the islands during Period III ($27^{\circ} 30' 4''$ N; $15^{\circ} 44'$ 32'' W, 2500m bottom depth). The mooring accommodated Indented Rotating Sphere Carousel (IRSC) sediment traps [*Peterson et al.*, 2005] at 260m, with the capacity of separating particles into discrete classes as a function of their sinking velocity. Using a protocol similar to that described by *Lee et al.* [2009], one of the traps was programmed to collect particles in a time-series mode (TS), while the other two were programmed to collect particles based on their settling velocities (SV). In situ SV separation was accomplished by

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Table 1	. Average	Fluxes ^a
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Period	Mass Flux (mg $m^2 d^{-1}$)	POC Flux (mg $m^2 d^{-1}$)	POC (%)	PON Flux (mg $m^2 d^{-1}$)	PON (%)	C/N _m
I(n = 11)	63.7 (2.8)	5.8 (0.2)	9.1	0.92 (0.30)	1.4	7.3 (0.6)
II(n = 11)	57.8 (4.3)	5.1 (0.3)	8.8	0.72 (0.17)	1.2	8.5 (0.6)
III $(n = 11)$	128.0 (9.2)	1.63 (0.1)	1.3	0.23 (0.04)	0.2	8.0 (0.9)

^aAverage (± 1 SD) fluxes and contribution (%) of POC and PON to the total mass for each period. I, June 2005 to December 2005; II, December 2005 to June 2006; III, June 2006 to December 2006.

rotating the IRS once each day and then rotating the sample carousel, corresponding to a minimal settling velocity for each sample tube of >980, 490–980, 326–490, 196–326, 140–196, 98–140, 49–98, 22–49, 11–22, 5.4–11, and 0.68– 5.4 m d^{-1} .

[7] All sediment trap cups were poisoned with mercuric chloride released "in situ" into each cup from a small vial containing 14 mg HgCl₂ in a solid pellet of NaCl. Upon recovery, samples were visually checked and the supernatant removed. Swimmers were rarely present, but when so (only in the TS trap) were handpicked under a dissecting microscope. A high precision peristaltic pump was then used to obtain subsamples through repeated splitting of the raw samples. Subsamples for total mass, POC, PON, chloropigment and amino acid analyses were filtered onto pre-combusted GF/F filters.

2.2. POC and Biomarker Analysis

[8] The carbon analyses were performed with a Perkin-Elmer 2400 CHN elemental analyzer. DOC sorption onto GF/F filters (<3.5% of the POC signal) was subtracted from samples to avoid overestimation of POC.

[9] Chlorophyll *a*, pheophytin *a*, pheophorbide *a*, and pyropheophorbide *a* were determined using reverse-phase

High Performance Liquid Chromatography (HPLC) [Lee et al., 2000; Wakeham et al., 2009].

[10] Amino acids were measured by HPLC on the same filters analyzed for pigments, using pre-column *o*-pthaldialdehyde (OPA) derivatization after hydrolysis [*Lee et al.*, 2000; *Wakeham et al.*, 2009].

2.3. Integrated Mass Flux Density Calculation

[11] Integrated Mass Flux Density Calculation (IMFD) is the mass of any constituent per square meter of trap area integrated over the length of the deployment time and divided by the width of the SV interval, which is defined here as the dimensionless log_{10} of the ratio of the highest and lowest settling velocities in each SV interval ($log_{10}(SV_{max}) - log_{10}(SV_{max}) = log_{10}(SV_{max}/SV_{min}))$ [*Armstrong et al.*, 2009].

3. Results

3.1. Fluxes and Current Velocity Variability

[12] From June to December 2005 (Period I) the time average (6-months) mass flux was 63.7 mg m⁻² d⁻¹ while the mean particulate organic carbon (POC) flux was 5.8 mg C m⁻² d⁻¹, yielding a %POC of 9.1 (Table 1). These average values were almost the same in December 2005 to June 2006 (Period II). However, from June to December 2006



Figure 1. Seasonal variability of variables measured with IRSC sediment traps. Mass flux (grey squares); POC fluxes (grey bars); mol% glycine (grey dots); current velocity measured with current meters at 275 m depth (black dots). (a) Period I: from June 2005 to December 2005. (b) Period II: from December 2005 to June 2006. (c) Period III: from June 2006 to December 2006. (d) POC flux versus current velocity for periods I and II.



Figure 2. Settling velocity groups. Time-integrated mass flux density (IMFD) versus particle settling velocity for (a) period I, (b) period II, and (c) period III. Black lines correspond to each of the SV traps (SV1 and SV2), grey bars stand for the average of SV1 and SV2 and grey lines stand for the relative contribution (in %) of each of the velocity-classes of particles to the total POC flux. See Figure 1 for period dates. (d) Mass flux density normalized to total mass flux, for the RODA, Medflux and VERTIGO deployments.

(Period III) the average mass flux was two fold higher than Periods I and II, while mean POC flux and %POC were lower (Table 1). Figure 1 shows the seasonal variability of POC fluxes, glycine (mol%) and current velocity. POC fluxes during Period I ranged from 2.8 to 10.3 mg C m⁻² d⁻¹ (Figure 1a), while during Period II fluxes were low, 2–3 mg C $m^{-2} d^{-1}$, except in March, when values reached 24 mg C m⁻² d⁻¹ (Figure 1b). During Period III POC fluxes were lower than in the first two periods, ranging from 0.45 to 4.1 mg C m⁻² d⁻¹ (Figure 1c). Average (15 days) current velocities during Period I ranged from 5 to 12 cm s⁻¹, yielding an average current velocity for the whole period of 7.18 ± 2.1 cm s⁻¹ (Figure 1a). During Period II, current velocities ranged from 6.5 to 14 cm s⁻¹ (Figure 1b), yielding a higher average current velocity (10.2 ± 2.3 cm s⁻¹) compared to Period I.

3.2. Particle Settling Velocity Spectrum

[13] In spite of the different locations, during both Periods I and III, time-integrated mass flux densities (IMFD) calculated from SV sediment traps exhibited an exponential tail at lower settling velocities $(0.7-11 \text{ m d}^{-1})$ that explains 68–75% of total mass flux and a smaller Gaussian portion at the higher end of the SV spectrum (Figures 2a and 2c). In contrast, the settling velocity spectrum from Period II presented a different shape, with a peak of rapidly settling particles (>326 m d^{-1}) that explains 41% of total mass flux and a roughly constant IMFD over the other SV groups (Figure 2b).

[14] The relative contribution (in %) of each of the velocityclasses of particles to the total POC flux also exhibited different distributions between periods I-III and period II. Periods I and III showed a bimodal distribution with the highest amount of total POC (62%) in the slowest settling velocity groups (0.7–11 m d⁻¹), and lower amounts (~25% of total POC) in the highest settling velocity classes (>326 m d⁻¹). Each of the intermediate SV groups (11–326 m d⁻¹) contained less than 5% of total POC (Figures 2a and 2c). On the contrary, during period II most of the total POC (53%) collected by SV traps was in the highest settling velocity classes (>326 m d⁻¹). Each of the other SV groups represented less than 10% of total POC (Figure 2b).

[15] To evaluate the degradation state of these two different classes of settling particles we selected four biomarkers: chlorophyll-*a*, pheophytin-*a*, pheophorbide-*a* and γ -aminobutyric acid (Table 2). During Period I, biomarkers indicated that the dominant slowly settling particles were fresher than the rapidly settling particles (the latter enriched in pheophytin and Gaba mole%), whereas the opposite pattern was found during Period II. Additionally, glycine, a diatom indicator, was used to evaluate the contribution of this phytoplankton group to the carbon fluxes. During period II, mole% glycine and POC flux follow a similar behavior characterized by a directly proportional relationship (r² = 0.84; p < 0.05).

4. Discussion

4.1. Effect of Current Velocity on POC Fluxes

[16] Previous laboratory and field analysis regarding the effects of flow velocity on the collection efficiency of

Table 2. Biomarkers^a

	Settling Velocity Group (m d^{-1})						
	Period I		Period II		Period III		
	>326	0.7-11	>326	0.7 - 11	>326	0.7-11	
Chl-a (mole%) (Phytoplankton marker)	-	-	9.8	ND	15.0	12.9	
Pheophytin-a (mole%) (Microzooplankton grazing marker)	76.7	52.5	36.3	46.3	31.8	17.5	
Pheophorbide-a (mole%) (Zooplankton marker)	10.62	13.6	30.9	7.9	16.6	24.8	
GABA (mole%) (Microbial decomposition marker)	0.69	0.47	0.25	0.31	0.68	1.07	

^aPigment and amino acid biomarkers used to evaluate the degradation state of the two different settling velocity groups (>326 and 0.7–11 m d⁻¹). See Table 1 for period dates. Dash indicates not determined; GABA, γ -aminobutyric acid; ND, not detected.

sediment traps have shown conflicting results (see reviews by Gardner [2000] and Buesseler et al. [2007b]). Here we report new results that fuel this controversy, but may represent a step forward in understanding the complex mechanisms that control sediment trap collection efficiency. Our observed correlations between flow velocity and POC flux also show contradictory results (Figure 1d). Period I shows a decrease in POC flux with increased flow velocity (Pearson's r = -0.64, p < 0.05), while during Period II no statistically difference was found. This change in the flux-flow velocity relationship could be explained by the modifications that the ecosystem undergoes with time. Period I is dominated by slow sinking particles which are susceptible to lateral advection, while Period II is dominated by fast sinking particles that are presumably less affected by current velocity. According to these results, particle-settling velocity is a key factor controlling the hydrodynamic biases affecting sediment traps, in agreement with Gust and Kozerski [2000].

4.2. Particle Settling Velocity Spectra

[17] The analysis of the temporal evolution of near-surface Chl-a and depth of the mixed layer (MLD) and euphotic zone (Ze) (Text S1 and Figure S1) reveal that the depth interval between the bottom of the MLD and the depth of the sediment trap is higher during Periods I and III (when slow sinking particles dominate), suggesting that these particles were passively collected, rather than mixed down from surface to the trap depth.¹

[18] A comparison of the sinking rate spectra observed here with those obtained using IRSC traps at approximately the same depth (\sim 300 m) in the subarctic K2, subtropical ALOHA (North Pacific) and DYFAMED (Mediterranean) stations reveals important findings (Figure 2d). The DYFAMED station showed particle-sinking spectra similar to our Period II, characterized by a Gaussian portion of fastsettling particles, which dominate sinking fluxes, and a tail of slowly settling particles [Armstrong et al., 2009]. More interesting is the fact that these studies were carried out in the same season as our Period II. This suggests that a large fraction of the surface primary production generated during the late-winter bloom (Figure S1) is rapidly (~1 month) exported to the dark ocean via fast-settling particles. This phenomenon is induced by a higher contribution of large phytoplankton cells and zooplankton fecal pellets to the sinking flux as indicated by the contributions of glycine (Figure 1b) and pheophorbide to the organic matter (Table 2).

[19] On the other hand, the SV spectra at both Pacific stations, determined in the same season that our Periods I and III (ALOHA, June 2004 and K2, July 2005) showed a contribution of slowly settling particles (2–13 m d⁻¹) to the total POC flux ranging from 15 to 50% [*Trull et al.*, 2008]. In addition to this significant contribution, the authors indicated that the addition of brine solution into the cups could have affected the entry of slowly settling particles. In our case, we used HgCl₂ diffusers within the cups, thus avoiding such problems [*Peterson et al.*, 2005]. Moreover, the short rotation cycle of the IRSC valve (6 hours) used at the Pacific stations limited the minimum-settling rate that can be resolved to 2 m d⁻¹ (versus 0.68 m d⁻¹ with the 24 h cycle used in our study). Taking into account all these factors, it is reasonable to think that slowly settling particles could be a major fraction of the mass flux in those stations. Overall, these studies suggest that particle settling velocities in the ocean vary seasonally and with location, with profound implications for carbon sequestration in the deep ocean.

4.3. Implications of Slowly Settling Particles Dominating the Size Spectrum

[20] Our results give evidence that slowly settling particles dominated the carbon flux in our study during summer and autumn. In such a situation, sediment traps may miss a fraction of the exported POC in the smallest particles. Thus, if vertical carbon fluxes derived from sediment traps are used to construct budgets for different biogeochemical processes, strong imbalances may arise. Indeed, recent studies have reported important discrepancies between the mesopelagic metabolic carbon demand (MCD) of planktonic communities and the vertical carbon supply [Steinberg et al., 2008; Baltar et al., 2009]. We suggest that this "apparent" mismatch between MCD and vertical POC fluxes would presumably be less noticeable when fast-sinking particles dominate the flux and/or current velocities are low, as lateral transport would be relatively less important. The consumption of the undersampled slowly settling carbon pool could be therefore an additional mechanism buffering this imbalance by uncoupling MCD from vertical fluxes. However, considering the slow sinking rate of these particles, the effect of this undersampled carbon pool would be restricted to the upper mesopelagic waters (the place where the MCD is higher and the major decrease in molecularly-characterized material occurs) [Baltar et al., 2009; Lee et al., 2004].

[21] Biomarkers indicate that the slowly settling particles have the same degradation state, or are even fresher, than the rapidly settling particles during the summer-autumn (Table 2). This observation raises the questions of how can a carbon pool that sinks at $1-10 \text{ m d}^{-1}$ be very labile? Could it be that slow sinking particles are in fact broken parts of larger particles, which were formed during rotation of the IRS ball? To test if the signal of fresh particles in a slow velocity class reflects these biases in the SV trap, we performed a principal components analysis (PCA) to quantitatively assess variation in the organic composition of the different settling particle classes. PCA indicates that the two velocity groups (slowly and fast sinking particles) differ in organic matter composition, giving evidence against this hypothesis (Text S2 and Figure S2).

[22] Other studies [*Goutx et al.*, 2007; *Wakeham et al.*, 2009] reached the same conclusion after analyzing the composition of particles collected at 200 m in the Mediterranean Sea and separated by settling velocity. Samples from the Pacific Ocean also showed that material collected by in situ filtration, assumed to be suspended or with low settling rates, contained a remarkable abundance of labile organic compounds [*Lee et al.*, 2000; *Sheridan et al.*, 2002]. Therefore, the high bioavailability of slowly settling particles seems likely to be a general feature rather than an isolated case.

[23] Small "suspended" particles may result from sinking particles disaggregated by physical forces [*Burd and Jackson*, 2009] or the activity of microbes and zooplankton [*Sheridan et al.*, 2002], but also by self-assembly of dissolved organic material yielding porous microgels [*Chin et al.*, 1998]. In all cases these small particles seem to be a suitable nutrient-rich habitat to be colonized by microorganisms. Indeed, recent

¹Auxiliary materials are available in the HTML. doi:10.1029/2010GL043827.

studies have demonstrated a strong association between suspended particles and dark-ocean prokaryotic metabolism, supporting the view that microbial life is mainly dependent on small buoyant particles [e.g., *Baltar et al.*, 2009]. The high microbial activity reported during summer and autumn in the mesopelagic zone of the Canary region [*Arístegui et al.*, 2005], would support our observations of a greater contribution of slowly sinking particles during these periods.

[24] In terms of carbon sequestration, the depth of organic matter decomposition determines whether respired CO_2 may be exchanged quickly with the atmosphere or rather be sequestered over long periods of time [*Armstrong et al.*, 2001]. Thus, if slowly settling particles dominate the exportable carbon pool, most organic matter would be respired in the epipelagic and upper mesopelagic zones, acting as a biological source of CO_2 susceptible to exchange with the atmosphere. On the contrary, if fast-sinking particles contribute largely to the carbon flux, the carbon transfer efficiency to the mesopelagic waters increases, resulting in an enhanced carbon sequestration in the deep ocean.

[25] The implications of this work for understanding regional and global ocean carbon balances are profound if slowly settling particles are a significant portion of the exportable carbon pool. This phenomenon may explain several unresolved issues of the ocean carbon cycle. In the context of climate change, if the predicted changes in phytoplankton community structure occur, slowly settling particles would be favored, modifying the strength of the biological pump in the ocean. Our results also highlight the urgent need to extend our regional database of the sinkingparticle velocity spectrum, as well as to develop new technologies to measure and collect the total spectrum of sinking particles in the ocean.

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References

- Arístegui, J., et al. (2002), Dissolved organic carbon support of respiration in the dark ocean, *Science*, 298, 1967, doi:10.1126/science.1076746.
- Arístegui, J., C. M. Duarte, J. M. Gasol, and L. Alonso-Sáez (2005), Active mesopelagic prokaryotes support high respiration in the subtropical northeast Atlantic Ocean, *Geophys. Res. Lett.*, 32, L03608, doi:10.1029/ 2004GL021863.
- Armstrong, R. A., C. Lee, J. I. Hedges, S. Honjo, and S. G. Wakeham (2001), A new mechanistic model for organic carbon fluxes in the ocean: based on the quantitative association of POC with ballast minerals, *Deep Sea Res., Part II*, 49, 219–236, doi:10.1016/S0967-0645(01)00101-1.
- Armstrong, R. A., M. L. Peterson, C. Lee, and S. G. Wakeham (2009), Settling velocity spectra and the ballast ratio hypothesis, *Deep Sea Res., Part II*, 56, 1470–1478, doi:10.1016/j.dsr2.2008.11.032.
- Baltar, F., J. Arístegui, J. M. Gasol, E. Sintes, and G. J. Herndl (2009), Evidence of prokaryotic metabolism on suspended particulate organic matter in the dark waters of the subtropical North Atlantic, *Limnol. Oceanogr.*, 54, 182–193.
- Bopp, L., O. Aumont, P. Cadule, S. Alvain, and M. Gehlen (2005), Response of diatoms distribution to global warming and potential impli-

cations: A global model study, *Geophys. Res. Lett.*, 32, L19606, doi:10.1029/2005GL023653.

- Boyd, P., and P. Newton (1995), Evidence of the potential influence of planktonic community structure on the interannual variability of particulate organic-carbon flux, *Deep Sea Res., Part I*, 42, 619–639, doi:10.1016/0967-0637(95)00017-Z.
- Buesseler, K. O., et al. (2007a), Revisiting carbon flux through the ocean's twilight zone, *Science*, *316*, 567–570, doi:10.1126/science.1137959.
- Buesseler, K. O., et al. (2007b), An assessment of the use of sediment traps for estimating upper ocean particle fluxes, J. Mar. Res., 65, 345–416.
- Burd, A. B., and G. A. Jackson (2009), Particle aggregation, Annu. Rev. Mar., Sci., 1, 65–90.
- Chin, W.-C., M. V. Orellana, and P. Verdugo (1998), Spontaneous assembly of marine dissolved organic matter into polymer gels, *Nature*, 391, 568–572, doi:10.1038/35345.
- Gardner, W. D. (2000), Sediment trap technology and sampling in surface waters, in *The Changing Ocean Carbon Cycle: A Midterm Synthesis of the Joint Global Ocean Flux Study*, edited by R. B. Hanson et al., p. 240–281, Cambridge Univ. Press, New York.
- Goutx, M., et al. (2007), Composition and degradation of marine particles with different settling velocities in the northwest Mediterranean Sea, *Limnol. Oceanogr.*, 52, 1645–1664.
- Guidi, L., et al. (2009), Effects of phytoplankton community on production, size, and export of large aggregates: A world-ocean analysis, *Limnol. Oceanogr.*, 54, 1951–1963.
- Gust, G., and H.-P. Kozerski (2000), *In situ* sinking-particle flux from collection rates of cylindrical traps, *Mar. Ecol. Prog. Ser.*, 208, 93–106, doi:10.3354/meps208093.
- Lee, C., S. G. Wakeham, and J. I. Hedges (2000), Composition and flux of particulate amino acids and chloropigments in equatorial Pacific seawater and sediments, *Deep Sea Res., Part 1*, 47, 1535–1568, doi:10.1016/S0967-0637(99)00116-8.
- Lee, C., S. Wakeham, and C. Arnosti (2004), Particulate organic matter in the sea: The composition conundrum, *Ambio*, 33, 565–575.
- Lee, C., M. L. Peterson, S. G. Wakeham, R. A. Armstrong, J. K. Cochran, J. C. Miquel, S. W. Fowler, D. Hirschberg, A. Beck, and J. Xue (2009), Particulate organic matter and ballast fluxes measured using time-series and settling velocity sediment traps in the northwestern Mediterranean Sea, *Deep Sea Res.*, *Part II*, 56, 1420–1436, doi:10.1016/j.dsr2.2008. 11.029.
- Peterson, M. L., S. G. Wakeham, C. Lee, M. A. Askea, and J. C. Miquel (2005), Novel techniques for collection of sinking particles in the ocean and determining their settling rates, *Limnol. Oceanogr. Methods*, 3, 520– 532.
- Ploug, H., M. Iversen, and G. Fischer (2008), Ballast, sinking velocity, and apparent diffusivity within marine snow and zooplankton fecal pellets: Implication for substrate turnover by attached bacteria, *Limnol. Oceanogr.*, 53, 1878–1886.
- Sheridan, C. C., C. Lee, S. G. Wakeham, and J. K. B. Bishop (2002), Suspended particle organic composition and cycling in surface and midwaters of the equatorial Pacific Ocean, *Deep Sea Res., Part I*, 49, 1983–2008, doi:10.1016/S0967-0637(02)00118-8.
- Steinberg, D. K., et al. (2008), Microbial vs. zooplankton control of sinking particle flux in the ocean's twilight zone, *Limnol. Oceanogr.*, 53, 1327–1338.
- Trull, T. W., et al. (2008), In-situ measurement of mesopelagic particle sinking rates and the control of carbon transfer to the ocean interior during the Vertical Flux in the Global Ocean (VERTIGO) voyages in the North Pacific, *Deep Sea Res., Part II*, 55, 1684–1695, doi:10.1016/j. dsr2.2008.04.021.
- Wakeham, S. G., et al. (2009), Organic biomarkers in the twilight zone: Time series and settling velocity sediment traps during MEDFLUX, *Deep Sea Res., Part II*, doi:10.1016/j.dsr2.2008.11.030.

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