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Quantification of the lithogenic carbon pump following a simulated dust-deposition event in large mesocosms

M. Bressac[1,2], C. Guieu[2], D. Doxaran[2], F. Bourrin[3], K. Desboeufs[4], N. Leblond[5], and C. Ridame[6]

[1]ACRI-ST, BP 234, 06904 Sophia-Antipolis, France
[2]CNRS-INSU, Université Pierre et Marie Curie-Paris 6, UMR7093, Laboratoire d'Océanographie de Villefranche/Mer, Observatoire Océanologique, 06230 Villefranche-sur-Mer, France
[3]Université de Perpignan Via Domitia, CEFREM, CNRS-UPVD, UMR5110, 52 avenue Paul Alduy, 66860 Perpignan, France
[4]Université Paris Diderot, Sorbonne Paris Cité, Université Paris Est Créteil, UMR CNRS 7583, Laboratoire Interuniversitaire des Systèmes Atmosphériques (LISA), 61 av. Gal de Gaulle, 94010 C France
[5]Observatoire Océanologique de Villefranche/Mer, CNRS, Université Pierre et Marie Curie-Paris 6, 06230 Villefranche-sur-Mer, France
[6]CNRS-INSU-IRD, Université Pierre et Marie Curie, UMR7159, LOCEAN: Laboratoire d'Océanographie et du Climat: Expérimentation et Approches Numériques, 4 Place Jussieu – 75252 Paris Cedex 05, France

Correspondence to: M. Bressac (bressac@obs-vlfr.fr)

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Abstract. Lithogenic particles, such as desert dust, have been postulated to influence particulate organic carbon (POC) export to the deep ocean by acting as mineral ballasts. However, an accurate understanding and quantification of the POC–dust association that occurs within the upper ocean is required in order to refine the "ballast hypothesis". In the framework of the DUNE (a DUst experiment in a low-Nutrient, low-chlorophyll Ecosystem) project, two artificial seedings were performed seven days apart within large mesocosms. A suite of optical and biogeochemical measurements were used to quantify surface POC export following simulated dust events within a low-nutrient, low-chlorophyll ecosystem. The two successive seedings led to a 2.3–6.7-fold higher POC flux than the POC flux observed in controlled mesocosms. A simple linear regression analysis revealed that the lithogenic fluxes explained more than 85 % of the variance in POC fluxes. On the scale of a dust-deposition event, we estimated that 42–50 % of POC fluxes were strictly associated with lithogenic particles (through aggregation and most probably sorption processes). Lithogenic ballasting also likely impacted the remaining POC fraction which resulted from the fertilization effect. The observations support the "ballast hypothesis" and provide a quantitative estimation of the surface POC export abiotically triggered by dust deposition. In this work, we demonstrate that the strength of such a "lithogenic carbon pump" depends on the biogeochemical conditions of the water column at the time of deposition. Based on these observations, we suggest that this lithogenic carbon pump could represent a major component of the biological pump in oceanic areas subjected to intense atmospheric forcing.

1 Introduction

The magnitude of downward particulate organic carbon (POC) export and its subsequent sequestration depends on the flux generated within the euphotic zone, the velocity at which it sinks, and the rate at which it decomposes (De La Rocha and Passow, 2007). Early studies showed strong correlations in the deep ocean between mineral (biogenic calcite, biogenic opal, and lithogenic particles) and POC fluxes (e.g., Deuser et al., 1981, 1983). To explain this predictive power, a "ballast hypothesis" was proposed, and it has been suggested that the downward POC flux is partly driven by associations with denser mineral particles that increase the overall sinking velocity for aggregates and that provide physical protection against the remineralization of labile organic

matter (OM) (Ittekkot, 1993; Hedges et al., 2000; Armstrong et al., 2002; Francois et al., 2002; Klaas and Archer, 2002). Although little evidence for a direct protective mechanism has emerged from in situ observations (Ingalls et al., 2006; Ploug et al., 2008; Iversen and Ploug, 2010), laboratory-controlled experiments have demonstrated the potential for minerals to inhibit the microbial degradation of OM (Arnarson and Keil, 2005; Engel et al., 2009a; Le Moigne et al., 2013). On the other hand, it has been demonstrated that minerals could increase the velocity at which aggregates sink (e.g., De La Rocha and Passow, 2007; De La Rocha et al., 2008; Thomalla et al., 2008; Engel et al., 2009b; Iversen and Ploug, 2010) and drive large POC flux events (e.g., Thunell et al., 2007; Lee et al., 2009; Sanders et al., 2010; Ternon et al., 2010). Such fast-sinking POC, negligible within the euphotic zone, is sufficient to explain deep-ocean POC fluxes (Honda and Watanabe, 2010; Riley et al., 2012); this emphasizes the importance of the mode by which carbon is transferred downward when considering carbon flux parameterization.

Atmospherically and river-derived lithogenic material could act as an important carrier phase for POC to the deep ocean (Dunne et al., 2007; Salter et al., 2010). Often characterized by extreme events (Mahowald et al., 2003), atmospheric dust-deposition could induce a sudden and drastic increase in particle concentration and pronounced differential settling rates within surface waters. Such physical perturbation could profoundly change collision and coagulation rates, and, therefore, act as a catalyst during the aggregation process (Hamm, 2002; Lee et al., 2009). Atmospheric desert dust particles also constitute an important external source of new nutrients in large oceanic areas (Duce et al., 1991; Mahowald et al., 2009) that may alleviate biological limitation (Boyd et al., 2010 and references therein) and enhance export production (e.g., Bishop et al., 2002). Therefore, such a fertilization effect coupled with lithogenic ballasting has major consequences on ocean biogeochemistry and particle flux. However, while these simultaneous POC fluxes are selectively removed with respect to the ballast hypothesis, the difficulty of rigorously quantifying lithogenic ballasting due to this coupling of biotic and abiotic contributions remains.

As implicitly suggested by the ballast hypothesis, it has been demonstrated that POC–ballast associations take place within the upper ocean (Lee et al., 2009; Iversen et al., 2010; Sanders et al., 2010; Le Moigne et al., 2012) (i.e., before aggregates reach the mesopelagic depths where processes are determinant in setting the fraction of OM that reaches the deep ocean; Boyd and Trull, 2007). Although our mechanistic understanding of such an association must be improved, it seems that most lithogenic particles are not directly attached to biogenic particles, but form clusters that are likely bound by extracellular organic material (Hamm, 2002). In light of this fact, an alternative explanation states that correlations between POC and mineral fluxes may result from OM, which acts as "glue" for aggregate minerals that would otherwise not sink (Passow, 2004; Passow and De la Rocha, 2006). Without determining the catalyst for aggregation, Ternon et al. (2010) concluded that the simultaneous presence of OM and lithogenic particles is required for the formation of large and fast-sinking particles in the western Mediterranean Sea. Considering the strong spatial and temporal variability of dust-deposition events (Jickells et al., 2005; Mahowald et al., 2009), the water column into which atmospheric particles are deposited is characterized by a wide-ranging OM composition and abundance. Therefore, the intensity of the aggregation process and subsequent particulate export could vary, limiting the relevance of a global scale approach for estimating the contribution of lithogenic ballasting to POC export (Ragueneau et al., 2006; Boyd and Trull, 2007; De La Rocha and Passow, 2007).

Since only a few studies have reported the enhancement of export production following dust-deposition pulses in low-nutrient, low-chlorophyll (LNLC) areas (e.g., Ternon et al., 2010), we sought to improve our understanding of this mechanism through this work. As a result of the episodic nature of dust deposition, artificial seeding in mesocosms constitutes a suitable approach for following, on an environmentally relevant timescale, the surface POC export associated with dust-deposition events. In this study, particulate export was investigated using two complementary approaches, as follows: (1) optical measurements were used to assess the rapid transfer of suspended particulate matter occurring a few hours following seeding, and (2) daily sediment trap samples were used to discriminate organic and lithogenic fractions, and to provide a global view of the flux that occurs following seedings. While determining surface fluxes is subject to trapping artefacts (Gardner, 2000; Scholten et al., 2001; Yu et al., 2001), such an experimental approach enabled us to investigate particulate fluxes using vertical coherence and a higher time resolution than that feasible with sediment traps. The objectives of the study are to determine (1) the causality of the relationship between dust deposition and subsequent POC export increase, (2) the respective contribution of biotic (fertilization) and abiotic (lithogenic ballasting) processes to total POC export, and (3) the variability of these processes for different initial biogeochemical conditions.

2 Materials and methods

2.1 Experimental setup and sampling

In the framework of the DUNE (a DUst experiment in a low-Nutrient, low-chlorophyll Ecosystem) project, a first artificial seeding experiment was performed in 2008 (DUNE 1) and a second in 2010 (DUNE 2). Since no optical measurements were performed during the DUNE 1 experiment, only the results from the DUNE 2 experiment are reported here. The mesocosm's experimental design and the methodology used to produce dust analog are reported in Guieu et al. (2010). Seven large mesocosms (height: 14.7 m, diameter:

2.3 m, surface area: 4.15 m^2, volume: 52 m^3) were deployed within a coastal area (Corsica; 42.374° N, 8.554° E) during the summer oligotrophic period. Three mesocosms kept without seeding (here referred to as "control mesocosms") and three seeded mesocosms (here referred to as "+ dust mesocosms") were devoted to biogeochemical studies. A seventh mesocosm, also seeded, was utilized for the deployment of optical instruments.

The mesocosms ended with a sediment trap (a 250 mL high-density polyethylene bottle) from which divers collected material every 24 h. Optical measurements were performed at high spatial and temporal resolutions during the first ∼ 24 h of each experiment for ∼ 2 days following each seeding, whereas biogeochemical parameters were sampled daily during the week. Primary production measurements were performed every 24 h at a depth of 5 m (Ridame et al., 2014). The data were integrated over the water column (0–12.5 m in depth) by assuming a homogeneous profile.

2.2 The dust analog and the seeding

The finest dust fraction (< 20 µm) was separated from the bulk soil samples – dominated by quartz (40 %), calcite (30 %) and clays (25 %) – by grinding and dry-sieving. Then the dust analogs were processed to simulate cloud evapocondensation cycles. The physicochemical characteristics of the dust analog are reported in Desboeufs et al. (2014). The resulting dust population presented a volume median diameter around 6.5 μm and a peak at ∼ 10 µm, while the particle number size distribution peaked at 0.1 µm (Guieu et al., 2010a).

The DUNE 2 experiment lasted 14 days, from 26 June to 9 July 2010. Two artificial seedings were successively conducted seven days apart within the same mesocosm and consisted of mimicking realistic wet deposition events with a dust flux of 10 g m^{-2}. Such a flux corresponds to 41.5 g of evapocondensed dust diluted in 2 L of ultrapure water and sprayed onto the surface of each of the mesocosms for a total duration of ∼ 40 min.

In the Mediterranean Basin, dust is mainly derived from the Sahara desert in the form of strong pulses (Loÿe-Pilot et al., 1986; Bergametti et al., 1989; Guerzoni et al., 1999). Between 1984 and 1994, Loÿe-Pilot and Martin (1996) reported a mean annual flux in Corsica of 12.5 g m^{-2} yr^{-1}, mainly attributed to pulses > 1 g m^{-2}. According to the same authors, this deposition is mainly wet deposition and may occur only with few drops of rain, meaning that a high amount of dust can be deposited in time scales of minutes. Similar strong and sudden (few-hour-long) events have been recorded over the past decade, with African dust-deposition fluxes as high as 22 g m^{-2} (Bonnet and Guieu, 2006; Guieu et al., 2010b; Ternon et al., 2010). Our simulation, which allowed us to seed all the + dust mesocosms in a quasi-synoptic way, therefore appears realistic in terms of flux magnitude and duration (Guieu et al., 2013a).

2.3 Optical measurements

Optical instruments, measurements, data processing and corrections are described in detail in Bressac et al. (2012). Briefly, an optical profiling package, including an ECO-BB3 (WET Labs, Inc.) backscattering sensor and a LISST-100 type B device (Sequoia Scientific Inc.), was deployed inside and outside the "optical" mesocosm. To minimize perturbation inside the mesocosm when profiling, vertical profiles were performed from 0 to 10 m depth at a speed of 0.1 m s^{-1} at the center of the bag. Vertical profiles, performed every hour using both sensors, consisted of continuous measurements for approximately 20 min between the subsurface and 10 m depth. For the remaining 40 min, measurements were performed continuously at 0.5 m depth. Control profiles were performed outside the mesocosm in the same manner. The particulate backscattering coefficient ($b_{bp}(\lambda)$, m^{-1}) was obtained from the light backscattered at 117° (β (117°), m^{-1} sr^{-1}), measured using the ECO-BB3 sensor. Because of a logistic constraint, two different backscattering sensor were employed: a visible (440, 532, and 660 nm) sensor and a near-infrared (720, 770, and 870 nm) sensor; these were deployed during the first and second seeding experiment, respectively. Only measurements performed at 660 (first seeding) and 720 nm (second seeding) are reported here and compared to their respective initial values (see Sect. 3.3.2); indeed, the results at other wavelengths were similar. The LISST-100 type B sensor measured the beam attenuation coefficient at 670 nm along a path length of 5 cm. The ratio of the intensity of transmitted light in seawater to the intensity of light transmitted in ultrapure water was used to calculate the attenuation coefficient due to suspended particles, removing the attenuation due to water (Hill et al., 2011). Since light absorption by colored dissolved substances is negligible in the red spectral domain (Bricaud et al., 1981; Boss et al., 2009), the measured attenuation was assumed to be the particulate beam attenuation (c_p, m^{-1}).

2.4 Sediment traps: sample treatment, elemental analyses, and calculations

Samples from sediment traps were analyzed within the seven mesocosms. The means of POC and lithogenic fluxes measured in the "optical" and + dust mesocosms were not significantly different from each other (p values > 0.05). However, since primary production was not measured, data from the "optical" mesocosm are not reported here. Following collection, samples were preserved using a solution of 5 % buffered formaldehyde and stored in the dark at 4 °C until processed. Swimmers were carefully handpicked using a binocular microscope. The remaining sample was desalted using ultrapure water and freeze-dried. Mass flux was determined by weighing the entire freeze-dried sample five times, with the accuracy of the weighing being < 1 % over the whole data series.

The total concentration of carbon (TC) was measured in duplicate using a CHN analyzer (PerkinElmer 2400) on aliquots of desiccated samples (5–10 mg). HNO_3/HF acid-digestion was performed in 7 mL Teflon flasks at 150 °C on aliquots of desiccated samples ($\sim$ 20 mg). Following complete evaporation, samples were diluted in 0.1 M HNO_3 and analyzed for their calcium (Ca), aluminium (Al), and sulfur (S) concentrations by ICP–AES (inductively coupled plasma–atomic emission spectrometry) using the procedures described by Desboeufs et al. (2014). The detection limit of the apparatus for Ca, Al, and S was well below the lowest concentration of the digested aliquot (Desboeufs et al., 2014). Aliquots of the blanks and the certified reference materials (GBW07313) were digested and analyzed for Al, Ca, and S under the same conditions. In dust analogs Ca is present both as calcium carbonate and as calcium sulfate (Guieu et al., 2010a; Desboeufs et al., 2014). The part of Ca associated with sulfate (% Ca_{CaSO_4}) was estimated from the particulate S concentration within sediment traps. Therefore, the particulate Ca concentration as carbonate (% Ca_{CaCO_3}) corresponded to the difference between total % Ca and % Ca_{CaSO_4}. Then the carbonate fraction ($CaCO_3$) was determined from the %Ca_{CaCO_3} as follows:

$$\%\,CaCO_3 = 100/40 \times \%\,Ca_{CaCO_3}. \quad (1)$$

Particulate inorganic carbon (PIC) was deduced from the $CaCO_3$ fraction by assuming that, as follows:

$$\%\,PIC = 12/100 \times \%\,CaCO_3. \quad (2)$$

POC was determined by subtracting PIC from TC. The lithogenic fraction was determined from particulate Al concentrations measured in the + dust mesocosms by considering the Al composition of the dust analogs (3.32 %; Desboeufs et al., 2014). The protocol for the elemental analyses, the calculations for the various fractions, and the complete sediment trap data set are fully described in Desboeufs et al. (2014).

3 Results

Calculation and nomenclature – POC flux data are presented for all of the mesocosms (Figs. 5 and 6) or as the average of the three + dust and three control values (Figs. 1, 7, and 8). The difference between these averaged POC fluxes is referred to as "net" (Fig. 1). "T_x" represents the sampling time expressed in hours (x) since the first seeding. For samples from the second experiment, time (in hours) since the second seeding (y) is added in parentheses, as follows: "$T_{x(y)}$".

3.1 Evolution of the physical and biogeochemical parameters

Throughout the entire experiment, the seawater temperature ranged from 20.0 to 27.3 °C (Guieu et al., 2013a). The water column was well mixed during the first seeding experiment (T_0–$T_{166(0)}$). Toward the last day of the first experiment, solar heating within the surface layer led to the onset of stratification. The vertical temperature gradient was rapidly disrupted on the night after the second seeding ($\sim T_{190(24)}$–$T_{210(44)}$). The water column remained well mixed until the last day of the experiment, when a strong thermal stratification appeared. Stratification was higher during the second seeding experiment but interrupted by wind-driven mixing events.

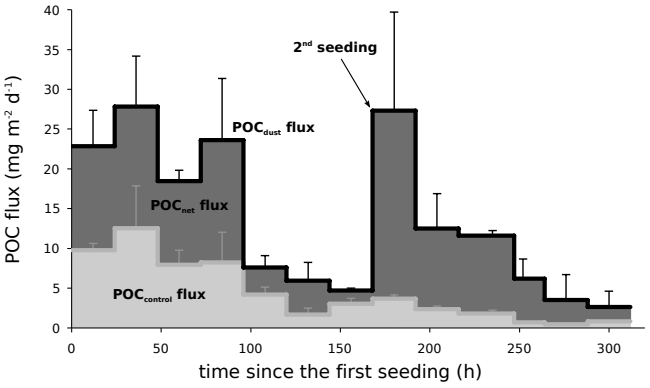

Fig. 1. Temporal evolution of the POC_{dust} flux (black line), the $POC_{control}$ flux (light-gray portion), and the POC_{net} flux (dark-gray portion). Data represents the average (+SD) of the three replicate mesocosms.

Considering the biological response to the first seeding (Giovagnetti et al., 2013; Ridame et al., 2014), the biogeochemical status of the water column changed between the experiments. Prior to the first seeding, the chlorophyll *a* concentration (Chl *a*) was characteristic of oligotrophic conditions (0.07 ± 0.02 mg m^{-3}). Seven days after the first seeding (i.e., prior to the second seeding), Chl *a* was $\sim$ 1.7 times higher (0.12 ± 0.04 mg m^{-3}). In the control mesocosms Chl *a* remained constant for the entire experiment (0.06 ± 0.01 mg m^{-3}), indicating that changes in the + dust mesocosms were directly linked to the input of new nutrients provided by the dust.

Initial conditions indicate (1) very low dissolved inorganic phosphorus concentrations ([DIP]) (5 ± 3 nM; Pulido-Villena et al., 2014), (2) dissolved inorganic nitrogen concentrations ([DIN]) below the detection limit (< 30 nM; Ridame et al., 2013), and (3) dissolved iron concentrations ([DFe]) typical of coastal area (3.3 ± 0.8 nM; Wuttig et al., 2013). Following the first seeding, a decrease in [DFe] due to scavenging by sinking dust (Wuttig et al., 2013) and a transient increase in [DIP] (Pulido-Villena et al., 2014) were observed. The second addition of dust induced a significant increase in [DFe] (Wuttig et al., 2013) and [DIP] (Pulido-Villena et al., 2014). Furthermore, significant increases in [DIN] were observed following both seedings (Ridame et al., 2013). By increasing [DIP] and [DIN], the seedings relieved the ambient nutrient limitation and strongly stimulated primary

production (see Sect. 4.1). Based on estimation of the new production, Ridame et al. (2013) observed a switch from a regenerated-production-based system to a new-production-based system 24 h after the seeding.

3.2 Evolution of the POC flux

The temporal evolution of the averaged POC fluxes in the dust-seeded (POC_{dust}) and control ($POC_{control}$) mesocosms, as well as the difference between both fluxes (POC_{net}), are reported in Fig. 1. It should be noted that the organic carbon contained in dust (0.31 %) constituted a very small fraction of the POC flux and is not discussed here since its fate remains unknown (Desboeufs et al., 2014). The first seeding resulted in a POC_{dust} flux (111 mg m^{-2}) 2.3 times higher than the $POC_{control}$ flux (47.4 mg m^{-2}). The POC_{dust} flux remained high during the first 96 h (> 18.5 mg m^{-2} d^{-1}), and then decreased by ∼ 16 mg m^{-2} d^{-1} from T_{96} (day 5). Until the end of the first experiment (T_{166}), the POC_{dust} flux remained higher than the $POC_{control}$ flux.

The second seeding strongly reactivated the downward POC export, while the $POC_{control}$ flux (on average, ∼ 6.5 times lower) continually decreased, reaching a near-zero value at the end of the experiment (∼ 0.8 mg m^{-2} d^{-1}). The increase in POC_{dust} flux was particularly significant during the first 24 h ($T_{166(0)}$–$T_{190(24)}$) following the second seeding (+22.6 mg m^{-2} d^{-1}), and was characterized by a larger variation (45 %) between + dust mesocosms than the variation observed 24 h following the first seeding (20 %).

During the first 24 h following the second seeding, the POC_{net} flux was 1.8 times higher than that 24 h after the first seeding. On days 2 and 3, POC_{net} fluxes were similar between both experiments (∼ 10–15 mg m^{-2} d^{-1}) but differed widely on day 4, as follows: 15.4 and 5.5 mg m^{-2} d^{-1} for the first and the second experiments, respectively. The POC_{net} fraction collected over six days was slightly higher following the first seeding (62 mg m^{-2}) than after the second seeding (54 mg m^{-2}). Although these POC_{net} fluxes were similar, export dynamics differed in magnitude and duration. The POC export that stretched over time following the first seeding was intense, but was shorter following the second seeding.

3.3 Evolution of the optical parameters

b_{bp} and c_p measurements are representative of the various fractions of particulate matter stock (e.g., Loisel et al., 2011). b_{bp} is highly sensitive to changes in the abundance of small non-living particles, such as dust (Stramski and Kiefer, 1991; Ulloa et al., 1994), while the c_p (670) is dependent on the entire particle assemblage, excluding dissolved matter (Bricaud et al., 1981; Boss et al., 2009).

3.3.1 Depth integration

Thanks to the high-resolution vertical coverage of the water column using optical measurements, the integration of c_p (670) from the surface to 10 m depth (c_p (0–10 m)) provides a record of particulate matter (of both biological and lithogenic origin) accumulation or depletion over time (Fig. 2). At T_0, the c_p (0–10 m) was very low (0.46 m^{-1}), consistent with the oligotrophic status of the water column, and immediately increased by 3.2 m^{-1} following the first seeding; subsequently it continually increased, reaching 8.7 ± 1.4 m^{-1} (T_{48}–T_{53}). At $T_{166(0)}$, c_p (0–10 m) was ∼ 10 times higher (4.93 m^{-1}) than the T_0 value. Immediately following the second seeding, c_p (0–10 m) increased by 4.28 m^{-1} (9.21 m^{-1}), and then continually decreased, reaching a lower value (2.62 m^{-1}) than the initial value.

3.3.2 The vertical particle profiles

The different initial values and the opposite evolution of c_p (0–10 m) during the two seeding experiments suggest a different behavior of the dust and/or biological communities. The calculation of Δc_p (670) (c_p (670)–c_p $(670)_{initial}$; m^{-1}) allowed us to investigate the net effect of seedings over time and depth (Fig. 3). Following the first seeding, the decrease (∼ 1 m^{-1}) of Δc_p(670) within surface waters was rapidly (T_6) followed by an increase (∼ 0.2 m^{-1}) at depth (i.e., by an accumulation of particulate matter in comparison to the initial inventory of the water column). Between T_{30} and T_{48}, high and homogeneous Δc_p (670) values were observed over the entire water column. The second seeding induced a higher accumulation of particulate matter within the first two meters of the water column (Δc_p (670) up to 2.4 m^{-1} at 0.5 m depth). As demonstrated by the dust profile issued from particulate Al measurements within the water column (Desboeufs et al., 2014), the accumulation of particulate matter is mainly associated with the addition of dust. Negative Δc_p (670) values were rapidly observed (T_3–T_8) at depth, demonstrating the rapid removal of particulate matter present before the second seeding. Between T_8 and T_{30} the decrease of Δc_p (670) at the surface was followed by an increase at depth, indicating that an important transfer of matter toward depth occurred. Two days following the second seeding, Δc_p (670) was homogeneous but negative along the 0–10 m water column, indicating that most of the particulate export occurred during this period, in agreement with the POC_{dust} flux trend (Fig. 1).

The evolution of $\Delta b_{bp}(\lambda)$ ($b_{bp}(\lambda)$–$b_{bp}(\lambda)_{initial}$ in m^{-1}; Fig. 4) was also investigated in order to focus on the fate of the added particles. The wavelength used differed between experiments (see Sect. 2.3); however, we assumed that this calculation allowed us to compare the respective evolution of Δb_{bp}. Differences in the $\Delta b_{bp}(\lambda)$ profiles between experiments were less marked as compared to the Δc_p (670) profiles. Decreases in the $\Delta b_{bp}(\lambda)$ within surface waters were not associated with a proportional increase at depth, and could indicate that the "cleaning effect" of the water column highlighted using Δc_p (670) profiles could result from the sinking of larger particles, such as mixed aggregates, that

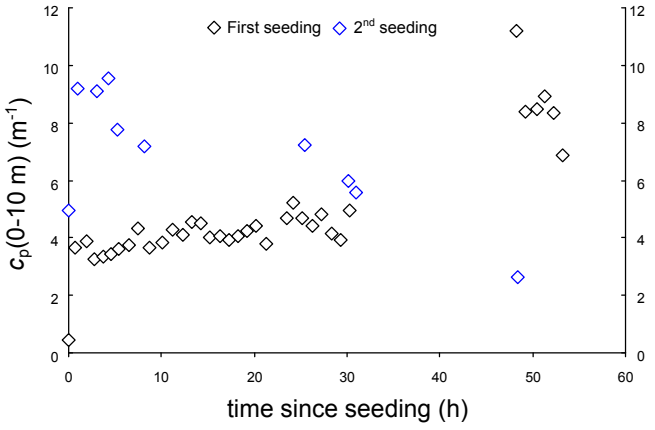

Fig. 2. Temporal evolution of the vertically integrated (0–10 m) particle attenuation coefficient (c_p (0–10 m)) during both seeding experiments.

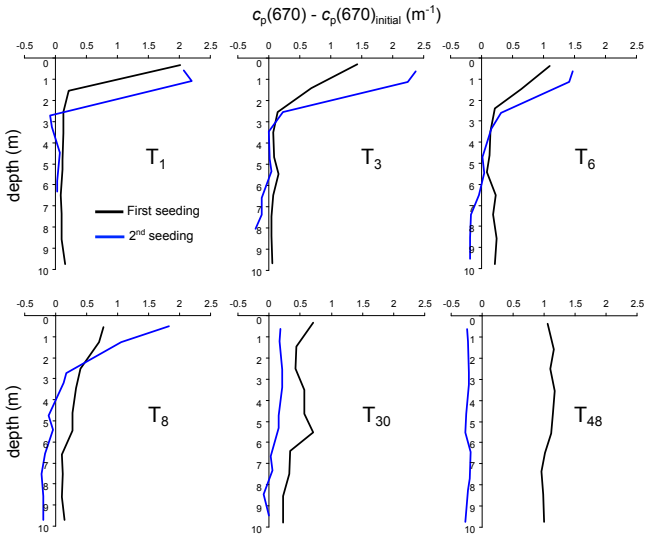

Fig. 3. The vertical profiles of Δc_p (670) (c_p (670)–c_p (670)$_{initial}$ in m^{-1}) for different times following both seedings. Negative values correspond to a decrease compared to the initial c_p (670) coefficient.

backscatter light less efficiently than small lithogenic particles (Twardowsky et al., 2001), as supported by particulate Al profiles showing a depletion of dust particles in the first 10 m between T_{24} and T_{48} (Desboeufs et al., 2014). Two days following both seedings, the $\Delta b_{bp}(\lambda)$ profiles were homogeneous along the water column and still positive, indicating that a portion of the lithogenic particle pool was still in suspension as suggested by Bressac et al. (2012).

4 Discussion

4.1 A comparison between primary production, POC, and lithogenic fluxes

The isolation of the water mass by the mesocosm could be conceptually compared to the effect of the strong stratification within the upper water column that typically occurs during the summer period. Within the sediment traps of control mesocosms, the observed very high POC to lithogenic ratio (not shown) indicated that lithogenic ballasting was negligible. In this context, $POC_{control}$ export can be considered as representative of the surface POC export that occurs in natural systems during oligotrophic periods without external forcing.

Since optical data was limited to the first 48 h of experiments, sediment trap data and primary production (PP) were used to determine the biological and lithogenic contributions in POC export over experiments. Similar increases in PP (by a factor of 2.3–2.4) were observed within + dust mesocosms following both seedings, while PP remained constant within control mesocosms (Ridame et al., 2014). Both data sets remained significantly different (p values < 0.05) throughout the experiment. The strong stimulation of PP went along with a rapid enhancement of the pigment content per cell and a rapid photoprotective response (Giovagnetti et al., 2013).

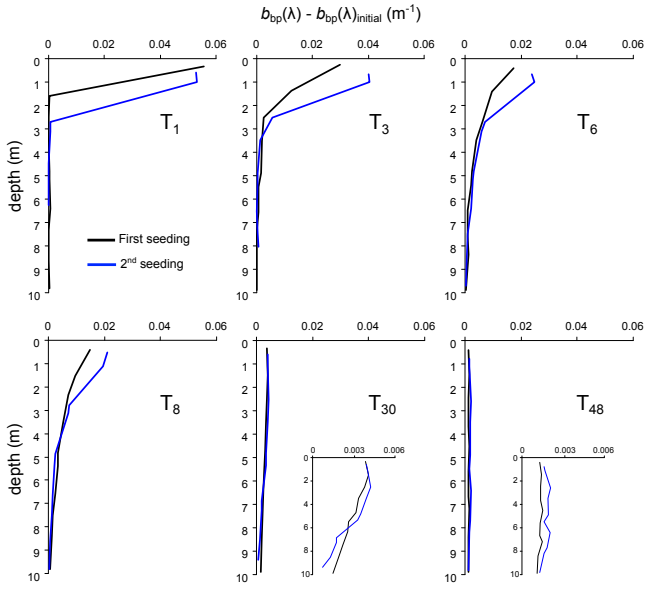

Fig. 4. Vertical profiles of $\Delta b_{bp}(\lambda)$ ($b_{bp}(\lambda) - b_{bp}(\lambda)_{initial}$ in m^{-1}) at different times following both seedings. The wavelength used for this calculation differed between experiments (see Sect. 2.3). The insets (the T_{30} and T_{48} panels) show a close-up of the 0–0.006 m^{-1} values.

Therefore, the increase in PP seems to have been favored by such physiological acclimation in relation to the high light environment (Guieu et al., 2013a).

The continual decrease in $POC_{control}$ flux during the experiment (Fig. 1) indicates that the constant primary production observed within control mesocosms was not sufficient to sustain the longevity of POC export throughout the

experiment, in agreement with the critical particle concentration concept which proposes that the (re)activation of the aggregation process and subsequent particulate export requires a particle concentration above a threshold value (Jackson and Lochmann, 1992; Boyd et al., 2005; Burd and Jackson, 2009). Atmospheric deposition could help to reach this threshold via the direct input of lithogenic particles, and indirectly through the supply of new nutrients, leading to an increase in algal biomass.

In the + dust mesocosms, a comparison between integrated PP data and POC fluxes indicated that no statistically significant relationship existed between these two parameters (p values > 0.05; Fig. 5). Introducing a time lag of 12 or 24 h between production and flux did not improve this relationship. The apparent decoupling between primary production and POC flux indicated that production alone could not be used to accurately predict POC fluxes.

Furthermore, following both seedings, the biomass of siliceous phytoplankton remained very low and a major response was observed for non-siliceous phytoplanktonic organisms (Giovagnetti et al., 2013). Although calcified organisms likely responded to the seedings, the fraction of biogenic $CaCO_3$ collected in sediment traps of + dust mesocosms remained negligible (3 ± 0.5 % in mass; Desboeufs et al., 2014). Therefore, biomineral ballasting was considered to be negligible and lithogenic particles were considered to be the main carrier phase of POC in + dust mesocosms, as confirmed by the scatter plot of the POC_{dust} flux versus the lithogenic flux, which indicated a statistically significant correlation (p value, < 0.0001; Fig. 6). For these analyses we assumed that the regressions did not pass through the origin (i.e., that an additional POC fraction not directly associated with the lithogenic flux may be a significant component of the fluxes (Honda and Watanabe, 2010)), as follows:

$$\text{POC}_{\text{dust}} \text{ flux} = a \times \text{lithogenic flux} + b, \quad (3)$$

where a is defined as the carrying coefficient (Klaas and Archer, 2002) and b corresponds to the unassociated POC flux. A simple linear regression analysis revealed that the lithogenic fluxes explained more than 85 % of the variance in POC_{dust} fluxes. The ratios of the POC_{dust} flux to the lithogenic flux (i.e., the carrying coefficient a) ranged from 0.013 (during the second seeding) to 0.016 (during the first seeding). A possible explanation for the decrease in the carrying coefficient following the second seeding is discussed later (see Sect. 4.3.2).

4.2 The dynamics and timing of particulate export

The c_p (670) coefficient, usually associated with the particle concentration (< 20 µm) (Chung et al., 1998), is widely used to follow particulate export (e.g., Bishop et al., 2002; Smetacek et al., 2012). As with the POC_{dust} fluxes and optical parameters, the phytoplankton community responded differently to both seedings with a distinct magnitude, timing, and composition change (Giovagnetti et al., 2013).

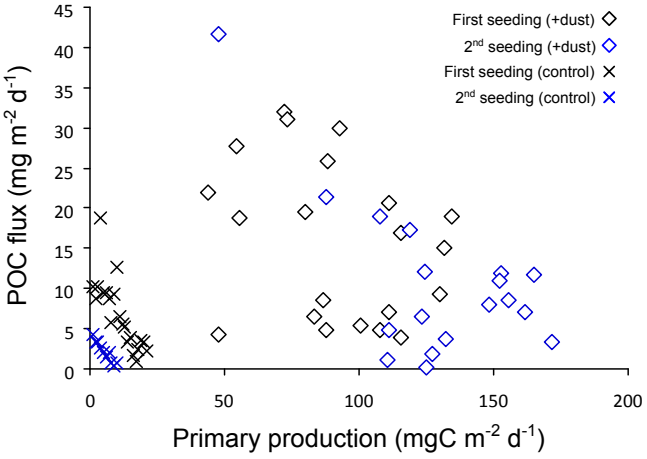

Fig. 5. POC flux for all of the mesocosms versus integrated primary production (PP). No significant correlation existed between PP and the POC flux in the + dust mesocosms (Fisher test, p values > 0.05).

Although optical measurements revealed rapid particulate export following the first seeding (Bressac et al., 2012), c_p (0–10 m) continually increased during the T_0–T_{53} period (Fig. 2). This increase, particularly marked between T_{48} and T_{53}, was consistent with an increase in picophytoplankton biomass (< 3 µm) that occurred two days following the first seeding, while larger cell-sized phytoplankton (> 3 µm) needed three days to increase in terms of biomass (Giovagnetti et al., 2013). The c_p (0–10 m) evolution indicated that biological production exceeded and masked particulate export, explaining the longer duration of POC_{dust} export during the first experiment (Fig. 1). The long time lag between the first seeding and biological response (2–3 days) and immediate POC_{dust} export activation (Fig. 1) highlighted the decoupling between POC export and biological production. On the basis of these observations, we suggest that the immediate twofold increase in POC_{dust} flux resulted from abiotic processes such as lithogenic ballasting (i.e., by aggregating cells and increasing particle sinking velocity), in agreement with the strong correlation observed between the POC and lithogenic fluxes during the entire first experiment (Fig. 6).

The opposite evolution of c_p (0–10 m) following the second seeding (Fig. 2) indicates that particulate export exceeded biological production ($T_{166(0)}$–$T_{214(48)}$). Even if a stronger biological response was observed (a threefold Chl a increase), dominated by the nano- and microphytoplankton communities (> 3 µm), it only occurred 24–48 h after the second seeding (Giovagnetti et al., 2013). Therefore, the negative Δc_p (670) values rapidly observed (T_3–T_8) at depth following the second seeding suggest that this immediate "cleaning effect" resulted from lithogenic ballasting. On a longer timescale, we can hypothesize that the preferential response of large cells, more prone to be exported, may have

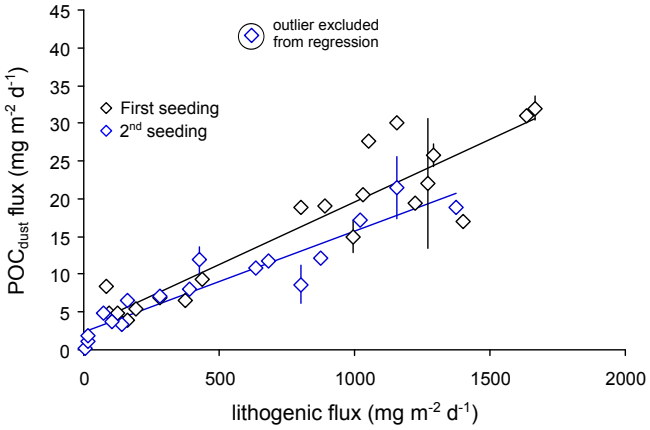

Fig. 6. POC_{dust} versus lithogenic fluxes. Solid lines represent linear regressions with the following slopes, intercepts, determination coefficients, and probabilities (Fisher test). First seeding: $N = 21$, slope = 0.016 ± 0.002, intercept = 3.11 ± 1.48, $R^2 = 0.85$, $p < 0.0001$. Second seeding: $N = 17$, slope = 0.013 ± 0.001, intercept = 2.41 ± 0.80, $R^2 = 0.88$, $p < 0.0001$. The highlighted outlier was excluded from the linear regression for second seeding data. Uncertainties correspond to the standard deviation of one sample measured two times.

increased the budget of exported carbon and changed the "biotic contribution" to POC export.

These observations suggest that a sequence of mechanisms controlled the particulate export. While the biological response was delayed, particulate export driven by algal aggregation during the first 48 h following both seedings is unlikely (e.g., Prieto et al., 2002). On the other hand, the input of 41.5 g of dust (with a grain size distribution from < 0.1 to ~ 20 µm) likely catalyzed the aggregation and adsorption processes on a short timescale (e.g., Lee et al., 2009) and activated particulate export. Thus, abiotic processes were likely dominant during the first 24–48 h until the biological contribution became significant and stretched over the time of particulate export. The decline could finally result from the imbalance between production and export, leading to a lower particle concentration within the water column than that required for the aggregation process.

4.3 The relationship between POC and lithogenic fluxes

The first general assessment for the carrying coefficients of ballast minerals was performed on a global scale (Klaas and Archer, 2002). Others studies that have generally focused on biominerals allowed these coefficients to vary in space (Ragueneau et al., 2006; Le Moigne et al., 2012; Wilson et al., 2012), or assessed them from individual sites (Wong et al., 1999; Conte et al., 2001; Honda and Watanabe, 2010). All of these analyses, performed at an annual timescale, reflect average fluxes during both productive and oligotrophic periods missing important temporal variability within the flux relationships. Therefore, we focused on specific dust-deposition events on timescales on the order of a week, representative of the residence time for dust within surface waters estimated from days to month (Buat-Ménard et al., 1989; Bory and Newton, 2000; Croot et al., 2004; Frew et al., 2006). During this artificial seeding experiment in LNLC ecosystems, the lithogenic fluxes were high and the algal biomass was likely too low to drive large POC flux events. Therefore, the low carrying coefficients estimated in this study (0.013–0.016; Fig. 6) did not correspond to a low absolute associated POC flux but rather suggested a low lithogenic normalized POC flux. Despite the strong and statistically robust relationships observed in the + dust mesocosms between POC and lithogenic fluxes (Fig. 6), the mechanistic basis for these OM-lithogenic particle interactions remains uncertain. The correlations could result from (1) the lithogenic ballasting of organic matter (Armstrong et al., 2002; Francois et al., 2002; Klaas and Archer, 2002), (2) the inclusion of lithogenic particles within organic matter (freshly produced) (Passow and De La Rocha, 2006); or (3) the coupling of both processes. To determine the respective contribution of these biotic and abiotic processes to POC export, two comparative approaches were successively employed.

4.3.1 The effect of biogeochemical conditions

As a result of the high variability in physical conditions during the course of this experiment (Sect. 3.1), a direct comparison of POC_{dust} fluxes between both experiments could bias our interpretation. Therefore, the POC_{dust} fluxes were compared to the respective $POC_{control}$ fluxes, first highlighting the global effect (the biotic plus abiotic processes) of both seedings (Fig. 7). For the same initial biogeochemical conditions (i.e., the first seeding), the POC_{dust} flux was, on average, 2.33 ($\pm$ 0.12) times higher than the $POC_{control}$ flux. Under different initial biogeochemical conditions (i.e., the second seeding), the POC_{dust} flux was, on average, 6.68 ($\pm$ 0.51) times higher than the $POC_{control}$ flux. On the basis of these observations, we conclude that the net effect of a dust-deposition event on POC export depends, in part, on the biogeochemical properties of the water column (the organic matter pool, the phytoplankton community) at the time of deposition. Among these biogeochemical parameters, the stronger increase in large cell (> 3 µm) biomass (Giovagnetti et al., 2013) could partly explain the larger difference observed during the second experiment.

Sorption of dissolved organic matter (DOM) from solution onto mineral surfaces could reach equilibrium very rapidly (within ~ 1 h; Arnarson and Keil, 2000, 2005). This process likely contributed to the downward POC export in the first 24 h following the seedings. By using the same dust analog and flux in 0.2 µm filtered seawater, Bressac and Guieu (2013) quantified this abiotically driven organic carbon export and its variation as a function of the composition and abundance of DOM. During this abiotic experiment, the

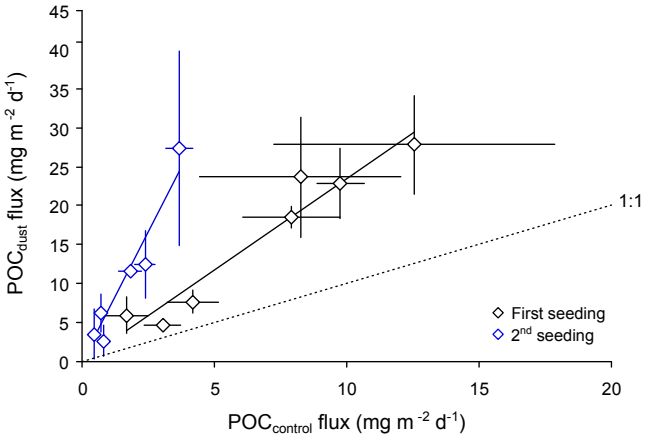

Fig. 7. POC_{dust} versus $POC_{control}$ fluxes (mean fluxes and standard deviations of the mesocosm triplicates). The best linear regressions and the 1 : 1 lines are shown. First seeding: $N = 7$, slope = 2.33 ± 0.12, $R^2 = 0.94$, $p < 0.0001$ (Fisher test). Second seeding: $N = 6$, slope = 6.68 ± 0.51, $R^2 = 0.93$, $p < 0.0001$ (Fisher test).

amount of organic carbon adsorbed onto dust particles and exported downward was of the same order of magnitude as the POC fluxes observed in the + dust mesocosms. Furthermore, sticky particles such as transparent exopolymer particles (TEP), known for promoting the aggregation process (Chin et al., 1998; Passow, 2002; Engel et al., 2004; Verdugo et al., 2004), could also have indirectly influenced the particulate export. Although DOM and TEP concentrations were not measured during this experiment, the abundance of such organic material prior to the second seeding was likely higher within the + dust than within the control mesocosms, contributing to the larger difference in POC fluxes observed following the second seeding.

Although lithogenic ballasting cannot be strictly considered as a pump (as surface primary production is required to sustain it), Bressac and Guieu (2013) introduced the concept of the "lithogenic carbon pump" in order to highlight the fact that aggregation and adsorption processes could trigger a dust-induced POC export event. As with the fertilization effect (e.g., Marañón et al., 2010), POC export abiotically triggered by dust deposition could vary according to the biogeochemical state of sea surface waters at the time of deposition (Bressac and Guieu, 2013).

4.3.2 Biotic and abiotic contributions to POC export

With the objective of determining the strength of this "lithogenic carbon pump", the second comparative approach consisted of a deconvolution of the "ballasted" and "unballasted" POC fluxes. For this purpose, the POC_{dust} flux could be partitioned into two pools, a fraction associated with lithogenic particles (POC_{lith}) and a "freshly" produced one induced by the input of new nutrients (POC_{ferti}), as follows: $POC_{dust} = POC_{lith} + POC_{ferti}$. Also known as the particle export efficiency (e.g., Buesseler, 1998; Lutz et al., 2002; Henson et al., 2012), POC_{lith} was estimated by normalizing the POC_{dust} fluxes to the respective integrated PP value (Fig. 8). As biomineral ballasting was negligible during this experiment (Sect. 4.1), the difference in this parameter between the control and + dust mesocosms was assumed to result from lithogenic ballasting. POC_{lith} was 1.17 ($\pm$ 0.19) (during the first seeding) and 2.84 ($\pm$ 0.19) (during the second seeding) times higher than the control's POC_{lith}. According to the relationships obtained using both comparative approaches (Figs. 7 and 8), POC_{lith} represented 50 ± 8 and 42 ± 3 % of the POC_{dust} fluxes after the first and the second seeding, respectively; consistent with a higher biological contribution to POC export following the second seeding (Sect. 4.2). A possible explanation of the relative decrease in the POC_{lith} after the second seeding is the scavenging of most of the biogenic particles from the water column following the first seeding. Such a decrease was observed by Lee et al. (2009) following successive dust-deposition events and suggests that POC_{lith} following the second seeding was allowed by the OM production induced by the first pulse of new nutrients, reflecting a highly dynamic system. A second key finding is that POC_{ferti} largely exceeded the variance in POC fluxes unexplained by lithogenic fluxes ($\sim$ 15 %; Fig. 6), demonstrating that the carrying coefficient should be carefully interpreted. Such a finding calls into question whether or not a simple fertilization mechanism exists or whether the lithogenic ballasting of POC_{ferti} could occur and favor its downward export.

4.4 One dust-deposition event, several particle settling populations

Both the coupling (e.g., Jickells et al., 1998; Migon et al., 2002; Ternon et al., 2010; Brust et al., 2011) and decoupling (e.g., Buat-Ménard et al., 1989; Migon et al., 2002; Ternon et al., 2010) of dust deposition and particulate export have been reported. During our experiment, only $\sim$ 57 and 41 % (by mass) of the lithogenic particles initially added were recovered in the sediment traps six days after the first and second seedings, respectively (Desboeufs et al., 2014). Neuer et al. (2004) collected samples at $\sim$ 500 m depth with between 13 and 20 % of lithogenic material deposited, and concluded that a large fraction of lithogenic matter was not removed by particle sedimentation. Based on Stokes' law, we estimated that approximately half (in mass) of the dust population was large enough (> 5 µm) to settle without being included in aggregates, and would reach the sediment traps of mesocosms before the end of the experiment. The smaller lithogenic particles (< 5 µm) that were numerically dominant likely remained in suspension, in agreement with Δb_{bp} (660), still positive at $T_{166(0)}$ (not shown). The result could have been influenced by ephemeral dust-induced phytoplankton blooms, which did not supply a sufficient amount

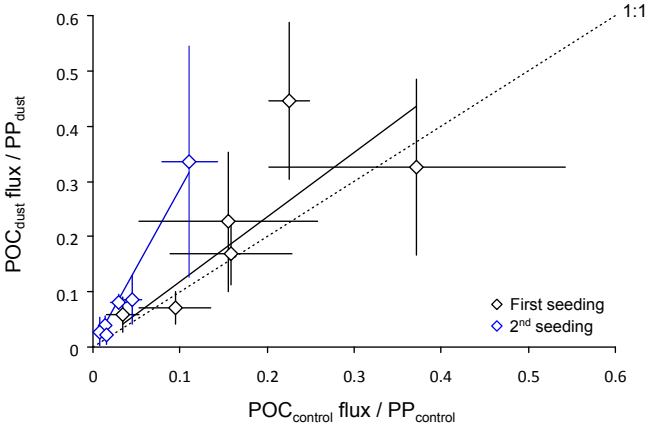

Fig. 8. POC_{dust} versus $POC_{control}$ fluxes, both normalized with respect to integrated primary production values (PP). The best linear regressions and the 1 : 1 lines are shown. First seeding: $N = 6$, slope = 1.17 ± 0.19, $R^2 = 0.56$, $p < 0.0001$ (Fisher test). Second seeding: $N = 6$, slope = 2.84 ± 0.19, $R^2 = 0.96$, $p < 0.0001$ (Fisher test).

of OM "glue", and by the rapid scavenging of most of the biogenic particles following both seedings.

In the open ocean, this pool of small lithogenic particles remains stored within surface layers during the stratification period until either the onset of vertical convection during winter (e.g., Migon et al., 2002), or their inclusion into faecal pellets (e.g., Buat-Ménard et al., 1989) or larger aggregates (e.g., Burd and Jackson, 2009). For this last case, POC fluxes could scavenge these slow-settling lithogenic particles from the water column and determine their flux (Passow and De La Rocha, 2006). The particle population could also act as a nucleation point for aggregate formation, and, therefore, contribute to a second POC export event (e.g., Ternon et al., 2010). Actually, a decoupling between the deposition and export of this particle population will occur, preventing a direct temporal comparison. Finally, the long residence time within surface waters for such highly refractive submicron lithogenic particles has been advanced as an explanation of the color anomaly of the ultra-oligotrophic waters of the Mediterranean Sea (Claustre et al., 2002; Loisel et al., 2011). Our observations demonstrated the possible lasting impact of atmospheric lithogenic particles on seawater optical properties.

5 Conclusions

By combining the use of sediment traps and high-resolution vertical optical profiles inside large mesocosms deployed within a LNLC system, we report surface particulate export following two successive dust-deposition events. Although the mechanism driving the relationship between POC and ballast material remains uncertain (De La Rocha and Passow, 2007), we have demonstrated in the present study that (1) dust deposition catalyzes particle-sinking events (e.g., Lee et al., 2009; Ternon et al., 2010), and (2) the intensity of POC–lithogenic particle association depends on the biogeochemical conditions of surface seawater at the time of deposition. The results obtained could be used to parameterize surface POC export in oligotrophic systems receiving high rates of dust deposition (e.g., the Mediterranean Sea) and to better predict the effects of future changes in atmospheric dust fluxes (Mahowald et al., 2009).

The lack of a significant relationship between POC flux and primary production combined with the high degree of covariance between POC and lithogenic fluxes adds further support to the ballast hypothesis. The probable composition of sinking aggregates (the high content of lithogenic material and the low amount of relatively buoyant OM), as well as their sinking velocity ($\sim$ 24–86 m d^{-1}; Bressac et al., 2012) suggest low specific carbon remineralization (Riley et al., 2012). Furthermore, the inherent sporadic character of the lithogenic carbon pump may play a fundamental role in carbon sequestration (Ragueneau et al., 2006) since episodic events may lead to the rapid sinking of particles that will not be fully exploited by the deep sea bacterial community (Hansell and Ducklow, 2003; Nagata et al., 2000, 2010). As a result, the major fraction of the deep sea POC flux following dust-deposition events likely corresponds to the remnants of surface ballasted POC stocks (e.g., Thunell et al., 2007; Honda and Watanabe, 2010).

Impacts on heterotrophic activity must be taken into account in order to achieve connections between dust-deposition and ocean carbon cycling (Pulido-Villena et al., 2008). Both seedings maintained the strong net heterotrophic character of the ecosystem, indicating that bacteria are key players in the ecosystem response to dust depositions (Pulido-Villena et al., 2014), which leads to the remineralization of a fraction of fixed algal carbon, and, therefore, to a decrease in the amount of exported organic carbon (Guieu et al., 2013b). While dust deposition can have a fertilization effect on the phytoplankton compartment by bringing new nutrients, the labile OM produced could escape being remineralized within the upper ocean through its physical associations (i.e., aggregation and adsorption processes) with dust particles and subsequent lithogenic ballasting.

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