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Dust deposition in an oligotrophic marine environment: impact on the carbon budget

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Abstract

By bringing new nutrients and particles to the surface ocean, atmospheric deposition impacts biogeochemical cycles. The extent to which those changes are modifying the carbon balance in oligotrophic environments such as the Mediterranean Sea that receives important Saharan dust fluxes is unknown. DUNE project provides the first attempt to evaluate the changes induced in the carbon budget of an oligotrophic system after simulated Saharan dust wet and dry deposition events. Here we report the results for the 3 distinct artificial dust seeding experiments in large mesocosms that were conducted in the oligotrophic waters of the Mediterranean Sea in summer 2008 and 2010. Simultaneous measurements of the metabolic rates (C fixation, C respiration) in the water column have shown that the dust deposition did not change drastically the metabolic balance as the tested waters remained net heterotroph (i.e. net primary production to bacteria respiration ratio < 1) and in some cases the net heterotrophy was even enhanced by the dust deposition. Considering the different terms of the carbon budget, we estimate that it was balanced with a dissolved organic carbon (DOC) consumption of at least 10 % of the initial stock. This corresponds to a fraction of the DOC stock of the surface mixed layer that consequently will not be exported during the winter mixing. Although heterotrophic bacteria were found to be the key players in the response to dust deposition, net primary production increased about twice in case of simulated wet deposition (that includes anthropogenic nitrogen) and a small fraction of particulate organic carbon was still exported. Our estimated carbon budgets are an important step forward in the way we understand dust deposition and associated impacts on the oceanic cycles. They are providing knowledge about the key processes (i.e. bacteria respiration, aggregation) that need to be considered for an integration of atmospheric deposition in marine biogeochemical modeling.

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1 Introduction

Atmospheric deposition provides new nutrients to the marine environment and, in a number of oligotrophic environments submitted to significant deposition, those new nutrients are likely able to relieve on going (co)limitations by providing available nitrogen, phosphorus, iron and other micronutrients (de Leeuw et al., 2013). The response of the biota to such input (natural, polluted or mixed aerosols) has been explored in a number of experimental artificial aerosols addition and in situ observations. In a recent paper, Guieu et al. (2014a) have synthetized the results from 26 of those studies showing that biota in Low-Nutrients and Low-Chlorophyll (LNLC) areas positively responds to aerosol addition, with bacterial production and N_2 fixation showing the strongest responses. Increases in chlorophyll *a* (Chl *a*) have also been seen but to a lesser extent. In fact, this synthesis shows that changes in biological standing stocks tend to be smaller than changes in metabolic rates (i.e. chlorophyll *a* vs. primary production, and bacterial abundance vs. bacterial respiration and/or production). Indeed, this could be due to the effect of grazing by zooplankton on phytoplankton and bacteria, (i.e. Bonnet et al., 2005; Herut et al., 2005; Marañón et al., 2010) which may increase turnover at the expense of stocks and rapidly propagate responses through the whole food web. This may result in an experimental artifact in that Chl *a* concentration may increase in experiments where grazers are filtered, but remains unchanged in natural waters, possibly explaining the variable and low response of satellite-derived chlorophyll signals to dust events (Volpe et al., 2009). This indicates that the use of metabolic rates instead of stocks seems more appropriate in tackling the response of biota to atmospheric deposition. Unfortunately, only a couple of studies have so far considered together the changes in metabolic rates induced by atmospheric deposition for both autotrophic and heterotrophic communities: for example, Herut et al. (2005) show that both communities were highly stimulated after fresh dust addition to surface seawater in microcosm experiments with bacterial production (BP) stimulated twice as much as primary production (PP) in the ultra-oligotrophic eastern Mediterranean Sea (increase

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of 770 % and 450 %, respectively). Marañon et al. (2010) conducted eight bioassay experiments, over the basin-wide geographical range in the tropical Atlantic and have shown that the effect of Saharan dust deposition on the biological activity of the surface ocean may vary with the degree of oligotrophy of the tested waters. For four out of the eight addition experiments, the relative change in response to dust exceeded a value of 200 % for BP and community respiration (CR), whereas PP never increased by more than 100 % (Marañon et al., 2010). In the western Mediterranean Sea, Pulido-Villena et al. (2008) also show a strong stimulation of bacterial respiration (BR) after dust deposition either in microcosms (125 % average increase in BR) or in situ (100 % increase), the stimulation being proportional to the intensity of the dust flux. Unfortunately no autotrophic metabolic rate was measured during that study. Depending on the balance between the heterotrophic vs. autotrophic community, the stimulation by atmospheric deposition may thus either result in a CO_2 input or a CO_2 output in oligotrophic environments. Such opposite effects in terms of carbon (C) fate deserve to be explored if we want to understand the role of atmospheric deposition in marine ecosystem functioning, C cycling and feedbacks on climate.

Finally, it has been shown recently that aggregation and sorption processes between atmospheric lithogenic particles and in situ (dissolved and particulate) organic matter and subsequent ballasting can induce a strong and rapid particulate organic carbon (POC) export independently of a fertilization effect (Ternon et al., 2010; Bressac and Guieu, 2013; Bressac et al., 2014; Desboeufs et al., 2014). So far, the balance between the different main processes involved in the C cycle after a dust deposition has never been explored. As shown in Guieu et al. (2014b), the 52 m^3 mesocosm strategy developed during the DUNE (a DUst experiment in a low Nutrient, low chlorophyll Ecosystem, http://www.obs-vlfr.fr/LOV/DUNE/index.html) project allows us to consider a number of stocks and fluxes after a representative simulation of atmospheric deposition performed in situ at the surface of a large body of water. In particular considering the vertical transport of particles within the 12.5 m depth of the mesocosms over a rep-

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resentative length of time (7 days after the deposition) is an important improvement compared to the microcosm strategy.

Here we first explore how the balance between bacterial respiration and net primary production evolve after the dust deposition. We then attempt to use the numbers obtained (stocks and fluxes), along with estimates, to quantify how the carbon budget modified by the introduction of dust simulating wet and dry deposition events can be balanced. We report the results for the 3 distinct artificial seeding experiments that were conducted in the frame of the DUNE project in the oligotrophic waters of the Mediterranean Sea in summer 2008 and 2010.

2 Methods

2.1 Three seeding experiments during oligotrophic period in the oligotrophic waters of the Mediterranean Sea

The methodology concerning the "large clean mesocosms" (diameter: 2.3 m, surface area: 4.15 m^2, and volume: 52 m^3) setup is fully described in Guieu et al. (2010) and the 2 field campaigns main features are described in a companion paper (Guieu et al., 2014b). In this paper we will report on primary production (PP), bacterial respiration (BR) and particulate organic carbon export (POC_{export}) data acquired during the campaigns DUNE-1 in June 2008 and DUNE-2 in June–July 2010. DUNE-1 consisted in two distinct 8 day experiments: a first simulation of a Saharan wet deposition event (hereafter named "DUNE-P") and a second simulation of a Saharan dry deposition event (hereafter named "DUNE-Q"). DUNE-2 consisted of a single 16 day experiment (hereafter named "DUNE-R") with 2 successive dust wet deposition simulations with 7 days between each seeding (respectively named "R1" and "R2"). Mineral dust deposition was mimicked using the finest fraction (< 20 µm) of alluvial soils collected in a desert soil source area in south Tunisia known to export Aeolian dust to the western Mediterranean (Guieu et al., 2010). Dry deposition was mimicked using the raw

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soil dispersed in surface seawater whereas wet deposition was mimicked using the same sieved soils after a chemical treatment reproducing cloud water processing by condensation-evaporation. This "evapo-condensed" dust is named hereafter "EC-dust". The methodology to produce those proxies of wet and dry dust deposition is fully described in Guieu et al. (2010). Both dust types had similar chemical composition for nutrients i.e. P, Fe and C, but not for N because of the addition of HNO_3 in the simulated cloud water used to process dust for wet deposition simulation (Guieu et al., 2010). Their respective detailed composition is reported in Desboeufs et al. (2014). For each experiment, 3 mesocosms "CONTROL" without dust addition and 3 mesocosms "DUST" seeded each with a dust flux of $10\,g\,m^{-2}$ were deployed. In addition for DUNE-R, a fourth mesocosm was seeded with EC-dust and was devoted to optical measurements (see details in Bressac et al., 2012). The ways the dust was seeded and the mesocosms sampling strategy are fully described in Guieu et al. (2010, 2014). Sampling is summarized hereafter.

2.2 Methodology for sampling and measuring bacteria respiration (BR), net primary productivity (NPP) and particulate organic carbon flux (POC_{export})

The methods are described in companion papers of this special issue (see for bacteria respiration: Pulido-Villena et al., 2014, net primary productivity: Ridame et al., 2014 and POC_{export}: Bressac et al., 2014, and Desboeufs et al., 2014). The main points are summarized here. The sampling was done every day at the same hours.

BR – Briefly, BR was determined on 5 m depth samples from each mesocosm gently filtered through a 0.8 µm polycarbonate filter under low vacuum pressure and siphoned into a set of six BOD (biological oxygen demand) bottles. Three BOD bottles from each mesocosm were immediately fixed with Winkler reagents. The other 3 were incubated during 24 h in the dark in a tap water bath to minimize temperature variations and were then fixed with Winkler reagents. Oxygen concentration was measured through a spectrophotometric approach based on measuring the absorbance at 466 nm of the colored I_2 and I_3^- (Labasque et al., 2004, Reinthaler et al., 2006). There is growing evidence

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that the used technique, involving pre-filtration and long incubation time, can lead to an overestimation of the BR rates (see for example, Aranguren-Gassis et al., 2012). This potential overestimation should not be a big problem as far as results are compared with literature data (mostly obtained with the same method) and/or relative changes after dust addition are concerned. We are aware, however, that absolute values of BR or net CO_2 fluxes must be taken with caution.

NPP – One sample per depth was collected at both 0.1 and 5 m depth during DUNE-P and -Q and at 5 m depth only during DUNE R, for the determination of NPP using the ^{13}C uptake determination method. Immediately after sampling, ^{13}C tracer was added to obtain a final enrichment of about 9 atom% excess. Then, the ^{13}C-amended bottles were incubated under in situ conditions on a mooring line for 24 h at the corresponding sampling depths. Incubations were ended by filtration onto pre-combusted 25 mm glass fiber filters. Sample filters were stored at −20 °C and dried at 40 °C for 48 h before analysis. Concentration of carbon in particulate matter and ^{13}C-enrichment were quantified using a ThermoFisher Scientific™ (Bremen, Germany) isotope ratio mass spectrometer (IRMS) Delta plus, coupled with a C/N analyzer Flash EA via a type III-interface. This net primary productivity corresponds to the net particulate primary productivity.

POC_{export} – Samples from sediment traps were preserved using a 5 % buffered solution of formaldehyde. Swimmers were carefully handpicked and the remaining sample was desalted using ultrapure water and freeze-dried. Mass flux was determined by weighing the entire freeze-dried sample. The total concentration of carbon (TC) was measured using a CHN analyzer (Perkin Elmer 2400). HNO_3/HF acid-digestion was performed in 7-mL Teflon flasks at 150 °C. Following complete evaporation, samples were diluted in 0.1 M HNO_3 and analyzed for their calcium (Ca), and sulfur (S) concentrations by ICP-AES (Desboeufs et al., 2014). In dust analogs Ca is present both as calcium carbonate and calcium sulfate (Guieu et al., 2010; Desboeufs et al., 2014). The part of Ca associated with sulfate ($\%Ca_{CaSO_4}$) was estimated from the particulate S concentration. Therefore, the particulate Ca concentration as carbonate ($\%Ca_{CaCO_3}$) corresponded to the difference between total Ca (%Ca)

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and $\%Ca_{CaSO_4}$. The carbonate fraction ($CaCO_3$) was determined from the $\%Ca_{CaCO_3}$ ($\%CaCO_3 = 100/40 \cdot \%Ca_{CaCO_3}$). Particulate inorganic carbon (PIC) was then deduced from $CaCO_3$ ($\%PIC = 12/100 \cdot \%CaCO_3$). Finally, POC_{export} was determined by subtracting PIC from TC in sediment trap samples.

Dissolved Organic Carbon (DOC) – Samples were taken for DOC but we decided to not use the results as unexpected high concentrations and/or variability (either among the 3 depths in a same mesocosm or at the same depth in the triplicate mesocosm were found for many samples, randomly. Unfortunately, the same was observed for filtered samples either transferred in combusted glass ampoules (P and Q experiments) or in acid-washed HDPE bottles (R experiments). This kind of issue with DOC measurements from samples collected in mesocosms has already been reported and suspected to be attributed to contamination of samples during sample collection and transport as well as during instrument deployment inside the mesocosms (Engel et al., 2013). Only the measurements for in situ ("OUT") measured during DUNE-P will be considered here as a background reference for DOC concentration at the mesocosm site. The mean concentration 87 ± 9 µM ($n = 11$) was above the typical concentration of the oligotrophic situation at the DYFAMED site for the same season (75 µM; Lemee et al., 2002; Pulido-Villena et al., 2008) but lower than the maximum concentration measured during a 16-months time series in a station overlying a Posidonia Oceanica meadow at 8 m depth (135 µM, Bay of Blanes, Navarro et al., 2004). High abundances of Posidonia seagrasses also characterize our study site in Corsica.

2.3 Data integration

The whole data set is presented in Table S1. NPP and BR fluxes were integrated over the mesocosm depth (12.5 m) assuming that the measurement at 5 m is representative of the flux over the entire mesocosm based on the significant similarity ($p > 0.05$) of the Chl-*a* concentrations measured at 0.1, 5 and 10 m depth for NPP and on the homogeneity of bacteria abundance for BR (Pulido-Villena, 2013).

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2.4 Statistical tests

The mean relative changes (RC, in %) after the P, Q, R1 and R2 seedings were calculated as $(X_{Dust} - X_{Control}) \times 100/(X_{Dust})$ for each parameter (X = NPP, BR and POC_{export}), where $X_{Control}$ is the mean for the 3 mesocosms CONTROL. In order to compare the results between experiments), means were compared using a one-way ANOVA and a Fisher Least Significant Difference (LSD) means comparison test ($\alpha = 0.05$). When assumptions for ANOVA were not respected, means were compared using a Kruskal-Wallis test and a post hoc Dunn's test. The statistical tests and the box plots were performed using the Addinsoft™ XLstat software (http://www.xlstat.com).

3 Results

3.1 Orders of magnitude of the background fluxes

The orders of magnitude of all the POC export, NPP and BR fluxes measured in the CONTROL-mescosms and the DUST-mesocosms before seeding for the three experiments are reported in Table 1. Among the 3 parameters, NPP was the more stable flux in the tested waters over the 3 experiments (variation coefficient of 24 %). POC_{export} and BR were more variable but with variation coefficients below 100 % (82 and 68 % respectively).

For POC_{export}, no data are reported at such a depth as sediment traps are usually placed below 100 m depth (see synthesis data for the Mediterranean Sea in Ternon et al., 2010). Comparing POC export in surface waters (15 m in the DUNE experiments) and at 150–200 m is difficult as a high remineralization occurs reducing rapidly the amount of POC as a function of water depth, but at least our numbers can indicate orders of magnitude of the POC export from the surface mixed layer (SML) during summer in the western Mediterranean Sea (mixed layer depth from 10 to 15 m; D'Ortenzio et al., 2005). Ternon et al. (2010) measured an average POC flux at 200 m over 4 yr

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of $11 \pm 12\,mg\,C\,m^{-2}\,d^{-1}$ at the DYFAMED (DYnamique des Flux Atmosphériques en MEDiterranée) site located in the northwestern Mediterranean Sea, with the lowest values from July to December. Our values at 15 m are in the lower range of values reported for the Ligurian Sea at 200 m at the same period of the year, indicating that the POC export flux was extremely low in the tested waters during DUNE.

Net primary production measured over 7 yr at the DYFAMED site in the Ligurian Sea in the surface mixed layer after the spring period ranged from 2 to $10\,\mu g\,C\,L^{-1}\,d^{-1}$ (Marty and Chiaverini, 2002), which is in good agreement with the NPP rates measured in the tested waters during the DUNE experiments. Such values are typical of non-productive waters of the open ocean (del Giorgio et al., 1997).

Bacterial Respiration – A recent review on heterotrophic bacteria in the Mediterranean Sea (Pulido-Villena et al., 2012) indicates the scarcity of data on bacterial respiration compared to abundance and production, with only few studies focusing on the western basin, all showing high seasonal variability of BR for both coastal and open waters. BR values of the tested waters during the DUNE experiments were in the upper range of the most recent data obtained at the open sea DYFAMED site (Pulido-Villena et al., 2008) in the Ligurian Sea with values in May being $14.4 \pm 7.2\,\mu g\,C\,L^{-1}\,d^{-1}$. In particular, during DUNE-P, BR was higher than previously reported for the open Mediterranean Sea, with values more similar to coastal data as those reported by Navarro et al. (2004). As pointed out by these authors, the production of dissolved organic carbon (DOC) by seagrass meadows, highly abundant in the DUNE study site, may be responsible for such high BR rates.

All those comparisons indicate that our study site is a low productive oceanic system with low POC export.

Order of magnitude of induced changes – In order to evaluate the overall impact of the dust deposition on POC export, NPP and BR, the parameters were integrated (POC) or averaged (NPP, BR) over the same duration (7 days) after the artificial seedings. The relative changes (RC in %) compared to CONTROL-Meso are represented in Fig. 1.

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Average increases relative to CONTROL-meso over 7 days higher than 500 % were observed only for POC_{export}. NPP did not increase after seeding during the Q experiment (dry deposition) and for the other experiments it increased in the range 75–144 %. BR increased in the range 137–156 % in P, Q and R2; a factor 2 higher increase of BR was observed after the R1 seeding (291 %).

Heterotrophic character of the tested waters – In the literature, the NPP/BR ratio is commonly used to quantify the metabolic status of aquatic systems (see for ex. Del Giorgio et al., 1997; Duarte and Augusti, 1998). If NPP > BR, then the considered system would be a CO_2 sink and on the contrary, if NPP < BR, the ecosystem would be a CO2 source. During DUNE, the average NPP/BR ratio was always ≤ 0.5 in the CONTROL-meso (Fig. 2) indicating that the total carbon processed by bacteria exceeds by far the carbon fixed by phytoplankton: all the tested waters during DUNE before dust addition would thus be a source of dissolved CO_2. This is in good agreement with recent findings that unproductive aquatic systems are net heterotrophic (del Giorgio et al., 1997). This is reported for the whole Mediterranean sea (Duarte et al., 2013) and in the NW Mediterranean Sea (i.e. Lemee et al., 2002).

There are extremely large ranges of the gross primary production (GPP)/Community respiration (CR) ratio reported in the literature; for example, in open ocean, GPP/CR mean is 1.71 with values ranging from 0.05 to 45.7 (Duarte and Agusti, 1998). As a simplistic first approach, if we consider that the phytoplankton respiration accounts for about 20–40 % of GPP (Marra and Barber, 2004) and represents 10–20 % of total primary production, and that BR represents on average 50 % of CR in the western Mediterranean Sea (see for ex. Navarro et al., 2004; Obernosterer et al., 2010), our min-max GPP/CR would be 0.11–0.16 during DUNE-P, 0.3–0.45 during DUNE-Q, 0.22–0.33 during DUNE-R1,and 0.16–0.24 during DUNE-R2. This is lower than the ratio given for the Mediterranean Sea by Duarte et al. (2013): GPP/CR = 0.74 ± 0.22. DUNE data are also in the lower range of the data compiled in Giorgio et al. (1997).

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4 Discussion

4.1 A strong heterotrophic character remains after seeding

Although there are some variations in between the triplicate mesocosms as one may expect in natural systems responding to external forcing such as atmospheric deposition, the DUNE data show an increase in both BR and NPP fluxes after seeding (except for NPP for DUNE-Q). The first important point is to note that NPP/BR are below 1 with the average value for the whole data set being 0.32 ± 0.25. As seen on Fig. 3, NPP/BR tends to be significantly lower in DUST-Meso compared to CONTROL-Meso for P and Q indicating that the dust deposition induced an increase in the net heterotrophic character of the tested waters in these experiments.

Indeed, when normalizing to CONTROL values (Fig. 4), there is evidence that the net heterotrophic character of the waters is increasing after seeding for P and Q experiments. Normalized ratio are also on average below 1 after the first seeding of R, but after the second seeding, the ratio is found slightly above 1, signifying that the evolution of the NPP/BR ratio was roughly comparable in both seeded and non-seeded mesocosms. So except for the second seeding of DUNE-R experiment, the dust input did increase the net heterotrophic character of the tested waters.

DUNE setup offers the opportunity to quantify how the carbon budget is perturbed after a simulation by an intense dust deposition onto an oligotrophic system. As discussed in the introduction, until recently most of the studies on impact of dust deposition on the surface ocean have focused on the stimulation of phytoplankton. But a first comprehensive study has been published recently indicating how the bacteria community can be stimulated preferentially to autotroph community in the oligotrophic ocean, this stimulation being likely a function of the degree of oligotrophy status where and when the dust deposition does occur (Maranon et al., 2010). Our data are in very good agreement with this previous study as we show that both bacteria activity and primary production have been stimulated by the wet dust input, the stimulation of the bacterial respiration being either higher than that of net CO_2 fixation after the dust event (R1 ex-

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periment) or equivalent (P and R2). The dust deposition did not thus change drastically the metabolic balance as the tested waters remained net heterotroph. In the 2 cases of DUNE-1 (P, Q), the net heterotrophy was even enhanced by the dust deposition. But this simplistic picture is of course incomplete if other processes that alter the carbon balance are not taken into account.

4.2 Carbon balance

As argued in Guieu et al. (2014b), our large clean mesocosms are closed systems with no lateral advection, enclosing a body of water large enough to be representative of the water outside and where stocks and fluxes can be measured after a perturbation such as a simulated dust deposition. Here, we will attempt to use the numbers obtained along with estimates of unmeasured parameters in order to quantify how the carbon budget is affected after dust deposition.

The mass balance equation for organic carbon from the mesocosm approach can be written as follows:

$$(\delta C_{\mathrm{org}}/\delta t) = (\delta \mathrm{POC}/\delta t) + (\delta \mathrm{DOC}/\delta t) = \mathrm{NCP} - \mathrm{POC}_{\mathrm{export}} + \mathrm{At}_{\mathrm{input}} \quad (1)$$

with NCP, the net community production, $\mathrm{POC}_{\mathrm{export}}$, the particulate organic carbon exported downward as measured in the sediment traps, and $\mathrm{At}_{\mathrm{input}}$, the amount of organic carbon added by the top to the DUST-meso by seeding (0.31 % of the total dust as determined by Desboeufs et al., 2014).

NCP is the difference between gross community production (GCP) and community respiration (CR): NCP = GCP – CR. The gross community production can also be expressed by the sum of the net primary production (NPP) that corresponds to the particle primary production in stratified conditions, and of the dissolved primary production (DPP): GCP = NPP + DPP. The community respiration comprises the bacterial respiration, the phytoplankton respiration and the zooplankton respiration. Considering that bacterial respiration represents on average 50 % of the community respiration in the western Mediterranean Sea (see for ex. Navarro et al., 2004, Obernosterer et al., 2010,

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although a fraction of the BR can be missed as it was measured on the fraction < 0.8 µm that does not take into account the attached bacteria), CR ≈ 2 BR and Eq. (1) can be rewritten as:

$$(\delta C_{org}/\delta t) = (\delta POC/\delta t) + (\delta DOC/\delta t) = NPP + DPP - 2BR - POC_{export} + At_{input} \quad (2)$$

Photosynthetic production of dissolved organic carbon (DPP) has been found to be a non-negligible fraction of the total primary production (dissolved and particulate) (see for ex. Baines and Pace, 1991). A similar range of its contribution to total primary production has been found in situ for open ocean oligotrophic systems (i.e 22 % Maranon et al., 2005; 14 %±7 for 9 studies in marine systems reported in Baines and Pace, 1991) and, from a mesocosm study in a coastal productive ecosystem, (19 % Lopez-Sandova et al., 2010). According to recent work in the western Mediterranean Sea in summer (Lagaria et al., 2011), DPP was found to represent ∼ 10 % of the total photosynthetic production. The term DPP in Eq. (2) can thus be replaced by DPP = (0.1·NPP).

The calculation of $(\delta C_{org}/\delta t)$ is given in Table 2a. Results indicate that the organic carbon sinks, especially respiration, strongly dominate the organic carbon sources, demonstrating that the dust deposition induced a loss of organic carbon of the system in all the experiments, particularly marked after the 3 simulated wet deposition events (P, R). In an attempt to quantify dissolved and particulate partitioning of this organic carbon sink, we have first calculated the changes induced by the seeding inside the mesocosm in the particulate pool $(\delta POC/\delta t)$. $(\delta POC/\delta t)$ is the sum of (1) the changes in the organic carbon pools of phytoplankton, micro- and meso-zooplankton, and bacteria plus (2) a fraction of POC associated to added lithogenic material (POC_{dust}) (Bressac et al., 2012, 2013) and still in suspension inside the mesocosm at the end of the experiment (Desboeufs et al., 2014). Details on the quantification of $(\delta POC/\delta t)$ are given in Tables 2b and S2. Results show that changes in biomass are mostly due to an increase in phytoplankton biomass but that POC_{dust} dominates the particulate organic pool inside the DUST-meso at the end of the experiments (∼ 55–65 % for the 3 wet deposition

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simulations P and R, and 100 % for Q following the non-stimulation of autotrophs by the dry deposition; Ridame et al., 2014).

The remaining term of this carbon budget is the change in the dissolved carbon pool. As emphasized in the methodology section, unfortunately, the non-validated DOC data cannot be used to close this budget. Assuming that the budget is balanced, we deduced the loss in the DOC pool induced by the dust deposition from the available data (Table 2c): we found that the DOC loss was 43 g of C when considering the whole mesocosm, i.e 10 $\mu mol\,C\,L^{-1}\,d^{-1}$ for P experiment, 6 $g\,C\,mesocosm^{-1}$ or 1.4 $\mu mol\,C\,L^{-1}\,d^{-1}$ for Q experiment, and 17 $g\,C\,mesocosm^{-1}$ or 4 $\mu mol\,C\,L^{-1}\,d^{-1}$ for R experiment. The same order of magnitude for DOC consumption has been measured during heterotrophic phases at oligotrophic coastal Mediterranean site (Navarro et al., 2004), with a net DOC consumption as high as 18 $\mu mol\,C\,L^{-1}\,d^{-1}$ and an average consumption during heterotrophic phases of 3.24 ± 3.55 $\mu mol\,C\,L^{-1}\,d^{-1}$). The authors of this last study indicate that such a consumption implies that the system has to import DOC, either derived from land (storm runoff) or released by benthic communities. In our case, as our system does not allow allochtonous inputs, it means that our dissolved organic stock should have decreased during the course of the experiment. The question is raised whether the numbers are realistic. Our DOC consumption over the whole mesocosm during 7 days following the seeding would have been of 70, 10, and 27 $\mu mol\,C\,L^{-1}$ for P, Q, and R1 experiment, respectively, compared to an initial DOC concentration of 87 ± 9 $\mu mol\,C\,L^{-1}$ (see Sect. 2). For Q and R, our DOC consumption would indicate a decrease of 10 % (Q) and 30 % (R) of the DOC stock leading to plausible in situ final DOC concentrations (respectively 78 and 60 $\mu mol\,C\,L^{-1}$). However, the DOC consumption for P experiment appears unlikely as it would indicate that most of the DOC stock was consumed. This could well be explained by an overestimation of the BR whose value for the whole mesocosm was extrapolated from the rate measured at the depth of 5 m, meaning that BR was not homogeneous contrary to what was hypothesized in Sect. 2. This speaks for possible BR variations with depth in stratified waters.

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On the other hand, as reported by Pulido-Villena et al. (2013) after the 2nd seeding of R experiment, the viral lysis could have fed back in part the pool of DOC. Such mechanism could counterbalance in part the drawdown of DOC necessary to explain the net consumption observed in the absence of allochtonous input of DOC in our setup. Nevertheless, this budget illustrates that in the absence of lateral advection from coastal sources or upwelling from deep waters, such heterotrophic system boosted by atmospheric deposition could decrease significantly the stock of dissolved organic carbon in the surface ocean, a question largely debated at the moment (see for ex. Duarte et al., 2013; Ducklow and Doney, 2013).

Although the net heterotrophy character of the tested waters remained (or even was increased) after the dust addition, POC export was still observed: so the DUNE data also illustrate that a system can be dominated by heterotrophy and still maintain an export of particulate organic carbon even in the absence of allochthonous carbon inputs on the short time scale concerned by the dust deposition event. This is different for open systems that can be heterotrophic while exporting organic carbon vertically only if allochthonous carbon inputs support both fluxes (Cole et al., 2007).

5 Conclusions

DUNE project allows us the first attempt to evaluate the changes induced in the carbon budget of an oligotrophic system after a simulated Saharan dust deposition above a large body of water during a 7 days period and considering the vertical dimension. We show (i) that the organic carbon sinks dominate the organic carbon sources demonstrating that the dust deposition induced a loss of organic carbon of the system in all the experiments, and (ii) that this loss is due to dissolved organic carbon consumption. Indeed, an overall negative DOC production for the 3 experiments was found. Negative net DOC production indicating net consumption, each of the seeding resulted in a significant drawdown of the DOC stock over the course of the experiment. DUNE seeding experiments confirm that heterotrophic bacteria are key players in the response to dust

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deposition as it was previously shown by Pulido-Villena et al. (2008) and Marañón et al. (2010) using microcosm approaches.

DUNE is an important step forward in the way we understand dust deposition to the ocean in particular because the term "fertilization" is often associated with the a priori belief that dust deposition should increases chlorophyll biomass (despite some evidences of the contrary from satellite data; Dulac et al., 2004; Volpe et al., 2009) and carbon fixation (and thus increases atmospheric CO_2 drawdown). Instead, DUNE results have shown that by fertilizing predominantly heterotrophic bacteria, dust deposition induces the remineralization of DOC, thereby reducing atmospheric CO_2 drawdown (Rivkin and Anderson, 1997). As emphasized by Pulido-Villena et al., 2008 and this issue, this may reduce substantially the fraction of the dissolved organic carbon stock in the surface ocean that can be exported to deep waters at the time of the winter mixing. Nevertheless, according to the "microbial carbon pump hypothesis" (Jiao et al., 2010), information on the lability of the remaining DOC pool after the enhanced bacterial respiration would be needed to better assess the net effect of dust deposition on DOC export. Other interesting development of this study would be to predict possible scenario for the future using global biogeochemical models where dust pulses such as the ones simulated during DUNE are represented (Guieu et al., 2014a). Indeed on going environmental changes (i.e. increasing temperature and stratification, expansion of the oligotrophic ocean, changes in atmospheric deposition) could modify the role of atmospheric deposition on biogeochemistry of Low-Nutrient-Low-Chlorophyll ocean such as the Mediterranean Sea and an adequate representation of the input of atmospheric new nutrients and particles in those models is timely (Guieu et al., 2014a). In particular, biogeochemical models should consider the important processes highlighted by the DUNE results such as bacteria respiration and (organic matter-Dust) aggregation, a process that allow particulate organic carbon export even in heterotrophic systems.

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Supplementary material related to this article is available online at http://www.biogeosciences-discuss.net/11/1707/2014/bgd-11-1707-2014-supplement.pdf.

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Table 1. Average, standard deviation and coefficient of variation of all the measurements of POC_{export}, NPP and BR performed in both DUST-mesocosms before seedings and the CONTROL- during the DUNE experiments.

	$mg\,C\,m^{-2}\,d^{-1}$			$\mu g\,C\,L^{-1}\,d^{-1}$	
	POC_{export}	NPP	BR	NPP	BR
mean	4.4	57	241	4.6	19.3
standard deviation	3.6	13	163	1.1	13.0
variation coeff.	82 %	24 %	68 %	24 %	68 %

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Table 2a. Carbon mass budget. Data result from the integrated carbon fluxes over 7 days for DUST-Meso corrected from the integrated carbon fluxes over 7 days for the CONTROL-Meso. All data are in g C in the whole mesocosm. Budget of Organic Carbon according to Eq. (2).

Experiment	$\delta C_{org}/\delta t =$	(+)1.1·NPP	(−) 2 BR	(−) POC_{export}	(+)At_{input}
P	−41	1.9	−42.4	−0.48	0.128
Q	−4	0.1	−4.4	−0.05	0.128
R (1st seeding)	−17	1.8	−18.2	−0.24	0.128
R (2nd seeding)	−16	2.5	−18.8	−0.2	0.128

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Table 2b. Induced changes in the organic particulate pool inside the DUST-meso.

Experiment	$\delta POC/\delta t$ =	+Chl *a* C term	+Zooplankton C term		+Bacteria C term	$+POC_{dust}$
			meso-	micro-		
		(1)	(2)	(3)	(4)	(5)
P	2.6	0.7	0.04	0	0.2	1.7
Q	1.6	0	0	0	0	1.6
R (1st seeding)	0.9	0.35	0	0	0	0.5
R (2nd seeding)	1.3	0.55	0	0	0	0.7

(1) From [Chl *a*] (Guieu et al., 2013) with a conversion factor C/Chl *a* = 103 for cells < 2 µm and C/Chl *a* = 247 for cells > 2 µm (from Perez et al., 2006 in the Atlantic subtropical gyre, an oligotrophic environment dominated by picoplankton, which is similar to the conditions during DUNE; Ridame et al., 2014). Discrimination between size cells relies on Vasco et al. (2013) who report that Chl *a* in the < 3 µm fraction represents 70 % of the total Chl *a*.
(2) Biovolume of mesozooplankton with size > 200 µm was analyzed using a zooscan system (L. Stemmann, personal communication, 2013 and Service RADEZOO, OOV Villefranche-sur-Mer) from net sampling performed at the beginning of experiments outside the mesocosms and both inside and outside after the last sampling of the experiment. When significant difference was found between DUST-meso and CONTROL-meso, a ratio of biovolume to zooplankton carbon equal to 0.03 mg C mm^{-3} (Estrada, 1996) was taken to calculate the increase in zooplankton biomass.
(3) The abundance of heterotrophic nanoflagellates (HNFA) was determined at 5 m depth during the R experiment: as no significant difference between CONTROL- and DUST-meso at any of the seeding period was reported by Pulido-Villena et al. (2013), we conclude that the HNFA did not contribute to any significant change in the particulate organic carbon pool after the seeding. This conclusion was extrapolated to P and Q as no data were available for HNFA for those experiments.
(4) The abundance of heterotrophic bacteria (BA) was measured from samples collected at 0, 5 and 10 m (P, Q: Pulido-Villena, personal communication, 2013; R: Pulido-Villena et al., 2014). When a significant difference in BA was found between DUST-meso and CONTROL-meso, a factor of 12.4 fg C $cell^{-1}$ (Fukuda et al., 1998) was applied to determine the corresponding increase in biomass.
(5) The strong correlation between lithogenic and POC fluxes found in the sediment traps of the DUST-meso over the course of all the experiments after the seeding (Bressac et al., 2014; Desboeufs et al., 2014) was used to estimate the POC fraction associated to the remaining lithogenic pool (POC_{dust}) and still in suspension in the mesocosm at the end of the experiment (details of the calculation in Table S2).

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Table 2c. Estimation of the partitioning between dissolved and particulate carbon pool.

In g of C in the whole mesocosm	$\delta C_{org}/\delta t$	$(+)\delta POC/\delta t$	$(\delta DOC/\delta t)$
P	−41	2.6	−43
Q	−4	1.6	−6
R (1st seeding)	−17	0.9	−17
R (2nd seeding)	−16	1.3	−18

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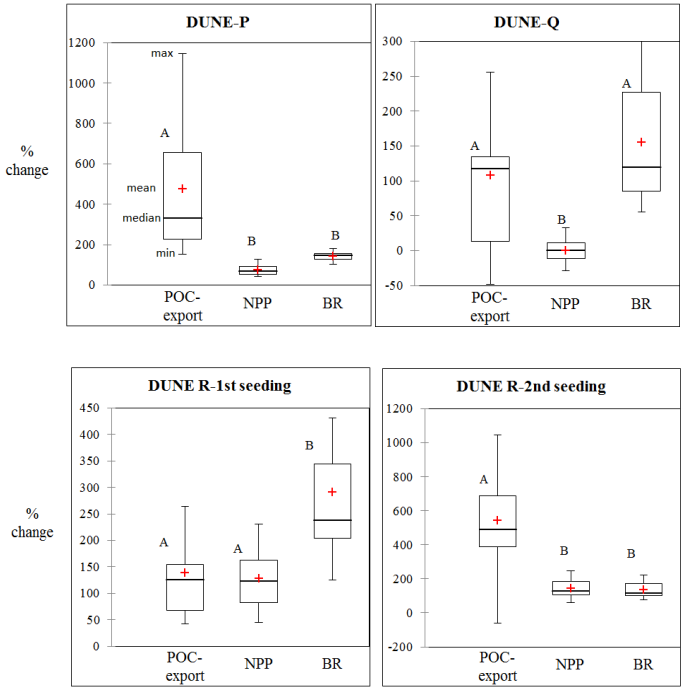

		C EXPORT	NPP	BR
Average Relative changes in %	P	476	75	143
	Q	107	0	156
	R1	138	128	291
	R2	544	144	137

Fig. 1. Box plots of the net fluxes expressed in Relative Change (%) and table with the average relative changes in percentage. The letters indicate the results of the statistical test in between the % change for the 3 parameters: means that were not significantly different between the different parameters ($p > 0.05$) were labeled with the same letter.

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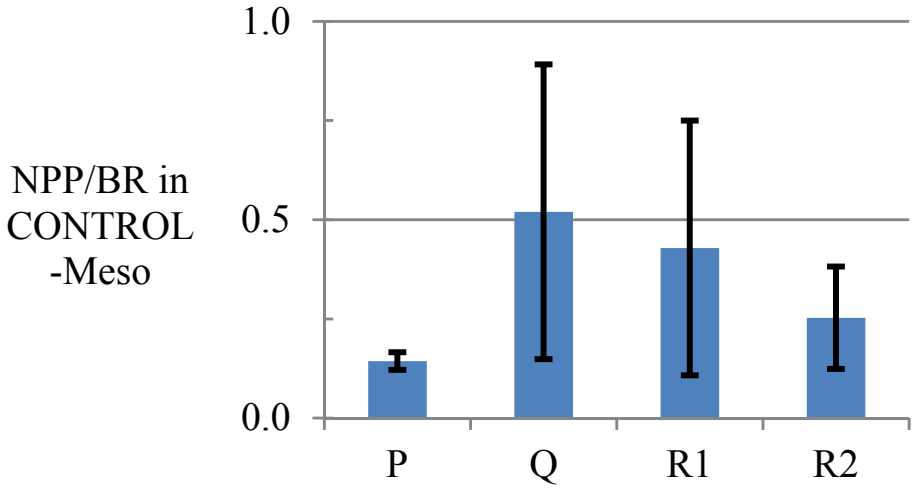

Fig. 2. Net primary production (NPP) to bacteria respiration ratio in the CONTROL-mesocosms averaged during the whole 7-d course of each experiment (bars indicate standard deviation).

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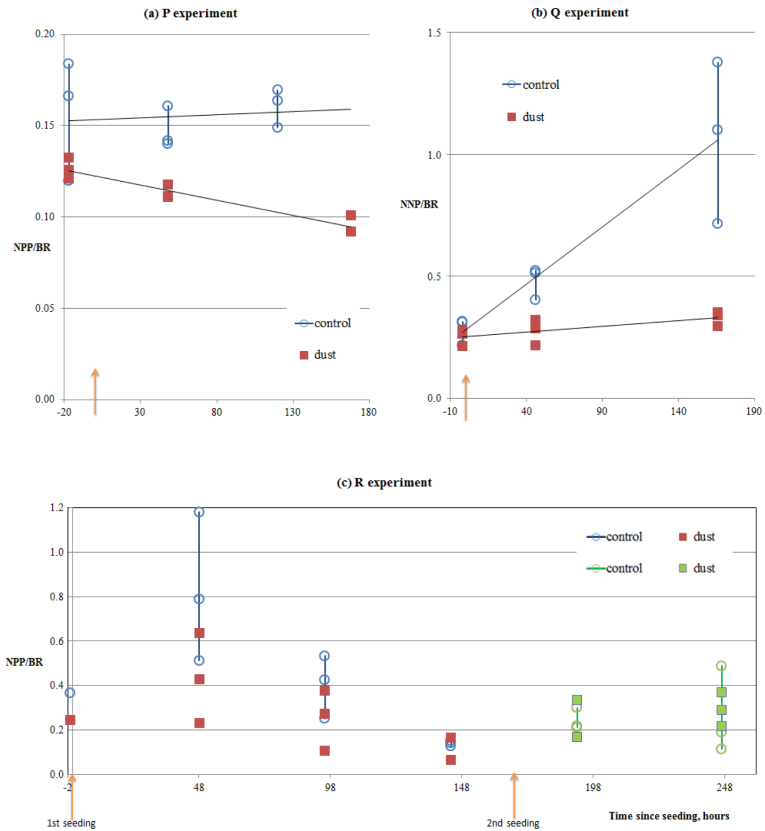

Fig. 3. Evolution of the ratio NPP/BR in CONTROL-meso and after seeding in DUST-Meso **(a)** during DUNE-P experiment, **(b)** during Q experiment and **(c)** during R experiment. Vertical arrows indicate seeding time (time origin for DUNE-P, -Q, and -R1, 172 h for DUNE-R2).

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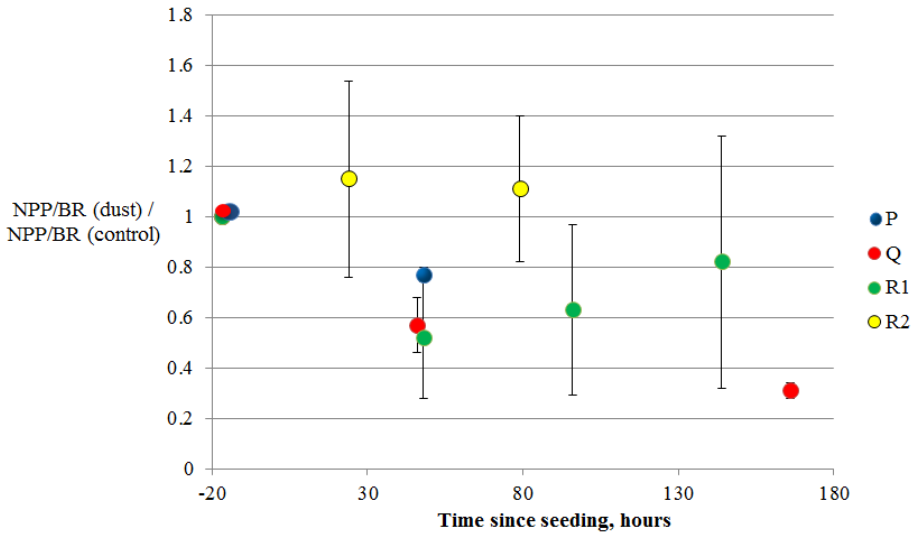

Fig. 4. Same ratio as in the previous figure but here the NPP/BR DUST-meso is normalized to the NPP/BR ratio in the CONTROL-Meso.

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