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Bacterial response to dust pulses in the western Mediterranean: Implications for carbon cycling in the oligotrophic ocean

Elvira Pulido-Villena,¹ Thibaut Wagener,¹ and Cécile Guieu¹

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[1] The bacterial response to dust pulses was investigated in the Mediterranean Sea through a combined field and experimental study. During the stratification period, characterized by a nutrient-starved mixed layer isolated from the depth, a Saharan dust event (2.6 g m^{-2}) induced a 1.5-fold increase in bacterial abundance (BA) and a 2-fold increase in bacterial respiration (BR). Experimental dust additions (equivalent to fluxes of 5 and 20 g m^{-2}) to bacteria natural assemblages also stimulated BA (between 2- and 4-fold increases) and BR (between 1.5- and 3-fold increases). Pooling the in situ and experimental data, linear relationships were obtained between dust concentration and BA ($r^2 = 0.86$; $p < 0.01$) and BR ($r^2 = 0.89$; $p < 0.001$). The dust-induced bacterial bloom resulted in a C mineralization of 0.5 g m^{-2} , which may represent up to 70% of bioavailable DOC annually exported to the depth in the Mediterranean. These results demonstrate that heterotrophic bacteria may play a much larger role in the connections between dust and the ocean carbon cycle than previously recognized and highlight the need for a more accurate understanding of how dust pulses may affect C export in the oligotrophic ocean.

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1. Introduction

[2] Nutrient cycles control the strength of the biological carbon pump through which CO_2 is consumed in surface water and transported as sinking organic carbon to the deep sea [Balino *et al.*, 2001]. Therefore understanding what governs nutrient cycles in the ocean and to which extent climate change plays a role in this schema is essential to understand the oceanic carbon cycle and to predict its evolution. Dust deposition is recognized as a significant source of phosphorus and other nutrients to the surface ocean [Duce *et al.*, 1991; Jickells, 1995]. The recent effort to understand the role of these inputs on ocean biogeochemistry has focused on the impact on autotrophic productivity, given their potential to generate new production. In oligotrophic oceanic regions, while the fertilizing effect of dust has been demonstrated [Ridame and Guieu, 2002] and a positive impact on autotrophic communities has been experimentally evidenced [Mills *et al.*, 2004; Bonnet *et al.*, 2005], no definite effect on C export has been reported yet. For significant C export to occur, the dust-derived nutrient input to the surface layer must escape heterotrophic bacteria uptake and subsequent C transfer through the microbial loop. Thus it is crucial to understand the impact of dust pulses on heterotrophic bacterial activity in order to achieve

an accurate comprehension of the connections between dust and ocean carbon cycling.

[3] There is a growing body of evidence of the potential for phosphorus limitation in the oligotrophic ocean [Rivkin and Anderson, 1997; Caron *et al.*, 2000; Ammerman *et al.*, 2003]. Limitation of bacterial growth by phosphorus constrains the amount of bioavailable dissolved organic carbon (DOC) that can be assimilated by bacteria and thus escape from being exported to depth through winter mixing. This may have important consequences on C cycling in oligotrophic oceanic regions where DOC export has been estimated to be equal to or greater than particle flux [Carlson *et al.*, 1994]. The open Mediterranean Sea, during the stratification period, exhibits a severe nutrient depletion after the spring bloom and both bacterioplankton and phytoplankton are strongly P-limited [Thingstad *et al.*, 1998]. This bacterial P limitation translates into a net accumulation of bioavailable DOC throughout the stratification period [Avril, 2002] that allows DOC export to the deep ocean through winter mixing [Thingstad *et al.*, 1997]. During this oligotrophic season, the atmosphere becomes the main external source of P and other nutrients to the mixed layer of the Mediterranean Sea, a region that receives one of the highest rates of aeolian material deposition in the world [Guerzoni *et al.*, 1999] mainly in the form of strong pulses. By relieving bacteria P limitation, these dust pulses may directly modulate the amount of mineralized DOC and, hence, the magnitude of C export to the deep ocean.

[4] In this study, we evaluated the response of heterotrophic bacteria to Saharan dust pulses in the NW Mediterranean

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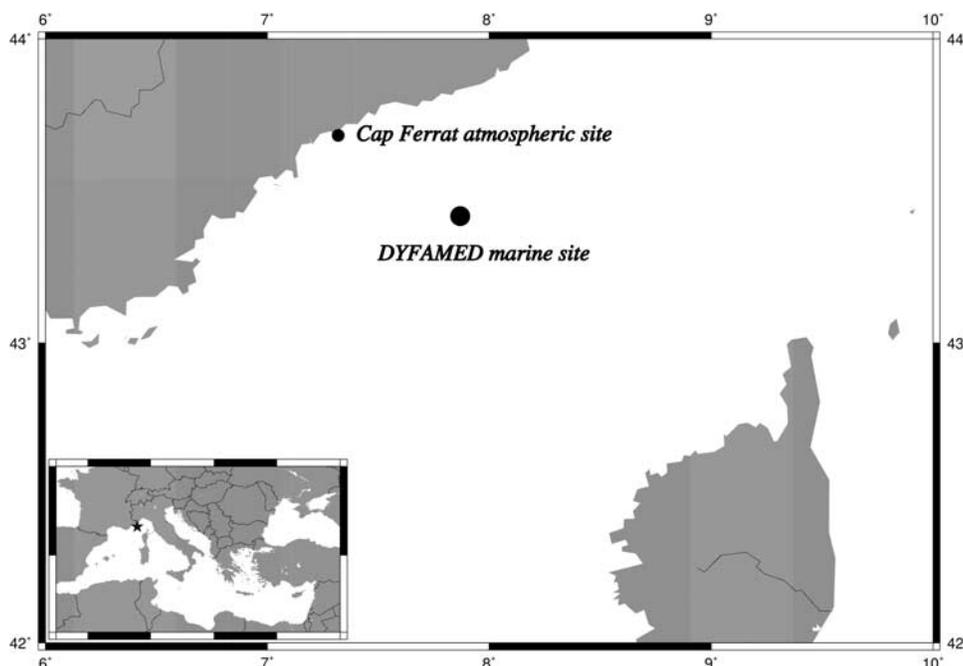


Figure 1. Location of the sampling sites: Atmospheric deposition sampling at the Cap Ferrat station and seawater sampling at the DYFAMED site.

Sea. For this purpose, we used a dual approach which combined field observations of atmospheric fluxes of nutrients and bacterial dynamics in the surface layer with a microcosm experiment in which realistic amounts of Saharan dust were added to bacterial natural assemblages. The aims of this combined study were (1) to quantify the dust-derived inputs of P and DOC to the mixed layer; (2) to assess the potential of Saharan dust pulses to induce heterotrophic bacteria blooms during the oligotrophic season; and (3) to estimate the consequences of dust-induced bacteria blooms on the C export.

2. Material and Methods

2.1. Atmospheric Deposition

[5] Total atmospheric deposition was collected at the Cap Ferrat site (43°41'N, 7°19'E, altitude 138 m, Figure 1). The atmospheric sampling was performed continuously from December 2005 to December 2006 and 26 samples representing time periods of about 14 d were analyzed. The sampler consisted of a 4L polyethylene bottle placed at 3 m from the ground. A polyethylene funnel was placed on the top of the bottle (surface 302 cm²) and 20 μm mesh covered the funnel exit in order to prevent insects and organic debris from falling inside the bottle. Samples were poisoned in situ by filling the 4 L bottles with 100 mL of HgCl₂ solution (10 μg mL⁻¹). Once in the laboratory, the funnel was rinsed with 100 mL of ultrapure water and the bottle was then ultrasonicated in order to collect all the particles stuck to the walls. The sample was filtered through a precombusted and preweighed GF-F filter for dissolved organic carbon (DOC) and soluble reactive phosphorus (SRP) analyses. The filter

was used to determine particulate matter (PM) content as dry weight (60°C, 24 h).

2.2. Water Sampling

[6] Seawater was collected on board R/V Tethys II in the northwestern Mediterranean Sea at the permanent time series DYFAMED site (43°25'N, 7°52'E, 50 km off Nice, France, Figure 1). This open ocean site (2350 m depth) is protected from coastal inputs by the Ligurian coastal current. The sampling took place monthly between December 2005 and December 2006. Seawater was collected at five different depths (surface, 5, 10, 20 and 40 m) using a trace metal clean Teflon pump system. Inline filtration was performed through a 0.2 μm cartridge (Sartorius Sartobran-150) to collect duplicate samples for soluble reactive phosphorus (SRP) and dissolved organic carbon (DOC) analyses. Unfiltered samples were collected in duplicate for bacterial abundance (BA) determination. At four sampling dates, 6 May, 10 June, 30 June, and 2 August, unfiltered seawater from 10-m and 40-m depth was additionally collected to determine bacterial respiration (BR). Water was gently filtered on board through a GF/F filter under low vacuum pressure and the filtrate was used to fill a set of six BOD bottles. Two BOD bottles were immediately fixed with Winkler reagents and the rest were taken to the laboratory and incubated in the dark at controlled temperature. After 30 and 48 h, two BOD bottles were fixed with Winkler reagents. Filtered seawater was also sampled for BA in order to determine the efficiency of recovery after filtration (67 ± 5% of total bacteria).

[7] Seawater sampling to perform the dust addition experiments was carried out on 2 August 2006. Inline

filtration was performed through a 0.65 μm cartridge (Sartorius Sartopure-PP2) under a laminar flow hood to collect seawater at 8-m depth (above the thermocline) and it was dispensed into acid-washed 20 L bottles. Water was stored in the dark until arrival at the laboratory (ca. 6 h later).

2.3. Dust Addition Experiment

[8] Once in the laboratory, the collected seawater was dispensed into acid-washed 4 L bottles and amended with two types of Saharan dust: (1) a composite of fine fractions ($<20 \mu\text{m}$) of surface soils collected in the Hoggar region (south Algeria) representative of the Saharan aerosol carried over the NW Mediterranean Sea [Guieu *et al.*, 2002]; and (2) the particulate fraction of a Saharan rain collected in Corsica in November 2001 (C. Guieu, unpublished data, 2001). The utilization of these two types of Saharan dust would allow us to assess how representative the Saharan aerosol end-member (composite soil) was. Two amounts of each type of Saharan dust were added to the bottles in order to obtain two final different concentrations: 0.5 and 2 mg L^{-1} , representative of a medium (5 g m^{-2}) and high (20 g m^{-2}) intensity Saharan dust input theoretically diluted into the whole mixed layer (10-m depth, average value during stratification) and typically encountered in oligotrophic regions such as the Mediterranean Sea [Ridame and Guieu, 2002] or in the eastern tropical Atlantic [Torres-Padron *et al.*, 2002]. Overall, the experiment consisted of four treatments, corresponding to the following additions: Saharan dust end-member = 0.5 mg L^{-1} (hereafter, 0.5EM), Saharan dust end-member = 2 mg L^{-1} (hereafter, 2EM), collected dust = 0.5 mg L^{-1} (hereafter, 0.5CD), and collected dust = 2 mg L^{-1} (hereafter, 2CD). One unamended bottle was kept as a control (C). Immediately after the additions, all bottles were vigorously shaken and a volume of 250 mL from each treatment (including C) was subsampled for the determination of the initial conditions of the experiment. The remaining content was transferred to acid washed 250-mL polycarbonate flasks previously sterilized by microwaving [Keller *et al.*, 1988]. For each treatment (including C), four flasks ($\times 3$ replicates) were filled and incubated in the dark at 22°C. For each experimental treatment, three replicates were discarded at four selected times during the course of the experiment (T1 = 12h; T2 = 24h; T3 = 48h; T4 = 72h). Subsamples were used for the following measurements: dissolved organic carbon (DOC), soluble reactive phosphorus (SRP), bacterial abundance (BA) and oxygen concentration. Samples for DOC and SRP were simultaneously filtered through acid-washed polycarbonate 0.2 μm filters.

2.4. Analytical Methods and Calculations

[9] Samples for DOC analysis were collected in combusted ($>2 \text{ h}$ at 500°C) flasks, acidified with phosphoric acid to pH < 2 and stored at 4°C in the dark until analysis. DOC concentration was measured with a Shimadzu TOC-5000 total carbon analyzer. The instrument blank was assessed using two external standards (Certified Reference Material, Hansell Laboratory, Bermuda Biological Station). The instrument blank ranged between 8 and 12 $\mu\text{mol L}^{-1}$

and was subtracted from the measurements. Soluble reactive phosphorus (SRP) concentration was analyzed spectrophotometrically after Murphy and Riley [1962]. The reagent blank value was always below the detection limit of the method (20 nmol L^{-1}). The accuracy of the method was systematically checked against a secondary reference material (Merck Certipur[®]). Samples for bacterial abundance (BA) were fixed with neutralized 0.2- μm filtered formaldehyde and BA was determined by epifluorescence microscopy using DAPI fluorochrome stain [Porter and Feig, 1980]. At least 400 cells in 30 random fields were counted per filter. Dissolved oxygen concentration to determine bacterial respiration was measured after automated Winkler titration technique. Bacterial respiration rate (BR) was taken as the slope of O_2 versus time, assuming a respiratory quotient of 1 (del Giorgio and Cole 1998). In the dust addition experiment, bacterial growth efficiency (BGE), expressed in percentage, was calculated as $\text{BGE} = \text{BP}/(\text{BP} + \text{BR}) \times 100$, where bacterial production (BP) was taken as the increase in bacterial biomass over the incubations assuming a conversion factor of 12.4 fg C cell^{-1} [Fukuda *et al.*, 1998].

2.5. Contamination Control

[10] Given the severe oligotrophic conditions encountered in the NW Mediterranean Sea during the stratification season, all handling was performed under ultra clean conditions to avoid any contamination. All material used for the atmospheric and seawater sampling, as well as for the dust addition experiments was initially washed following an ultraclean protocol (see details given by Bonnet and Guieu [2006]). Sample manipulation was always carefully performed under a laminar flow hood (class 100). A set of blank controls was periodically performed at key moments of all manipulations (see Figure S1 and Text S1 for details).¹

3. Results

3.1. Atmospheric Fluxes

[11] Figure 2 shows the temporal evolution of atmospheric fluxes of particulate matter (PM), dissolved organic carbon (DOC) and soluble reactive phosphorus (SRP) for each 2-week sample. PM fluxes were highly variable throughout the year ranging from 0.03 to 2.58 g m^{-2} and most PM deposition (75%) occurred between June and October. DOC fluxes ranged from 0.5 to 16.8 mmol m^{-2} and SRP fluxes from 0.7 to 74.0 $\mu\text{mol m}^{-2}$. One Saharan dust event, which took place on the 26 June (Figure 3) accounted for 42% of annual PM deposition and was responsible for the highest DOC and SRP fluxes registered during the study period (Figure 2).

3.2. Nutrient and Bacterial Dynamics in the Surface Layer

[12] Concentration of soluble reactive phosphorus (SRP) in the 0–40 m layer was very low during most of the study period with values ranging from below detection limits

¹Auxiliary materials are available in the HTML. doi:10.1029/2007GB003091.

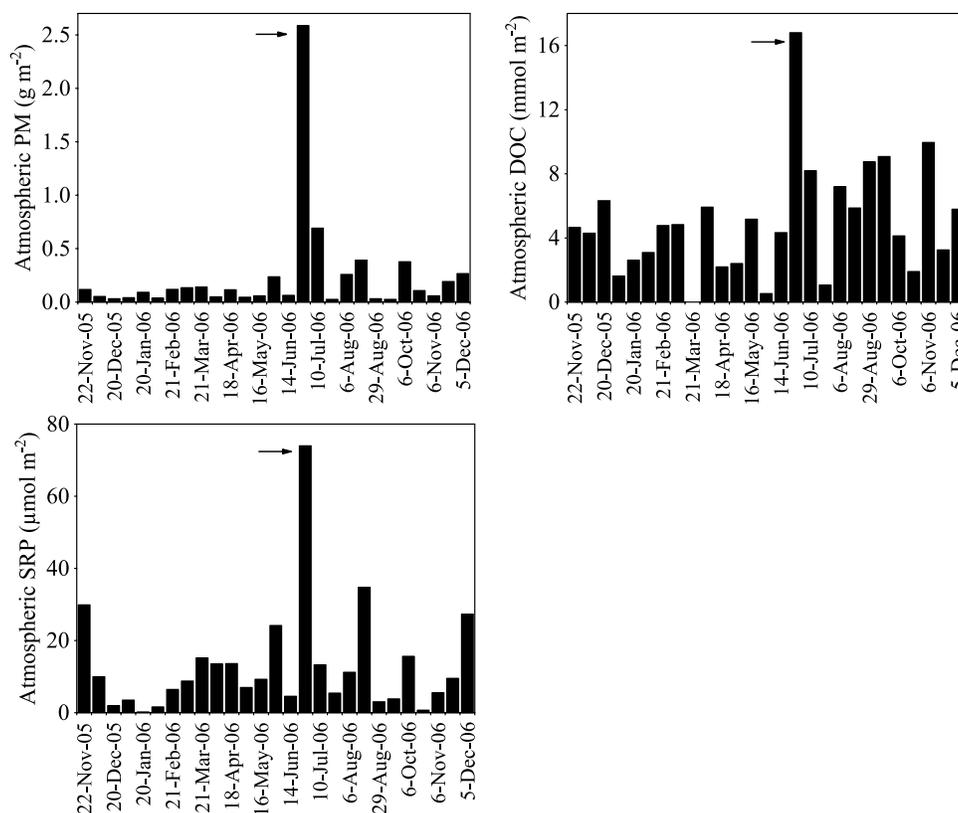


Figure 2. Temporal evolution of the atmospheric fluxes of particulate matter (PM), dissolved organic carbon (DOC), and soluble reactive phosphorus (SRP) for each 2-week sample collected at the Cap Ferrat station throughout the study year. Arrows point to a medium-intensity Saharan dust event registered on 26 June 2006.

(20 nmol L⁻¹) to 350 nmol L⁻¹. Minimum concentrations were observed just after the spring bloom and throughout the stratification period (Figure 4). Concentration of dissolved organic carbon (DOC) in the 0–40 m layer ranged from 36 to 107 μmol L⁻¹ and it exhibited the opposite seasonal trend to SRP, that is, maximum values just after the spring bloom and all throughout the stratification period (Figure 4). Bacterial abundance (BA) in the 0–40 m layer was highly variable ranging from 0.05 to 1.5 10⁶ cell mL⁻¹ (Figure 4). Seasonal variations were similar at all study depths, with minimum values at the beginning of the year and a first peak on 6 May 2006, just after the spring bloom. A second bloom of heterotrophic bacteria was observed at all depths on the 30 June, after which BA exhibited a progressive decrease until the end of the year (Figure 4). Bacterial respiration (BR) measured from May to August was more variable and exhibited lower values at 10-m depth than at 40-m depth (Table 1).

3.3. Bacterial Response to Saharan Dust: A Natural Fertilization

[13] Figure 5 shows the temporal variations of the mixed layer depth (MLD) at the study site and the atmospheric inputs of SRP and DOC predicted to accumulate in the mixed

layer. Because between June and October (stratification period) atmospheric deposition was maximum (Figure 2) and the mixed layer depth (MLD) was minimum, atmospheric nutrients predicted to accumulate in the ML were maximum during that period (Figure 5). Atmospheric SRP inputs to the mixed layer (ML) varied from 0.0004 to 12.4 nmol L⁻¹ and the cumulative input of SRP to the ML over 1 year was 31 nmol L⁻¹. Atmospheric inputs of DOC entering the ML ranged from 0.04 to 2.8 μmol L⁻¹ and the cumulative input of DOC to the ML over the study year was 9.6 μmol L⁻¹. The maximum input of SRP and DOC predicted to accumulate in the ML was induced by the Saharan dust event registered on 26 June. The routine cruise to the DYFAMED site took place 4 d after this Saharan dust event. This convenient circumstance allowed us to explore the response of heterotrophic bacteria to a Saharan dust-induced fertilization of the ML. Bacterial abundance (BA) in the 0–10-m layer was 1.5-fold higher just after the dust pulse than on the 10 June cruise, 20 d before (Figure 4). This increase (72%) was significant when compared to the whole variability of BA during the oligotrophic season within the mixed layer (CV = 23%, all measurements at surface, 5- and 10-m depth). Bacterial respiration (BR) at 10-m depth also exhibited a noticeable increase after the Saharan dust event,

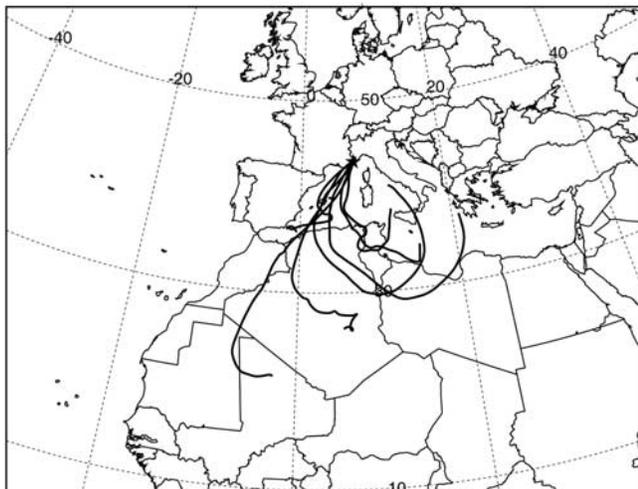


Figure 3. Five-day air back-trajectories arriving to the study site between 20 and 26 June corresponding to the Saharan dust event responsible for the highest fluxes of particulate matter, soluble reactive phosphorus, and dissolved organic carbon registered in the study period. Back-trajectories were calculated using the Hybrid Single-Particle Lagrangian Integrated Trajectories (HYSPLIT) trajectory model (R. R. Draxler and G. D. Rolph, 2003, NOAA Air Resources Laboratory, Silver Spring, Maryland, available at <http://www.arl.noaa.gov/ready/hysplit4.html>) provided by the NOAA Air Resources Laboratory (ARL).

boosting from $0.9 \mu\text{mol C L}^{-1} \text{d}^{-1}$ on 10 June to $2.1 \mu\text{mol C L}^{-1} \text{d}^{-1}$.

3.4. Bacterial Response to Saharan Dust: An Experimental Fertilization

[14] Experimental Saharan dust additions induced significant increases in dissolved organic carbon (DOC) and soluble reactive phosphorus (SRP) concentration in all experimental bottles. The increase in DOC was proportional to the amount of dust added and no significant differences were observed between either types of dust (Figure 6). SRP increased from below detection limit values ($\text{DL} = 20 \text{ nmol L}^{-1}$) in the control treatment to concentrations between 35 and 55 nmol L^{-1} in dust-amended bottles (Figure 6). At the end of the incubations, both DOC and SRP concentrations decreased in all experimental bottles, including control, falling down to below DL values in the case of SRP (Figure 6).

[15] During the incubations, bacterial abundance (BA) exhibited an initial phase of exponential growth followed by a stationary phase reached after ca. 48 h, especially in C, 0.5EM and 0.5CD treatments. At the end of the incubations, BA was higher in all spiked bottles than in control and it increased with dust concentration (Figure 7, left). Increases in BA were always accompanied by commensurate decreases in O_2 concentration (Figure 7, right), and therefore bacterial respiration rates (BR) were higher in all amended treatments than in control and increased with the amount of dust (Table 2). Bacterial growth efficiency (BGE)

was slightly higher in amended treatments than in control, although it remained very low ($< 10\%$) despite the amendments (Table 2).

4. Discussion

4.1. Natural Fertilization

[16] Atmospheric particulate matter (PM) fluxes registered in this study are in the range of previously reported data for the W Mediterranean [Guerzoni *et al.*, 1999, and references therein] as well as for other oligotrophic regions such as the eastern Atlantic Ocean [Torres-Padron *et al.*, 2002; Jickells *et al.*, 2005]. However, stronger Saharan dust pulses (up to 25 g m^{-2} , Loye-Pilot and Martin [1996]) have been previously reported for the study area and were not observed during the period of study. The strongest Saharan dust event recorded during the study period, on 26 June (see Figures 2 and 3), was responsible for the greatest flux of soluble reactive phosphorus (SRP). This agrees with the previous recognition that Saharan dust significantly contributes to atmospheric inputs of phosphorus [Bergametti *et al.*, 1992; Guieu *et al.*, 2002], an element of high biogeochemical interest which has stimulated the interest in the impact of dust inputs on ocean functioning [Ridame and Guieu, 2002, Markaki *et al.*, 2003]. The above mentioned Saharan event also delivered the largest flux of dissolved organic carbon (DOC) recorded during the study period, in agreement with previous reports of the organic content of Saharan aerosol, either as a primary component [Eglinton *et al.*, 2002] or as a result of heterogeneous reactions between organic compounds and mineral dust in the troposphere [Usher *et al.*, 2003, and references therein].

[17] The potential of atmospheric inputs to fertilize the mixed layer (ML) is a key question regarding its impact on ocean biogeochemistry. In this study, from June to October there was a concurrence of high atmospheric fluxes (Figure 2) and minimum MLD (Figure 3). Consequently, the maximum fertilizing effect of the atmosphere was encountered precisely during the summer, a period during which the water column is strongly stratified, with marked thermocline and pycnocline that isolate the surface water from the deeper water masses. The atmosphere would have been thus the main external source of DOC and SRP to the nutrient-starved surface waters of the NW Mediterranean Sea during that period. Atmospheric DOC inputs to the ML during the stratification period were small compared to in situ concentration (Table 3), suggesting a poor atmospheric contribution to DOC dynamics. Nevertheless, since only a small proportion of the DOC pool in oligotrophic waters is bioavailable (6–19%, Carlson and Ducklow [1996]), further research on the availability of atmospheric DOC would be needed to understand its actual contribution to the labile DOC pool. Conversely to DOC, atmospheric SRP inputs (particularly those associated to the above mentioned Saharan event) were substantial compared to in situ concentration during the stratification period which, despite not being measurable with the method used in this study, has been reported to be below 3 nmol L^{-1} [Moutin *et al.*, 2002].

[18] Atmospheric SRP delivered to the ML by the Saharan event on 26 June would have been rapidly uptaken by a starving bacteria and algae community since, during

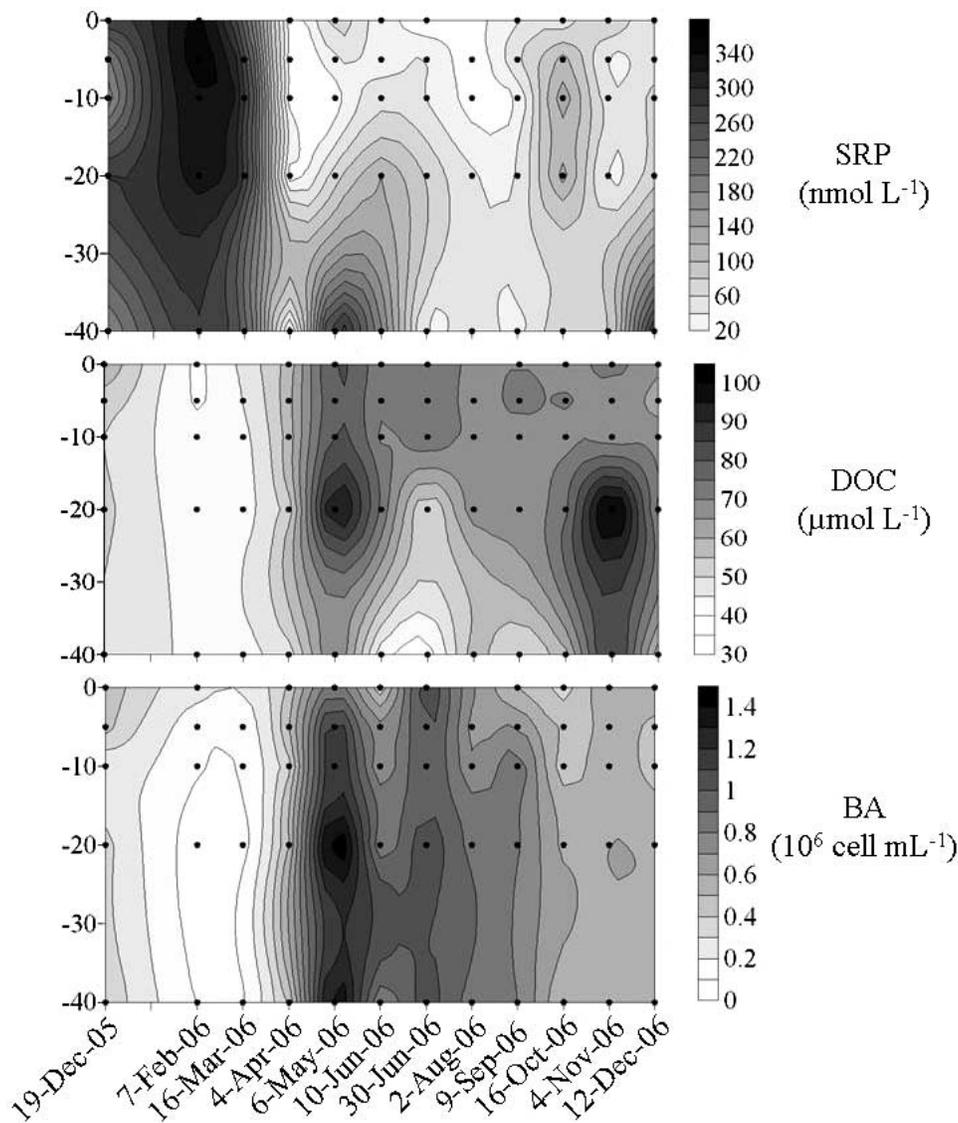


Figure 4. Soluble reactive phosphorus (SRP), dissolved organic carbon (DOC), and bacterial abundance (BA) in the 0–40 m layer throughout the study year. Points represent sampling depths.

stratification period in the NW Mediterranean Sea, both heterotrophic bacteria and phytoplankton are severely P-limited [Thingstad *et al.*, 1998] which translates into very short P turnover times [Moutin *et al.*, 2002]. Under this scenario of P limitation, heterotrophic bacteria have been observed to account for 60–100% of phosphate uptake and may even outcompete phytoplankton [Rivkin and Anderson, 1997]. After the dust pulse registered in this study, heterotrophic bacteria could have taken advantage of atmospheric SRP inputs, explaining why routine CTD fluorescence and pigment composition (data available at <http://www.obs-vlfr.fr/sodyf>) did not reveal any increase in total phytoplankton biomass or any shift in phytoplankton community structure after the Saharan dust event. The short lag time between the dust event and the observed bacterial response (4 d) rules out an indirect effect derived from an increase in phytoplankton biomass, in the way that has been observed

in Fe enrichment experiments performed in high-nutrient, low-chlorophyll regions [Cochlan, 2001; Arrieta *et al.*, 2004; Hale *et al.*, 2006]. By contrast, the observed bacterial response can be assimilated to the process in which P bypasses the phytoplankton compartment and enters the microbial loop, as has been proposed for the ultraoligotrophic eastern Mediterranean Sea [Thingstad *et al.*, 2005].

Table 1. Bacterial Respiration Rates Measured at the Study Site at 10 and 40-m Depth Between May and August 2006^a

	6 May 06	10 Jun 06	30 Jun 06	2 Aug 06
10-m depth	1.2 ± 0.6	0.9 ± 0.4	2.2 ± 0.4	0.9 ± 0.2
40-m depth	2.8 ± 0.6	2.7 ± 0.4	3.0 ± 0.2	2.6 ± 0.3

^aUnits are $\mu\text{mol C L}^{-1} \text{d}^{-1}$. The values represent the average±standard error of two replicates.

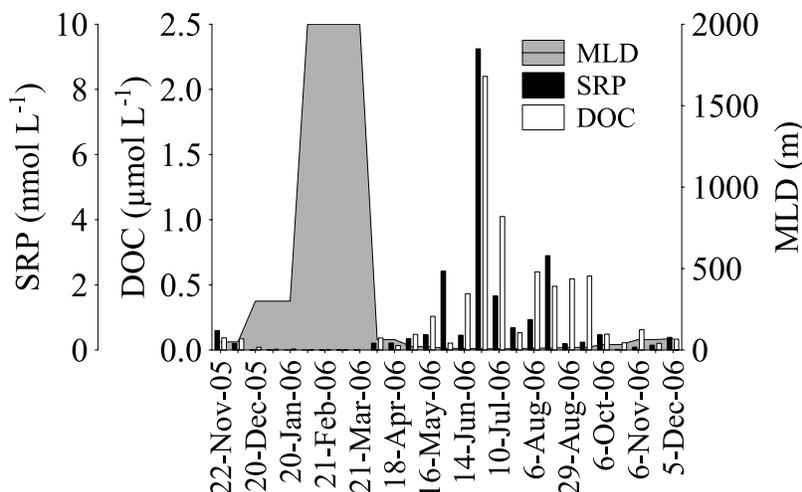


Figure 5. Atmospheric soluble reactive phosphorus (SRP) and dissolved organic carbon (DOC) resulting from the dilution of the atmospheric input into the whole mixed layer and calculated using the mixed layer depth (MLD) as follows: $\Delta\text{SRP}_{\text{ML}}$ or $\Delta\text{DOC}_{\text{ML}} = \text{SRP flux or DOC flux}/(\text{MLD} \times 1000)$. MLD (also represented in Figure 5) was calculated following the method used by *Levy et al.* [1998] (the depth at which density differs from surface density by 0.05 kg m^{-3}) as well as through visual examination of the density depth profiles.

The P limitation of bacterioplankton and a N, P colimitation of phytoplankton typically encountered in this part of the Mediterranean has been proposed to explain this bypass [*Zohary et al.*, 2005]. On the contrary, in the western basin, where both communities are P-limited [*Thingstad et al.*, 1998], the autotrophic versus heterotrophic response to dust pulses would be less dependent on the N:P ratio of the atmospheric input.

[19] Although bacterial P limitation was not explicitly assessed in this study, previous research on limitation conditions in the W Mediterranean Sea [e.g., *Thingstad et al.*, 1998] supports our hypothesis of a P-mediated impact of dust pulses on heterotrophic bacteria. The effect of other

dust-derived nutrients such as iron (Fe), despite significant in other regions of the world ocean [*Jickells et al.*, 2005, and references therein], is not expected to be substantial in the study area. Indeed, assuming a maximum Fe:C ratio of 44 ($\mu\text{mol}/\text{mol}$) [*Tortell et al.*, 1996], the Fe bacterial demand to sustain the bacterial bloom (0.02 nmol L^{-1}) would be well below the surface dissolved Fe concentration typically encountered in the study area during the stratification period ($0.5\text{--}1 \text{ nmol L}^{-1}$, *Bonnet and Guieu* [2006].) The observed heterotrophic bacterial bloom could have been theoretically sustained by Saharan dust-derived inputs of SRP to the ML (Table 3), confirming the potential of dust pulses to alleviate bacterial P limitation. In contrast, DOC

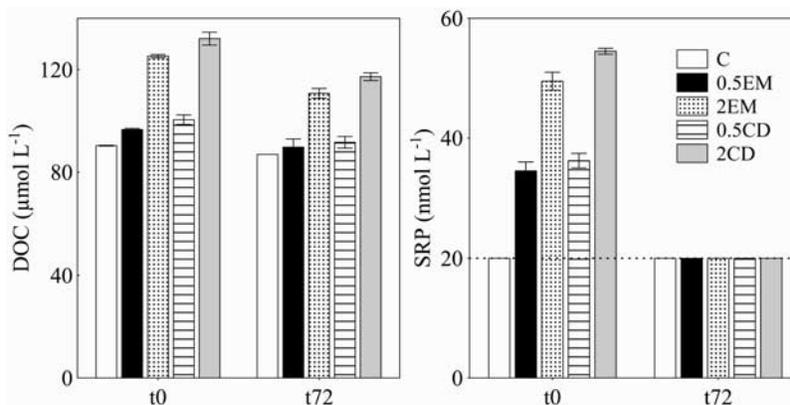


Figure 6. Concentration (mean value \pm standard error of three replicates) of dissolved organic carbon (DOC) and soluble reactive phosphorus (SRP) in the experimental bottles for each treatment at the beginning and at the end of the incubations in the dust addition experiments. Dashed line represents the detection limit of the method used to analyze SRP concentration.

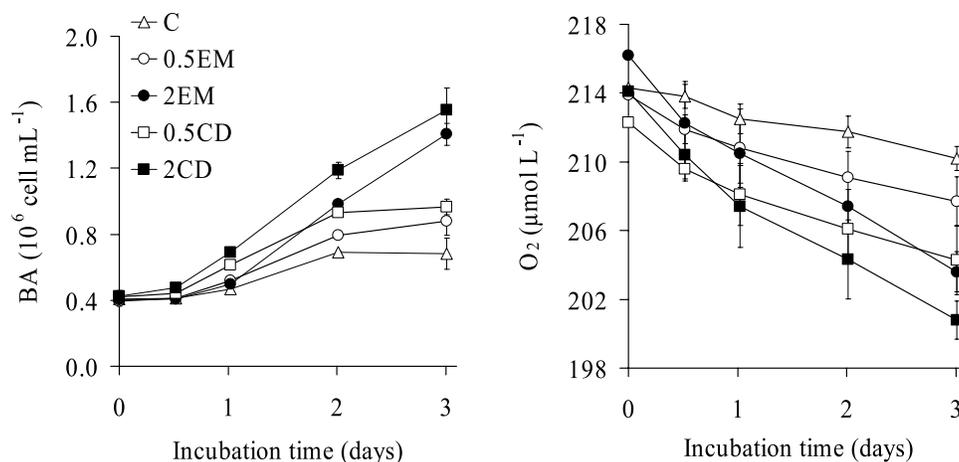


Figure 7. Changes in bacterial abundance (BA) and O_2 concentration (mean value \pm standard error of three replicates) versus incubation time for each experimental treatment in the dust addition experiments.

inputs could have barely satisfied the bacterial carbon demand (Table 3), probably leading to a dust-induced consumption of part of the autochthonous DOC pool by heterotrophic bacteria. Hence the suggested alleviation of bacteria P limitation by a dust pulse and the subsequent development of a bacterial bloom can have severe consequences on ocean carbon cycling that will be discussed further on.

4.2. Experimental Fertilizations

[20] The most generalized approach to tackle the biological impact of dust has been to perform experimental additions to natural whole assemblages [see, e.g., Mills *et al.*, 2004; Herut *et al.*, 2005; Bonnet *et al.*, 2005]. However, the biogeochemical impact of dust has turned out to be a question far more difficult than expected years ago and this approach has usually led to inconsistent results due to the difficulty to discriminate among the multiple processes taking place. Bacterial regrowth cultures used in this study may be less representative than the use of the whole assemblage, but, by discriminating bacterial response to dust inputs from other processes, they constitute an important step toward the understanding of the biogeochemical role of dust. The performed *in vitro* experiments supported the hypothesis of a response of heterotrophic bacteria to Saharan dust inferred from the study of a dust-derived natural bacterial bloom. Dust addition stimulated heterotrophic bacteria, provoking an increase in abundance and respiration rate in all treatments. Previously reported dust addition experiments to whole assemblages resulted in less

obvious responses of heterotrophic bacteria, with clear stimulation of production but no changes in biomass [Ridame, 2001; Bonnet *et al.*, 2005; Herut *et al.*, 2005]. These three studies pointed the predation by heterotrophic nanoflagellates as the major factor regulating bacterial biomass, which implicitly suggests that part of the dust-derived nutrients had been channeled through the microbial loop.

[21] The efficiency by which bacteria use the DOC pool is of critical importance in carbon cycling. Bacterial growth efficiency (BGE) is highly dependent on phosphorus availability, and hence oligotrophy appears to place high respiratory demands on bacterioplankton, resulting in very low growth efficiencies [del Giorgio and Cole, 1998; Smith and Prairie, 2004]. In the oligotrophic Mediterranean Sea, particularly during the stratification period, BGE is extremely low, with values not exceeding 20% [Lemée *et al.*, 2002] implying that heterotrophic bacteria behave as a sink of organic C rather than a link to higher trophic levels. Despite dust addition increased SRP concentration in experimental bottles, bacterial growth efficiency remained very low and the slight differences between treatments (7.7–9.7%) were largely below the *in situ* seasonal variation of BGE encountered in the western Mediterranean Sea (0.1–43%, Lemée *et al.* [2002]).

4.3. Natural Versus Experimental Fertilization

[22] In this study, two different and independent approaches resulted in a similar outcome: heterotrophic bacteria may respond to dust pulses in oligotrophic waters.

Table 2. Bacterial Respiration Rate and Growth Efficiency (BGE, %) in Control and Amended Treatments of the Dust Addition Experiments^a

	C	0.5EM	2EM	0.5CD	2CD
BR, $\mu\text{mol C L}^{-1} \text{d}^{-1}$	1.36 ± 0.21	1.96 ± 0.41	3.92 ± 0.44	2.50 ± 0.45	4.22 ± 0.51
BGE, %	7.7 ± 0.17	8.9 ± 0.41	9.3 ± 0.24	7.9 ± 0.31	9.7 ± 0.30

^aBR: bacterial respiration rate. BGE: bacterial respiration rate and growth efficiency.

Table 3. A Dust-Induced Bacterial Bloom: Increase in Bacterial Abundance (Δ BA), Bacterial Biomass (Δ BB), and Bacterial Respiration (Δ BR) in the Mixed Layer (ML) at the DYFAMED Site Between the 10 June Cruise (15 d Before the Saharan Dust Event) and the 30 June Cruise (4 d After the Dust Pulse): Comparison Between the Bacterial Carbon Demand (BCD) and Bacterial Phosphorus Demand (BPD) to Attain the Observed Increase and the Atmospheric Dissolved Organic Carbon (DOC) and Atmospheric Soluble Reactive Phosphorus (SRP) Resulting From the Dilution Into the Whole Mixed Layer (ML) of the Saharan Dust Event. The DOC and SRP in Situ Concentrations at the Time of the Pulse are Also Shown.

DOC and SRP in Situ Concentration	Atmospheric DOC and SRP Input to the ML ($\pm 30\%$) Derived From the Dust Pulse ^a	Bacterial Response to Dust Pulse
DOC = 75 μ mol C L ⁻¹	0.2–4 μ mol C L ⁻¹	Δ BA = 400 10 ⁶ cell L ⁻¹ Δ BB ^b = 455 nmol C L ⁻¹ Δ BR = 1.2 μ mol C L ⁻¹ d ⁻¹ BCD ^c = 5.2 μ mol C L ⁻¹
SRP < detection limit	9.5–17.6 nmol P L ⁻¹	BPD ^d = 9.1 nmol P L ⁻¹

^aAtmospheric input to the mixed layer was calculated as in Figure 5. In order to consider the uncertainties in the determination of the mixed layer depth (MLD), a range value of MLD $\pm 30\%$ (8 \pm 2.4 m) was carefully considered.

^bEstimated applying a conversion factor of 12.4 fg C cell⁻¹ [Fukuda *et al.*, 1998].

^cCalculated as the increase in BB plus the increase in respired carbon, conservatively estimated applying the measured BR rate for the four-day lag between the dust pulse and the 30 June sampling. This estimation is supported by the results of the dust addition experiment in which BR rates at the end of the incubations were lower than BR rates integrated during the whole duration of the incubations.

^dEstimated using a bacteria C:P ratio of 50 [Fagerbakke *et al.*, 1996].

The next logical step was to compare both “natural” and “experimental” dust-induced bacterial blooms. Natural Saharan dust input and associated SRP and DOC input to the whole mixed layer registered on 26 June 2006 were on the same order of magnitude as the lowest dust addition in the experimental fertilizations, allowing their comparison (Table 4). Plotting the observed responses of heterotrophic bacteria versus dust concentration in both natural and experimental fertilizations, linear relationships are obtained and the in situ response fits well with the experimental trend (Figure 8). The obtained linear relationships constitute a key aspect of this study since they report a comparable response of heterotrophic bacteria to dust pulses in both natural and experimental conditions.

[23] Overall, this study encompasses two key aspects regarding the potential link between dust and heterotrophic bacterial activity: first, it relates dust concentration to bacterial respiration, a parameter barely measured yet crucial in determining the fate of organic carbon [Jahnke and Craven, 1995; Rivkin and Legendre, 2001]; second, it reports an experimentally controlled response of heterotrophic bacteria to dust addition that may be comparable to natural bacterial blooms induced by dust pulses in the oligotrophic western Mediterranean. These two peculiarities shall allow us to estimate

the impact of bacterial response to Saharan dust inputs on carbon cycling in this oligotrophic, nutrient-starved oceanic system.

4.4. Implications for C Cycling

[24] Previous research on the biogeochemical impact of Saharan dust in oligotrophic regions has been commonly built on the assumption that dust-delivered nutrients to the surface ocean would boost autotrophic production and thus increase the capacity of the ocean to sequester atmospheric CO₂ [Ridame and Guieu, 2002; Markaki *et al.*, 2003]. In contrast, this study presents strong evidence that heterotrophic bacteria might preferentially respond to dust pulses with important consequences regarding the role of dust on the carbon cycling in the oligotrophic ocean. Heterotrophic bacteria response to Saharan dust may have implications on the amount of exported C in the form of DOC, which can be equal to or greater than particulate flux in oligotrophic oceans [Carlson *et al.*, 1994]. When bacterioplankton is P-limited, less DOC is mineralized and assimilated into bacterial biomass, thus increasing the amount of bioavailable DOC that can be exported to the ocean interior through vertical winter mixing [Rivkin and Anderson, 1997; Thingstad *et al.*, 1997; Tanaka and Rassoulzadegan, 2002]. Conversely, bacteria response to dust pulses will increase C mineralization thus reducing the amount of exported bioavailable DOC. Indeed, the experimental fertilizations revealed that dust-derived nutrient input does not appear to affect bacterial growth efficiency and thus would not induce a shift in the heterotrophic bacterial role on the C cycle from “sink” to “link”.

[25] In order to explore the impact of the dust-induced bacterial bloom on C export, we calculated the total amount of mineralized C from enhanced bacterial respiration assuming a minimum duration of the dust-induced bacterial bloom of 4 d (period between the dust pulse and the acquisition of bacteria data). This time period agrees with the experimental results where, after 3 d, BA entered a stationary phase that may be conservatively associated to the beginning of the bloom collapse. Assuming a constant BR rate during the 4-d bloom (see Table 3), the amount of

Table 4. Comparison of Dust Concentration and Increase in Dissolved Organic Carbon and Soluble Reactive Phosphorus Between Natural (Resulting From the Dilution Into the Whole Mixed Layer of the Atmospheric Input Delivered by the Saharan Event Registered on 26 June 2006) and Experimental Conditions

	Dust Input, mg L ⁻¹	Δ SRP, nmol L ⁻¹	Δ DOC, μ mol L ⁻¹
Natural event ^a	0.3	10	2.6
0.5EM ^b	0.5	13	4.8
0.5CD ^b	0.5	15	8.0
2EM ^b	2	30	8.5
2CD ^b	2	35	10.8

^aCalculated as in Figure 5.

^b Δ SRP and Δ DOC were calculated as the difference in SRP and DOC concentration between amended treatments and control at initial conditions of the experiment. Since SRP in control was below detection limit, we considered a maximum value of 20 nmol L⁻¹ (detection limit) to estimate Δ SRP.

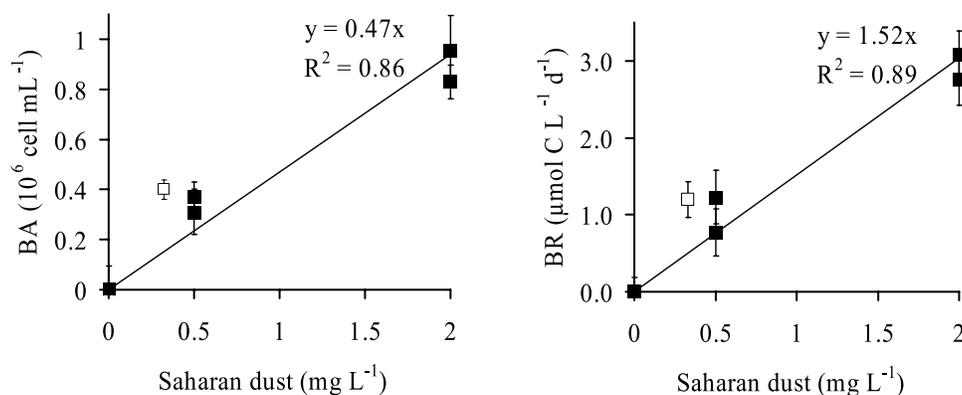


Figure 8. Increase in bacterial abundance (BA) and bacterial respiration rate (BR) between the end and the beginning of the incubations (dark symbols) versus Saharan dust concentration. BA and BR were normalized to the control treatment in order to represent the increase in BA and BR exclusively due to the addition of Saharan dust. Empty symbols represent the increase in BA and BR observed in natural conditions after the Saharan dust event registered on 26 June. Regression line obtained between dust concentration and increase in BA and BR pooling the in situ and the experimental data. Experimental values represent the average \pm standard error of three replicates and in situ values, average \pm standard error of two replicates.

respired carbon in the 8-m mixed layer would have been 0.5 g m^{-2} . This calculation was conservatively performed and results in a minimum value of C respired during the bloom because (1) the bacterial bloom could have certainly lasted longer than 4 d and (2) BR rates are expected to be higher during the first moments of the bloom than when the measurements were performed. In oligotrophic waters, labile DOC accounts for 6–19% of total DOC in surface waters, the rest being highly refractory [Carlson and Ducklow, 1996]. Since DOC export in the Mediterranean Sea has been recently estimated to average $12 \text{ g m}^{-2} \text{ a}^{-1}$ [Avril, 2002], the amount of bioavailable DOC susceptible to be exported to deeper waters would be between 0.7 and $2.3 \text{ g m}^{-2} \text{ a}^{-1}$. Therefore the medium Saharan dust event registered in this study would have induced a mineralization of between 22 and 70% of bioavailable DOC which, otherwise, would contribute to the transport of carbon to deep waters. The accuracy of the estimated percentages depends tightly on the fraction of bioavailable DOC considered which would ultimately determine the proportion of the labile DOC pool mineralized by a dust-induced bacterial bloom.

[26] Finally, in order to fully understand the consequences of a bacterial response to dust pulses for ocean C cycle, besides the proposed short-term effect (enhanced DOC mineralization), possible consequences at longer timescales must also be considered. For instance, bacterial biomass losses during the transfer of C through the microbial loop (up to 95%, Rivkin and Anderson [1997]) may increase the final amount of mineralized C. Conversely, bacterial release of DOC during exponential growth [Kawasaki and Benner, 2006] as well as after the bloom through intensive grazing [Strom et al., 1997] and viral lysis [Middelboe and Lyck,

2002] may counteract the observed DOC mineralization and even increase the amount of DOC susceptible to be exported to depth by winter mixing.

5. Conclusion

[27] Contrary to previous studies suggesting that dust inputs might increase autotrophic production, and hence the efficiency of the biological C pump in oligotrophic oceans, we have presented evidence that heterotrophic bacteria might preferentially respond to Saharan dust, reducing the amount of C exported to deeper waters. The quantitative implications for the global C cycle of both mechanisms may be very important since oceanic oligotrophic areas represent more than 75% of the global ocean [Berger, 1989] and an important proportion (e.g., North Atlantic Ocean) is submitted to dust pulses similar in magnitude to those encountered in the W Mediterranean Sea [Torres-Padron et al., 2002; Jickells et al., 2005]. It thus appears crucial to understand what determines the occurrence of an increase in autotrophic production or a stimulation of heterotrophic bacteria after a dust pulse. Among others, the status of the autotrophic and heterotrophic communities at the moment of atmospheric input as well as dust chemical characteristics (e.g., an important proportion of organic phosphorus would rather benefit heterotrophic bacteria) could determine the way of the biological impact of dust in oligotrophic waters. Our results demonstrate that heterotrophic bacteria may play a much larger role in the connections between dust and the ocean carbon cycle than previously recognized and highlight the need for a more accurate understanding of the role of dust pulses on ocean C cycling.

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