Bacterial response to dust pulses in the NW Mediterranean: Implications for C cycling in the oligotrophic ocean

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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.

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] (Fig. 1A). 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 the highest rate 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 (Fig. 1B).

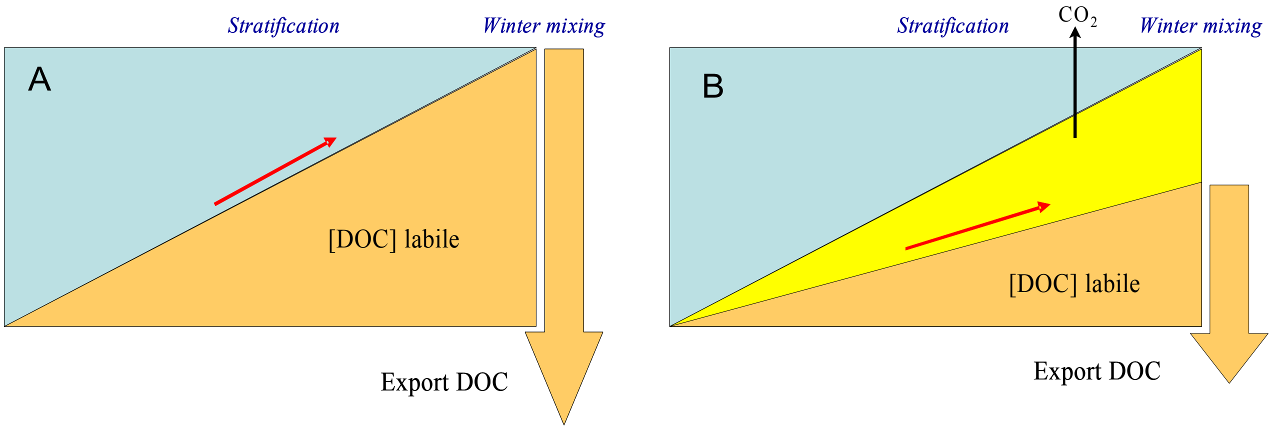

Figure 1. *Schematic representation of the DOC accumulation during the stratification period and subsequent export through winter mixing at two contrasting situations: A) Bacterial limitation by inorganic nutrients typically encountered in oligotrophic regions and B) relieve of bacterial limitation (e.g. by atmospheric input) during the stratification period*

In this study, we evaluated the response of heterotrophic bacteria to Saharan dust pulses in the NW Mediterranean Sea. For this purpose, we used a dual approach (Fig. 2) which combined field observations of atmospheric fluxes of nutrients and bacterial dynamics in the surface layer with microcosm experiments in which realistic amounts of Saharan dust were added to bacterial natural assemblages.

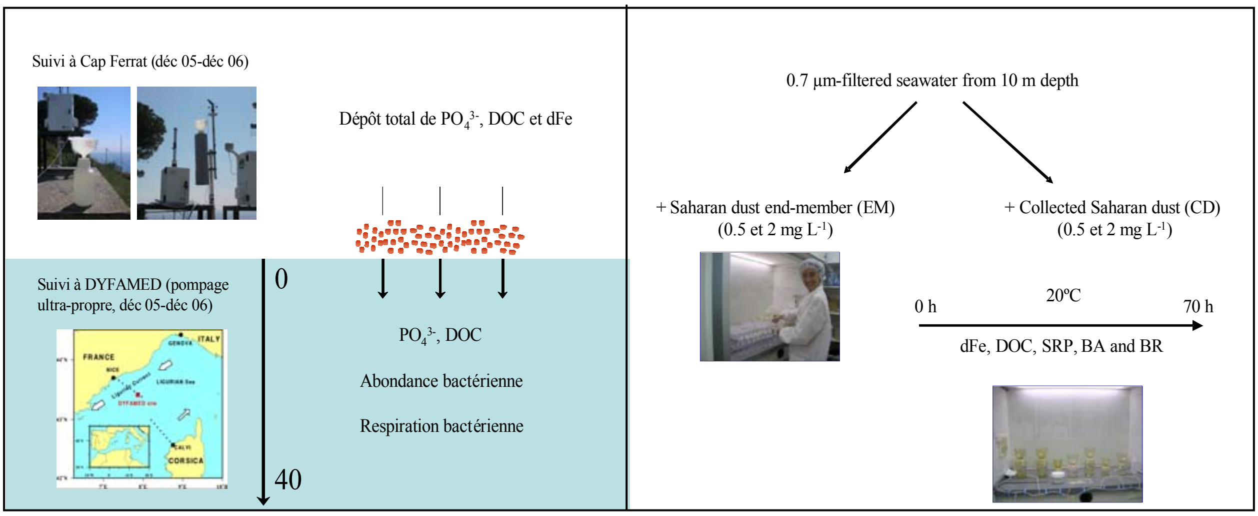

Figure 2. *Observational (left) and experimental (right) approach used in this study to assess the response of heterotrophic bacteria to Saharan dust pulses*

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 (Fig. 3). DOC fluxes ranged from 0.5 to 16.8 mmol m^{-2} and SRP fluxes from 0.7 to 74.0 µmol m^{-2}. One Saharan dust event, which took place on the 26th June accounted for 42% of annual PM deposition and was responsible for the highest DOC and SRP fluxes registered during the study period. Four days after this Saharan event surface BA and BR at the DYFAMED site exhibited a 1.5 and 2-fold increase, respectively (Fig. 3).

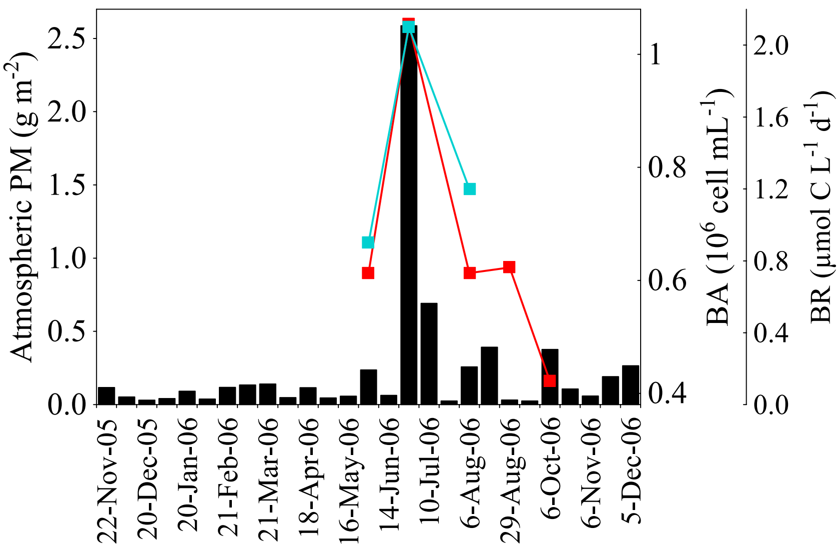

Figure 3. *Seasonal variability of atmospheric PM fluxes (black bars) and bacterial abundance (red line) and respiration (blue line) before and after the Saharan dust event registered on the 26th June (2.5 g m^{-2}).*

Experimental Saharan dust additions induced significant increases in dissolved organic carbon (DOC) and soluble reactive phosphorus (SRP) concentration in all experimental bottles. At the end of the incubations, both DOC and SRP concentration decreased in all experimental bottles, likely consumed by bacteria. During the incubations, bacterial abundance (BA) exhibited an initial phase of exponential growth followed by a stationary phase reached after ca. 48 hours, 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 (Fig. 4A). Increases in BA were always accompanied by commensurate decreases in O_2 concentration (Fig. 4B) and, therefore, bacterial respiration rates (BR) were higher in all amended treatments than in control and increased with the amount of dust.

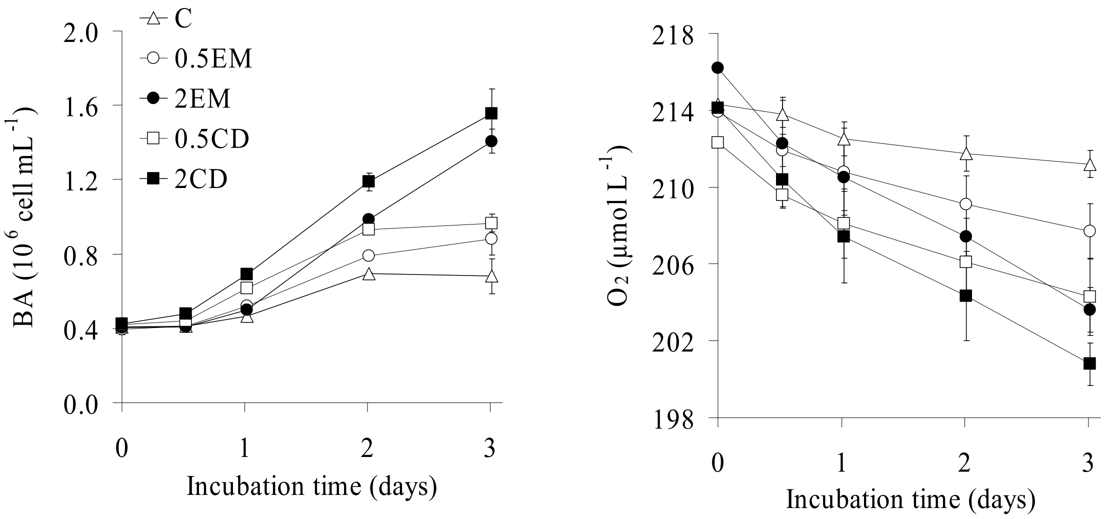

Figure 4. *Changes in bacterial abundance (BA) and O_2 concentration (mean value ± standard error of three replicates) versus incubation time for each experimental treatment in the dust addition experiments.*

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). These 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 and they allow us to estimate the impact of bacterial response to Saharan dust inputs on carbon cycling in oligotrophic, nutrient-starved oceanic systems. For this purpose, we estimated the total amount of mineralized C from both bacterial respiration and bacteria biomass losses during C transfer to higher trophic levels. The total amount of C mineralized in the mixed layer by the dust-induced bacterial bloom would have been > 0.6 g m^{-2}, more than 40% of the total amount of bioavailable DOC annually exported to depth in the Mediterranean Sea (Fig. 5).

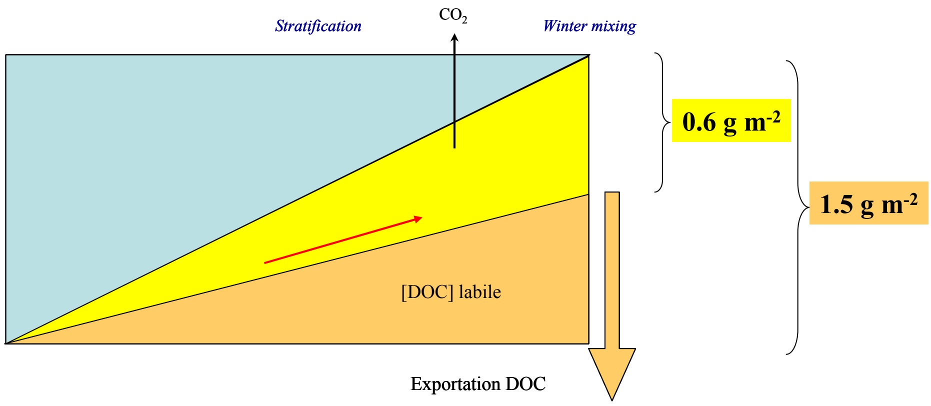

Figure 5. *Consequences for the C cycle in the Mediterranean Sea of a dust induced bacterial bloom. The amount of C annually exported to depth was estimated after Avril (2003) data assuming a mean 10% of bioavailable C in the oligotrophic ocean (Carlson and Ducklow, 1996)*

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. 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.