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Coastal Mediterranean plankton stimulation dynamics through a dust storm event: An experimental simulation

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ABSTRACT

An enhancement of aeolian inputs to the ocean due to a future increase in aridity in certain parts of the world is predicted from global change. We conducted an experimental simulation to assess the biological response of NW Mediterranean coastal surface waters to an episodic dust addition. On the assumption that planktonic growth was limited by phosphorus, dust effects were compared to those induced by equivalent enrichments of phosphate. The experiment analyzed the dynamics of several parameters during one week: inorganic nutrients, total and fractioned chlorophyll *a*, bacterial abundance, phytoplankton species composition, abundance of autotrophic and heterotrophic flagellates, particulate organic carbon and particulate organic nitrogen. The maximum addition of dust (0.5 g dust L^{-1}) initiated an increase in bacterial abundance. After 48 h, bacterial numbers decreased due to a peak in heterotrophic flagellates and a significant growth of autotrophic organisms, mainly nanoflagellates but also diatoms, was observed. Conversely, lower inputs of dust (0.05 g dust L^{-1}) and phosphate enrichments (0.5 μmol PO_4^{3-} L^{-1}) only produced increases in phototrophic nanoflagellates. In our experiment, dust triggered bacterial growth, changed phytoplankton dynamics and affected the ratio of autotrophic to heterotrophic biomass, adding to the variability in the sources that affect system dynamics, energy and carbon budgets and ultimately higher trophic levels of the coastal marine food web.

1. Introduction

The dynamics of plankton in temperate and subtropical oceanic waters has a strong seasonality driven mainly by the winter mixing that brings new nutrients to the upper euphotic layer. In coastal areas this seasonality tends to be smoothed without a clear pattern (Cloern and Jassby, 2008). Higher nutrient availability, multiple nutrient sources with their own dynamics and nutrient imbalances with respect to the Redfield ratio may increase the variability. As an example, the dynamics in Blanes Bay (NW Mediterranean) seems to be largely driven by specific events (Guadayol et al., 2009) on top of a seasonal background. Inorganic nutrients of terrestrial origin are supplied to the coastal system through runoff, driven in part by episodic meteorological phenomena. Nutrients are also resuspended into the water column through storm and wave action. Another potential event-driven source of nutrients is atmospheric deposition, with a highly variable component of dust from Saharan origin.

The Saharan and Sahel regions are two of the most active ones in terms of dust export (Prospero et al., 1996; Lee et al., 2006; Maher et al., 2010). Pérez et al. (2007) estimate that these two areas are responsible for more than half of the world's mineral dust emissions. A large part of this dust travels across the Mediterranean Sea and is deposited within its coastal area (Loÿe-Pilot and Martin, 1996; Guerzoni et al., 1999). Saharan dust is known to contain a variable amount of inorganic nutrients (Duce and Tindale, 1991; Bergametti et al., 1992; Jickells, 1995; Prospero et al., 1996). Several studies have been conducted to test aerosol effects in the Atlantic Ocean (Blain et al., 2004; Mills et al., 2004; Duarte et al., 2006; Marañón et al., 2010), in the eastern Mediterranean basin (Herut et al., 2005; Eker-Develi et al., 2006), and in the western Mediterranean Sea (Klein et al., 1997; Bonnet et al., 2005; Pulido-Villena et al., 2008, 2010). These studies, conducted within an open sea scenario, have shown variable results. A positive impact on autotrophic communities has been experimentally shown (Mills

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et al., 2004; Bonnet et al., 2005), and increases in bacterial activity and abundance following dust enrichments have also been reported, both in experiments and with direct measurements at sea (Herut et al., 2005; Pulido-Villena et al., 2008). Whether such biological responses are mutually exclusive, part of a seasonal and common ecological succession, or particular for certain locations or environmental conditions (Marañón et al., 2010) requires further study.

Stimulation of plankton components with dust is usually related to the alleviation of macro- or micro-nutrient limitation. The Mediterranean is an oligotrophic sea thought to be globally limited by phosphorus (Berland et al., 1980; Krom et al., 1991; Thingstad et al., 1998; Moutin et al., 2002), albeit inorganic nutrient concentrations are very low and the system is often found to switch between different limiting nutrients (Marty et al., 2002; Sala et al., 2002; Lucea et al., 2005; Pinhassi et al., 2006). The input of phosphorus is 82% of terrestrial origin, including atmospheric sources, compared to 2% for the global ocean (Bethoux and Migon, 2009). Terrestrial sources of nutrients have an N:P composition higher than the Redfield ratio of 16 for plankton thus exacerbating P-limitation in the long-term. Hence, phosphorus in atmospheric dust, even if present in relatively low amounts (Markaki et al., 2008), is a candidate for plankton stimulation events (Pulido-Villena et al., 2010). The importance of atmospheric dust loads may become even larger as desertification in the North African and Mediterranean regions increases in future climate scenarios (Gao and Giorgi, 2008).

The present study describes the response of a natural coastal planktonic community to large dust additions and hypothesises that the changes induced by dust are comparable to the effects of equivalent phosphate enrichments. Further results with particular focus on bacterial activity and composition are the subject of a companion paper published elsewhere (Lekunberri et al., 2010). The present experiment includes small-scale turbulence as a secondary environmental variable to test whether turbulent conditions, often accompanying dust storms, lessen or enhance the effects of dust on the planktonic community. The study further examines whether dust inputs can drive changes in biomass and structure within the microbial community of a particular NW Mediterranean coastal site, and if such changes may shift the balance between autotrophy and heterotrophy.

2. Materials and methods

2.1. Aerosol collection

Aerosols used in the experiment were gathered during an intense Saharan dust wet deposition event associated with a cold front in Nice, France (43°42′10″ N, 7°16′9″ E) on February 21, 2004. The Dust REgional Atmospheric Model (DREAM, www.bsc.es/projects/earthscience/DREAM) wet deposition forecast for this day shows a large area of Southern France, Northern Italy and the Northwest Mediterranean above 41°N with a deposition above 1 g m^{-2}. The mass flux was measured at the nearby meteorological station of Cap Ferrat during the event was 22 g m^{-2} (pers. comm. Christophe Migon [CNRS-UMPC Paris 06, UMR 7093, LOV, Observatoire océanographique, Villefranche/Mer, France]). We collected the dust in a plastic tray (ca. 0.28 m^2) exposed during the storm event (>1 day), with a locally estimated mass flux of 64 g m^{-2}. The dust was dried (60 °C, 48 h) and stored in an acid-washed polypropylene bottle. Before use, the dust was ground to homogenize the sample.

2.2. Water sampling and experimental setup

Water for the experiment was collected at the Blanes Bay Microbial Observatory (41°40′0″ N, 2°48′0″ E) on May 16th, 2006. Table 1 shows the N:P ratio for Blanes Bay. The mean molar N:P is 23 and shows no clear seasonal pattern (no significant seasonal autocorrelation), although the average summer value of 18 is slightly lower than for the rest of the year (24 in winter, 27 in spring and 22 in autumn). Inorganic phosphorus ranges from <0.02 (undetectable) to 0.94 μmol L^{-1} with an annual mean and standard deviation of 0.16 ± 0.10 μmol L^{-1}. Dissolved inorganic nitrogen ranges from 0.22 to 8.60 μmol L^{-1} with an annual mean and standard deviation of 2.60 ± 1.80 μmol L^{-1}. After screening the water through a 150 μm Nylon mesh, we filled 20 L plastic carboys that had previously been washed with a dilute solution of sodium hypochloride and thoroughly rinsed with tap water, milli-Q water and sample water. The water was taken to the laboratory, where 15 L cylindrical metacrylate containers were used for the experiment. Each of these containers was filled with 7.5 L of water, and they were subjected to experimental conditions in a light and temperature controlled environmental chamber during 7 days. We had eight experimental conditions (see Lekunberri et al., 2010) determined by three variables: levels of dust addition (DL, DH), phosphate enrichment (P) and absence/presence of turbulence (S, T). Controls (C) were not enriched with either phosphate or dust. We could not replicate all treatment combinations due to logistical constraints hence the compromise between the desired multifactor design and the number of feasible units was solved in favor of duplicating some of the combinations, namely CS, CT, DLS and DLT.

Small-scale turbulence was generated by means of vertically-oscillating grids with a mechanical device described in Peters et al. (2002). We used a turbulent kinetic energy dissipation rate of 10^{-2} cm^2 s^{-3}, estimated from the equations in Peters and Gross (1994). This value is within the range of turbulence intensities in coastal areas (Kiørboe and Saiz, 1995). Turbulence was only applied during the first three days of the experiment, a typical duration for turbulence events of the applied mean intensity in the Blanes area (Guadayol and Peters, 2006). Thereby, containers corresponding to T treatments underwent turbulent conditions for three days and remained still until the end of the experiment, whereas S treatments were kept still.

Both dust and phosphate were added as a unique dose at the beginning of the experiment. Ridame and Guieu (2002) suggest that 60% of 'Saharan rains' carry between 0.005 and 8 g of dust per liter. We did a preliminary nutrient release test for different dust concentrations in the water (Fig. 1) and found that a 0.05 g L^{-1} dust concentration released 0.38 ± 0.08 μmol PO_4^{3-} L^{-1}. We decided to use a dust addition of 0.05 g L^{-1} as our low addition level (DL) and 0.5 g L^{-1} as our high addition level (DH). To check whether a similar

Table 1
Nutrient data for Blanes Bay summarized from March 2001 to January 2008 (Blanes Bay Microbial Observatory). Data are means with standard errors in parenthesis.

Season	Day range (m/d)	*n*	NO_3+NO_2 (μmol L^{-1})	NH_4 (μmol L^{-1})	Si (μmol L^{-1})	P (μmol L^{-1})	N:P
All	1/1–12/31	108	1.52 (0.15)	1.08 (0.08)	1.64 (0.14)	0.16 (0.01)	22.6 (2.48)
Winter	12/21–3/20	26	2.34 (0.37)	1.21 (0.23)	1.96 (0.32)	0.17 (0.01)	24.5 (3.64)
Spring	3/21–6/20	25	1.86 (0.26)	1.07 (0.15)	1.97 (0.30)	0.19 (0.03)	26.7 (8.18)
Summer	6/21–9/20	25	0.54 (0.10)	1.00 (0.10)	0.92 (0.12)	0.13 (0.01)	17.7 (4.17)
Autumn	9/21–12/20	32	1.36 (0.25)	1.04 (0.12)	1.69 (0.30)	0.14 (0.01)	21.5 (3.26)

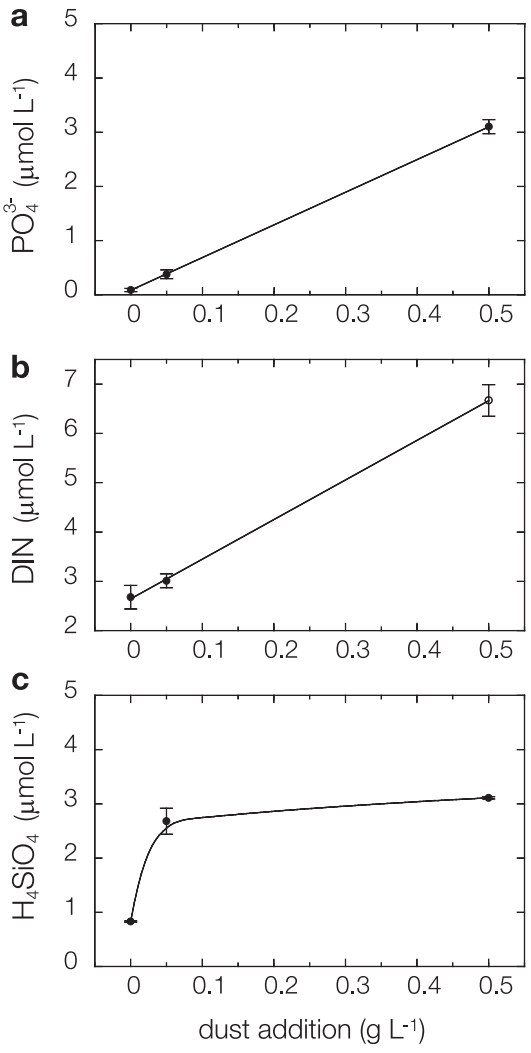

Fig. 1. Nutrient concentrations (a, phosphate; b, dissolved inorganic nitrogen; c, silicate) obtained in an abiotic test where different amounts of dust (0.05 g L^{-1}, 0.5 g L^{-1}) were diluted in seawater prefiltered by 0.2 µm. Analysis of inorganic nutrients was performed on samples taken 18 h after the additions. Error bars correspond to the standard deviation of two replicates and may be included within the size of the symbol.

addition of inorganic phosphorus produced the same effects on the planktonic community, P treatments were enriched with PO_4^{3-} at a concentration of 0.5 µmol L^{-1}. Our dust levels are somewhat high compared to previous experiments (e.g. Blain et al., 2004; Herut et al., 2005; Pulido-Villena et al., 2008). Unlike these, we aim to address the effects of dust in coastal waters, which may include very shallow areas such as coastal lagoons or estuaries where the effective water column can be as shallow as 1 m. Furthermore, even in somewhat deeper water columns, the distribution of particles may not be homogeneous and the dissolution of macronutrients from dust may occur in a shallow upper surface, not mixing in the whole water column, as has indeed been shown for phosphorus in mesocosm experiments (Pulido-Villena et al., 2010).

Temperature was adjusted to *in situ* water temperature (17 °C) and light conditions were set to 225 µmol photons m^{-2} s^{-1} inside the containers. The light:dark cycle (14.5 h:9.5 h) was also adjusted to that of the time of the year. The experiment started within 3–4 h of water collection. Samples for inorganic nutrients, total and fractioned chlorophyll *a*, and bacteria were taken daily (except for day 5). Samples for heterotrophic and autotrophic flagellates, particulate organic carbon, particulate organic nitrogen, and microphytoplankton were taken on days 0, 3 and 7.

2.3. Analytical procedures

Inorganic nutrients (nitrate, nitrite, ammonium, silicate and phosphate) were determined with an Alliance Evolution II autoanalyzer following the methods in Hansen and Koroleff (1999) with minor modifications. The detection limits in the lowest range (MDL) for the instrument are 0.01 (nitrate + nitrite), 0.0015 (nitrite), 0.034 (ammonium), 0.016 (silicate) and 0.02 (phosphate), all in µmol L^{-1}.

Total and fractioned (>3 µm, >10 µm) chlorophyll *a* was measured according to the procedure described in Yentsch and Menzel (1963). For total chl *a*, 20 mL samples were filtered through Whatman GF/F glass fiber filters. For the >3 µm and >10 µm fractions, 30–50 mL samples were filtered through 3-µm and 10-µm pore size Whatman Nuclepore polycarbonate filters respectively. All filters were then immersed in 90% acetone and left in the dark at 4 °C for 24 h. The fluorescence of the extract was measured with a Turner Designs fluorometer.

Bacteria were determined by flow cytometry (Gasol and Del Giorgio, 2000). Samples (1.8 mL) were fixed with 0.18 mL of a 10% paraformaldehyde and 0.5% glutaraldehyde mixture. Subsamples of 200 µL were stained with SYTO13 (Molecular Probes) at 2.5 µmol L^{-1} (diluted in DMS), left to stain for 15 min in the dark and then ran at low speed (ca. 12 µL min^{-1}) through a Becton Dickinson FACScalibur flow cytometer with a laser emitting at 488 nm. As an internal standard, we added 10 µL per sample of a 10^6 mL^{-1} solution of yellow-green 0.92 µm latex beads (Polysciences).

Autotrophic and heterotrophic nanoflagellates were estimated by epifluorescence microscopy (Porter and Feig, 1980). Samples for flagellates were fixed with glutaraldehyde (1% final concentration), stained with DAPI (5 µg mL^{-1}) and filtered on 0.8 µm black polycarbonate membranes. The filters were then mounted on microscope slides and kept frozen at −20 °C. Counts were done on a Nikon Labophot epifluorescence microscope at ×1250 magnification. Between 180 and 200 nanoflagellates were counted on each filter, and they were sized using a calibrated ocular micrometer in 4 classes (<4 µm, 4–8 µm, 8–16 µm, >16 µm). Autotrophic and heterotrophic organisms were distinguished by the red fluorescence of chlorophyll under blue light excitation.

Other phytoplankton cells (mainly diatoms and dinoflagellates) were enumerated in 50 cm^3 settling chambers using the Utermöhl technique (Utermöhl, 1958). Samples were fixed with a formalin-hexamine solution (0.4% final concentration) and kept at 4 °C until counting. The observed organisms were sized and classified to the highest possible taxonomic separation. Picophytoplankton was enumerated using flow cytometry and reported mainly elsewhere (Lekunberri et al., 2010).

Particulate organic carbon and nitrogen were collected (up to 500 mL) on pre-combusted Whatman GF/F filters. Samples were kept frozen at −80 °C until analysis. Measurements were carried out with a Perkin Elmer 2400 CHN analyzer; an acetanilide standard was used daily and the precision of the method is ±0.3 µmol C L^{-1} and ±0.1 µmol N L^{-1}.

For plankton biomass estimations, chlorophyll *a* values were converted to carbon using a factor of 50 µg of carbon per µg of chl (Eppley et al., 1977; Redalje, 1983). This is within the range of values reported by Delgado et al. (1992) for surface waters in the NW Mediterranean. Bacterial biomass was estimated by flow cytometry following the methodology described in Gasol and Del Giorgio (2000), using a carbon conversion factor of 0.35 pg C $µm^{-3}$ (Bjørnsen, 1986), which resulted in an average value of 21 fg C

cell^{-1}. Cell volume of flagellates was established from the mean value of each size class, assuming a prolate spheroid shape. In this latter case, conversion to carbon was calculated with the equation: pg C cell^{-1} = 0.433 · (μm^3)$^{0.863}$ (Verity et al., 1992). Similarly, carbon content of microphytoplankton was estimated applying the formula: pg C cell^{-1} = 0.109 · (μm^3)$^{0.991}$ (Montagnes et al., 1994) to biovolume determinations (Hillebrand et al., 1999).

2.4. Statistical analyses

Statistical analyses were performed with Statistica version 6 (StatSoft Inc., Tulsa, OK, USA) and JMP version 8 (SAS Institute Inc., Cary, NC, USA.). Significance was considered for probability values <0.05.

3. Results

3.1. Nutrient dynamics

Initial nutrient concentrations were low compared to averages for the season from 2001 to 2008 (Table 1). Nitrate plus nitrite showed a concentration of 0.51 μmol L^{-1}, ammonium of 0.73 μmol L^{-1}, phosphate of 0.04 μmol L^{-1} and silicate of 0.64 μmol L^{-1}. Although all inorganic nutrients showed lower concentrations than average for the time of the year, the largest imbalance was the ratio of nitrate plus nitrite to ammonium of 0.70 when the average is 1.72, more than double. The N:P ratio of the initial water was 31.

Concentrations of inorganic nutrients for all experimental conditions throughout the seven days of the experiment are shown in Fig. 2. Overall, non-enriched control treatments (C) showed the smallest variation amplitude over time, although their dynamics were similar to those in the DL and P containers. On the contrary, major differences were found in containers with large inputs of dust (DH), particularly for phosphate, ammonium and silicate (analysis of covariance, Bonferroni *post-hoc* test, *p-value* < 0.001).

Results from nutrient analyses performed 3 h after the enrichments (Fig. 2a) showed phosphate concentrations of 0.48–0.52 μmol PO_4^{3-} L^{-1} in P (the expected concentration was 0.5 μmol L^{-1}), 0.20 μmol PO_4^{3-} L^{-1} in DL (low dust) and 1.50–1.71 μmol PO_4^{3-} L^{-1} in DH (high dust). Note that, subtracting the phosphate measured in the controls (as a background concentration of phosphate in the seawater), we obtained a 10-fold increase of phosphate in containers with high concentration of dust compared to those with low dust inputs, in agreement with the amounts of dust added. The increase in the concentration of phosphate within the first three hours was followed by a rapid decrease in all treatments by day 1, and a recovery on days 3–4. Previous studies (Herut et al., 2002, 2005; Ridame and Guieu, 2002), indicate that phosphate is released from the dust shortly after its addition, sometimes peaking within 2 h.

The total amount of phosphate released within the experimental containers proved to be slightly lower than estimated from the abiotic test (Fig. 1). We obtained concentrations of 1.5 μmol PO_4^{3-} L^{-1} and 0.15 μmol PO_4^{3-} L^{-1} in the DH and DL experimental containers respectively (Fig. 2) indicating yields of ca. 3 μmol PO_4^{3-} g^{-1} dust, while the abiotic test showed yields of ca. 6 μmol PO_4^{3-} g^{-1} dust. However, one has to take into account that the experimental containers had a biological community dynamically reactive to phosphorus. In addition, in the abiotic test we analyzed nutrient concentrations after 18 h, which provides a much longer time for nutrients to be released from dust. Despite such differences, both experiments provided supporting evidence concerning nutrient supply: dust released ammonium, phosphate and silicate within the first hours, whereas nitrate increases following dust addition were minimal.

As mentioned above, the initial concentration of ammonium in the water was relatively high (0.73 μmol NH_4^+ L^{-1}) compared to the other nutrients during that time of the year. With the exception of treatments with the highest inputs of dust, ammonium remained stable in all containers during the first few days and tended to increase toward the end of the experiment (days 6 and 7). Where dust had been added in large concentrations, however, there was a sudden increase of ammonium within the first three hours and then a sharp decrease until the next day. The concentration reached then maximum values on days 3–4, and fell to initial values on days 6 and 7.

Nitrate and nitrite were least affected by the addition of dust. Even though nitrate reached slightly higher concentrations in DH treatments than in the controls, values did not differ significantly among experimental conditions (ANCOVA, *p-value* > 0.10). By the end of the experiment (from day 4 onwards), containers with either phosphate or low dust enrichments that had been under

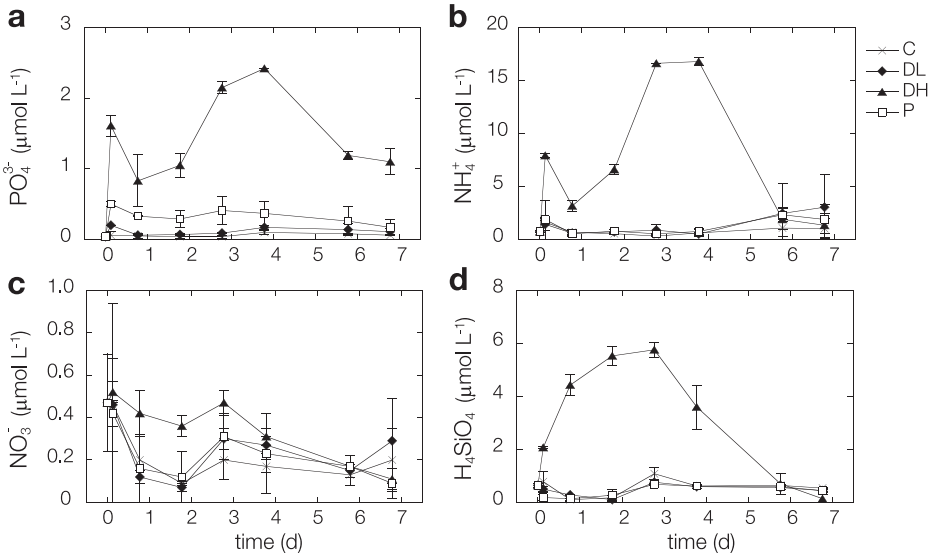

Fig. 2. Nutrient concentrations (phosphate, ammonium, nitrate and silicate) during the experimental simulation. Turbulence was not significantly different and consequently still and turbulent treatments were averaged for each nutrient amendment condition. Error bars represent the standard deviation of either 4 (in C and DL) or 2 (in DH and P) containers.

turbulence showed a steady increase in nitrite (data not shown). On the other hand, nitrate concentrations decreased with time in all treatments, with a steeper decrease during the first hours and a relatively small recovery between days 2 and 3 (Fig. 2c).

The case of silicate is of special interest. Whilst for most treatments changes in silicate concentration were similar, with concentrations decaying during the first two days and stabilizing thereafter, in those containers with high inputs of dust (DH) the concentration of silicate increased notably up to the third day (reaching values of about 6 μmol L^{-1}), and then decreased steadily to minimum values at the end of the experiment. The effect of turbulence on nutrient concentrations was non-significant (ANCOVA, *p-value* > 0.05 for each of the four nutrients).

3.2. Phytoplankton

The initial concentration of chlorophyll *a* was high (2.64 μg L^{-1}), close to typical spring bloom values in the area. During the first two days of the experiment chlorophyll concentration decayed in all treatments. While values remained low in the C, P and DL containers until the end of the experiment, chlorophyll increased by nearly 11-fold in the DH containers (Fig. 3). Likewise, the fraction of chl >10 μm fell to nearly 0 μg L^{-1} within 2 days in all experimental conditions except in those tanks with a high content of dust. In DH, the initial drop was followed by a peak on days 3 and 4. Although we did not sample daily for chl >3 μm, the results matched those of total chl and chl >10 μm: that is, a general decline of chlorophyll concentration except in DH treatments (Fig. 3). The percentages of each chlorophyll fraction throughout the experiment show a constant decrease of the pigmented organisms larger than 10 μm, independent of treatment, from 33% to a minor value of 5%. Chlorophyll of organisms larger than 3 μm also decreased, but their final proportion varied widely among experimental conditions (approx. 10–50%). Note that, in most cases, chlorophyll concentrations were higher under turbulence (*p-value* < 0.05, Table 2).

The initial dominance of diatoms (up to 85% of autotrophic carbon) gave way to a generalized dominance of small pigmented flagellates in the first few days (Fig. 4, and Lekunberri et al., 2010). Most of these initial diatoms were relatively large *Pseudo-nitzschia* spp. and chains of centric diatoms (Fig. 5) that settled to the bottom of the containers. Control treatments (CS, CT) showed trends similar to phosphate enrichments (PS, PT). After 3 days, total concentration of cells decreased nearly one order of magnitude with respect to initial values, and diatoms were replaced by a combination of autotrophic flagellates and dinoflagellates. In contrast, tanks enriched with low concentrations of Saharan dust increased the number of cells during the first days, though they also declined by the end of the experiment. Again, diatoms were replaced by flagellates and a few species of dinoflagellates. In containers with a high addition of dust, initial diatoms were replaced by smaller diatom species by day 3. Flagellates increased the most in DH treatments (Fig. 4), reaching final concentrations of about $5 \cdot 10^4$ cells mL^{-1}. It is

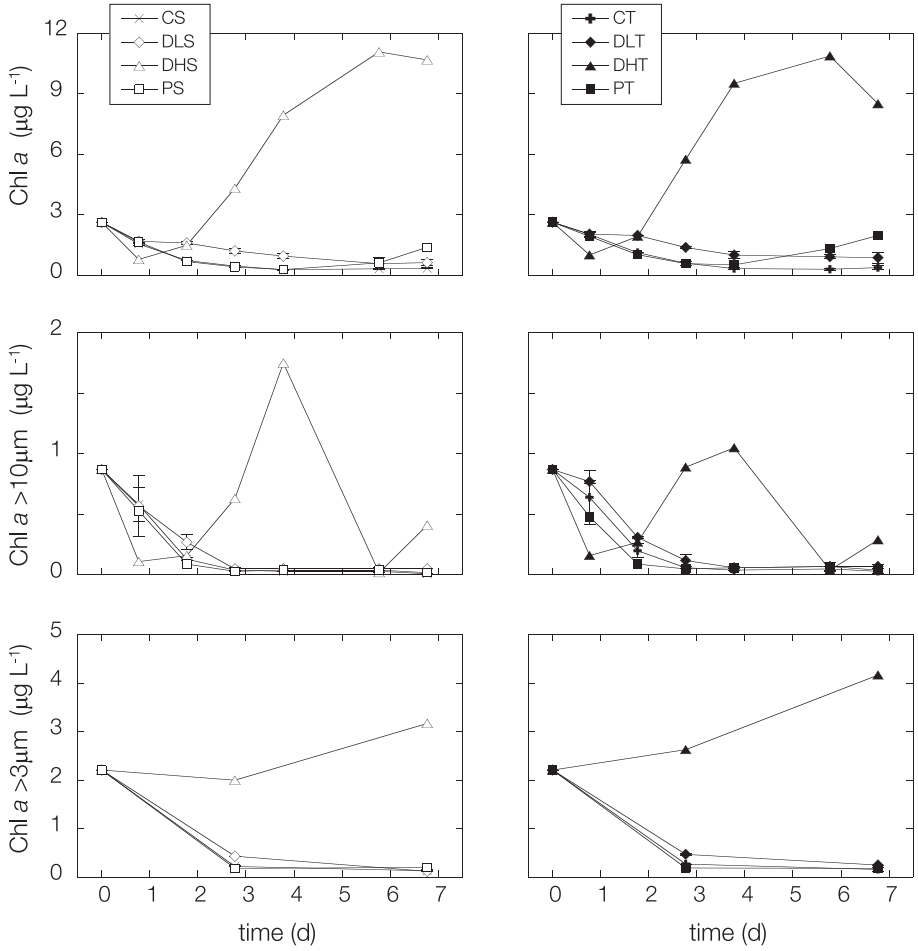

Fig. 3. Chlorophyll *a* during the experiment. Plots are for total chlorophyll *a* (see also Lekunberri et al., 2010), chlorophyll *a* >10 μm, chlorophyll *a* >3 μm. Left plots are for still water treatments and right plots for turbulent treatments. Error bars represent the standard deviation of two replicate containers in CS, CT, DLS and DLT. If not seen, error bars are small and contained within the symbol.

Table 2
Summary of ANCOVA tests for several biological variables. Asterisks denote significant levels where *** $p\text{-value} \leq 0.001$, ** $p\text{-value} \leq 0.01$, * $p\text{-value} \leq 0.05$; n.s. (not significant) refers to $p\text{-value} > 0.05$; N = number of samples. The final model was calculated excluding non-significant factors. Biological data were log-transformed prior to statistical analyses. Samples for autotrophic (ANF) and heterotrophic (HNF) nanoflagellates were only collected on days 0, 3 and 7 (see Materials and methods). Consequently, for the condition 'Time 0–3 days', time could not be included as a covariate and we performed ANOVA tests. The same is true for other phytoplanktonic groups data.

	chl ($\mu g\ L^{-1}$)	chl >10 μm ($\mu g\ L^{-1}$)	bact (cells mL^{-1})	ANF <16 μm (cells mL^{-1})	HNF <16 μm (cells mL^{-1})	ANF <4 μm (cells mL^{-1})	HNF <4 μm (cells mL^{-1})	Dinoflagellates (cells L^{-1})	Diatoms (cells L^{-1})
Time 0–3 days									
Time	***	***	n.s.	–	–	–	–	–	–
Addition	***	***	***	**	***	*	***	n.s.	**
Turbulence	***	***	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.
Addition · Turb	n.s.	n.s.	n.s.	–	–	–	–	–	–
Addition · Time	***	***	***	–	–	–	–	–	–
Turb · Time	n.s.	n.s.	n.s.	–	–	–	–	–	–
Time · Time	n.s.	n.s.	n.s.	–	–	–	–	–	–
Addition · Turb · Time	n.s.	n.s.	n.s.	–	–	–	–	–	–
R^2 adjusted	0.973	0.928	0.694	0.925	0.990	0.869	0.9856	0.558	0.953
N	36	36	48	8	8	8	8	8	8
p-value	***	***	***	**	***	*	***	*	**
All experiment									
Time	n.s.	***	***	n.s.	***	n.s.	n.s.	n.s.	***
Addition	***	***	***	***	***	n.s.	***	n.s.	***
Turbulence	*	*	n.s.	n.s.	n.s.	n.s.	n.s.	***	n.s.
Addition · Turb	n.s.	n.s.	n.s.	–	–	–	–	–	–
Addition · Time	***	*	n.s.	***	***	n.s.	***	***	n.s.
Turb · Time	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.
Time · Time	**	***	***	–	–	–	–	–	–
Addition · Turb · Time	n.s.	n.s.	n.s.	–	–	–	–	–	–
R^2 adjusted	0.848	0.637	0.641	0.889	0.977	–	0.926	0.826	0.915
N	72	72	84	16	16	15	16	16	16
p-value	***	***	***	***	***	–	***	***	***

to note that in treatments DHS and DHT, diatoms changed also in species composition: *Pseudo-nitzschia* spp. and centric diatoms were replaced by *Nitzschia* sp., *Skeletonema costatum* and *Chaetoceros* spp. (among others, see Fig. 5). Unlike the initial species, these diatoms are characterized by medium or small sizes and high growth rates (Eppley, 1977; Furnas, 1990), and their life strategy is considered to be similar to that of flagellates.

Whereas turbulence did not seem to significantly affect nutrient concentrations, it appeared to be responsible for some differences in phytoplankton concentrations. We observed a general trend for larger organism abundance and biomass concentration in turbulence versus still treatments for a particular time and nutrient amendment condition (Fig. 4). Perhaps this trend was most clear for diatoms at time 3 with an average of 2.6 times more abundant in T (highest difference of 4.9 times for DH). These differences were not apparent in the ANOVAs (Table 2) because of the large differences in response between the different amendment treatments.

As a whole, results were consistent with that found for bulk chlorophyll measurements: the bigger autotrophic cells (~chl > 10 μm) decreased rapidly in all treatments within the first days, and only recovered in the DHS–DHT (where chl > 10 μm peaked immediately afterwards, see Fig. 3). Except in DH, total chlorophyll *a* was low at the end of the experiment, as we would also expect from corresponding phytoplankton cell numbers. Finally, in both DHS–DHT treatments, high values of chlorophyll at the end of the experiment coincided with minimum values of chl >10 μm. Indeed, phytoplankton analysis showed that the major growth in these treatments corresponded to small flagellates, and additional flow cytometry measurements of picoeukaryotes and cyanobacteria confirmed these results (see Lekunberri et al., 2010).

3.3. Bacteria and heterotrophic nanoflagellates (HNF)

As with other variables, differences in the response of bacteria and HNF were maximal in tanks with the largest inputs of dust (Fig. 6, Table 2). In C, P, and DL treatments, bacteria and HNF remained in low numbers until day 3, and tended to increase toward the end of the experiment. In DH tanks, there was a rapid bacterial response within the first 24–48 h, and a subsequent decay 2 days after, following the maximum growth of HNF. Moreover, when the number of heterotrophic flagellates decreased in these treatments at the end of the experiment, the concentration of bacteria again increased.

3.4. Biomass ratios

There are two clearly distinct patterns in the proportion of bacterial biomass with respect to total biomass of osmotrophic organisms: in most treatments, bacterial biomass oscillated around 30% until day 3, and then increased up to 80% at the end of the experiment (Fig. 7). Conversely, large dust enrichments (DH) induced a rapid bacterial response during the first days (ca. 85% of total osmotrophic biomass were heterotrophic bacteria) and then the dominant changed to autotrophic organisms, with bacteria accounting for only 30% of total osmotrophic biomass ($p\text{-value} < 0.001$ for the cross-effect [addition · time]). Similarly, for the proportion of autotrophic biomass within total living biomass (Table 3), large dust additions maintained the autotrophic ratio over 50% at the end of the experiment, while in the other treatments autotrophic organisms decayed to ca. 20%. Consistent with biomass calculations based on cell abundances, particulate organic carbon and nitrogen increased notably in DH containers with regards to the other experimental conditions: nearly 5-fold on day 7 (Table 3).

4. Discussion

4.1. Initial conditions

The experimental simulation was conducted in late spring, after the usual spring bloom in this part of the NW Mediterranean Sea (Alonso-Sáez et al., 2008). This period of the year appears to be the

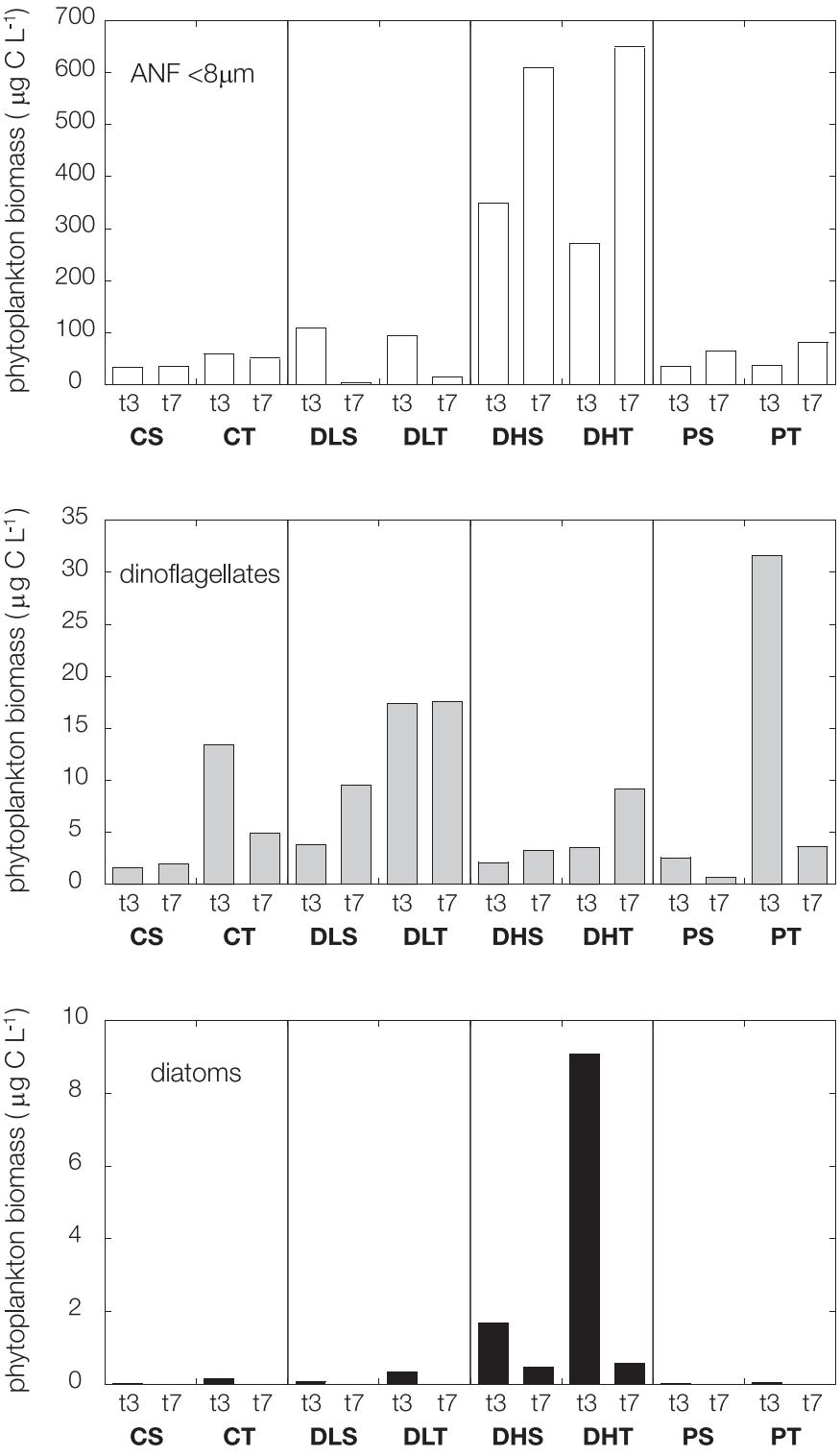

Fig. 4. Eukaryotic phytoplankton groups in units of carbon biomass (μg C L^{-1}) on days 3 and 7 for all experimental treatments.

ideal season for testing the potential effects of the dust to surface waters. Firstly, late spring–early summer is a very active period in terms of dust events over the Mediterranean (Guerzoni et al., 1997, 1999; Ridame and Guieu, 2002; Gkikas et al., 2009). Secondly, the water column is stratified and input of nutrients from deeper waters is limited (Marty et al., 2002). Under such circumstances, the atmospheric supply of nutrients could have a significant effect on plankton dynamics.

Inorganic nutrient concentrations at the beginning of the experiment were lower than the average for the season, but the ratio of ammonium to nitrate plus nitrite was 2.5 times higher than usual. The concentration of chlorophyll *a* was surprisingly high as compared to historical values for these waters at this time of the year. Some of the initial phytoplankton, mostly the larger centric diatoms, had partially damaged frustules, although the cells still showed high silicate content (Segura-Noguera, 2007). Thus, we

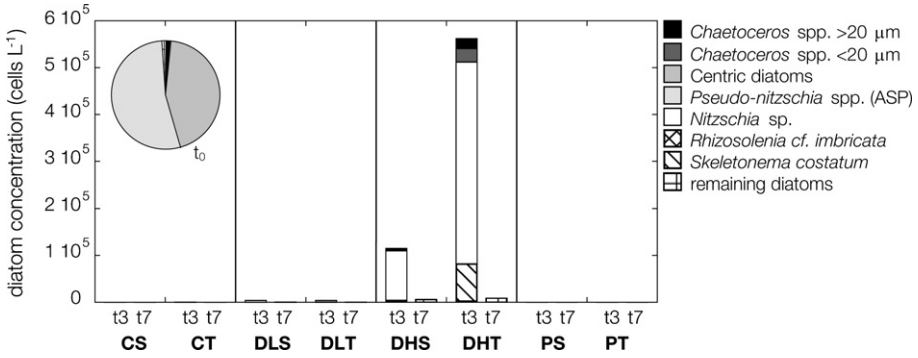

Fig. 5. Diatom species composition in the different experimental treatments. Relative diatom composition to initial (t_0) water is shown in pie chart inset.

hypothesise that the initial community was in a post-bloom state, with nutrients being depleted and some of the biggest diatoms already decaying, but still with high concentrations of autotrophic organisms. The fact that phosphate was extremely low (0.04 ± 0.01 µmol L^{-1}) could explain a growth limitation with excess ammonium being left over.

Mediterranean springtime conditions are characterized by few but severe episodes of rainfall, which lead to sudden river flushes in coastal areas. Previous studies have shown that these episodic freshwater inputs, with a high load of anthropogenic nutrients, can effectively boost diatom growth and induce short-term blooms (Guadayol et al., 2009). Whether the initial experimental conditions were a consequence of the general seasonal dynamics in the Mediterranean or a result of a more localized coastal event, we do not know. Whatever produced the previous growth, it seems clear that our initial conditions were characteristic of a decaying bloom state.

4.2. Potential release of inorganic macronutrients from the dust

Nutrient analyses after dust amendments showed major releases of silicate, phosphate and ammonium. Herut et al. (2005) also found important increases in phosphorus and nitrogen concentrations following dust additions (no analyses were done for silicate) but, contrary to our results, most of the leachable N was in the form of nitrate. This may be the consequence of the way we collected the dust, since the rainwater of the wet deposition probably washed out part of the nutrients present in the dust. The yield of leached phosphorus from dust was higher than that calculated from Ridame and Guieu (2002) and similar to values reported by Pan et al. (2002) and Herut et al. (2005). The particularly low nitrate yield suggests that, even considering differences in the dust composition that we collected, nitrate must have been washed out to an extent larger than the other nutrients.

The rapid increase of phosphate and ammonium in dust-amended treatments supports the idea that both macronutrients were quickly released from the dust, while the subsequent decay in their concentrations can be attributed to biological consumption. Contrary to this pattern, silicate increased steadily during the first 48 h in DH treatments, suggesting a much slower release. Note that a slower release at high dust concentrations would agree with the asymptote observed in the abiotic test, where analyses were limited to one sample 18 h after the dust addition. According to total and fractioned chlorophyll values, during the first days of the experimental simulation there was a concomitant drop of potential silicate consumers (chl $>$ 10 µm $\approx$ diatoms), and thus we could assume that the silicate accumulated after 48 h was approximately the total silicate released from the dust. Based on the highest dust enrichments (DHS, DHT), we can then estimate a concentration of ca. 10 µmol of silicate per gram of dust.

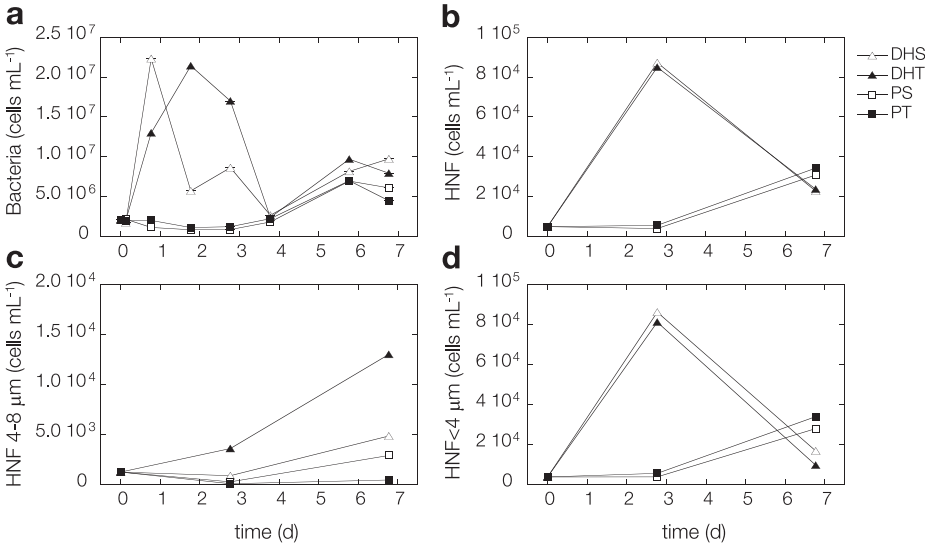

Fig. 6. Concentration of bacteria and heterotrophic nanoflagellates during the experimental simulation. Plots show bacterial abundance (a), concentration of heterotrophic nanoflagellates (b), concentration of heterotrophic nanoflagellates sized between 4 and 8 µm (c), and concentration of heterotrophic nanoflagellates $<$4 µm (d), C and DL treatments are not shown since they are almost identical to P for these parameters.

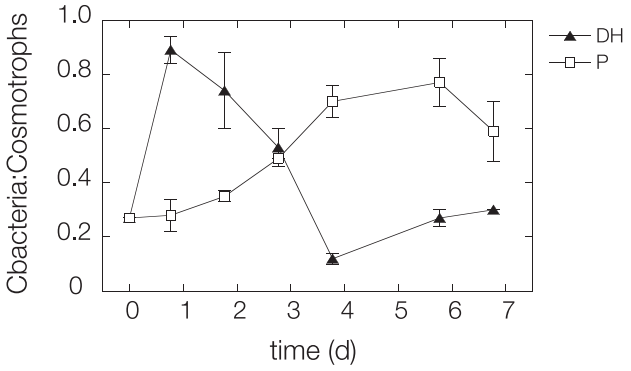

Fig. 7. Bacterial carbon as a fraction of osmotrophic carbon (Cbacteria:Cosmotrophs), both in units of μg C L^{-1}. Turbulence was not significantly different and consequently still and turbulent treatments were averaged for each nutrient amendment condition. Error bars represent the standard deviation of two containers. C and DL treatments are not shown since they are almost identical to P for these parameters.

4.3. Biological response

We have tested the fertilizing potential of dust aerosols collected during a Saharan wet deposition event on a coastal planktonic system, and compared it to a phosphate enrichment based on the possibility that this element was the main limiting nutrient. The response of organisms in dust-enriched containers departed from the dynamics within the rest of treatments, and the difference was particularly evident in tanks with the highest additions of dust.

In order to better understand the ecological response, it is critical to examine which part of the planktonic community benefitted most from the additions. In the controls, none of the planktonic groups increased in numbers: initial diatoms decayed rapidly, probably scavenging some nutrients from the water column and heterotrophic bacteria could not benefit from the potential release of dissolved organic matter (DOM) from the decaying diatoms. The simplest explanations are that either the carbon pool was rather refractory or bacteria were severely limited by phosphate. For the latter to hold true (i.e. P-limitation only), we would expect at least a significant bacterial response in tanks amended with phosphate. However, the pattern in P containers was fairly similar to that found in the controls. This suggests that bacteria may have been co-limited by another factor. Since the concentration of ammonium was high, nitrogen could be disregarded.

Some component of the dust did seem to alleviate microorganism growth limitations, since both autotrophic and heterotrophic cells managed to grow in dust-amended treatments. In the DL treatments, despite the increase in inorganic nutrients from dust being relatively low (phosphate values were, for instance, lower than in the P treatments), autotrophic nanoflagellates grew remarkably during the first three days, and a short peak in bacterial abundance appeared on day 1. The results agree with previous studies: Klein et al. (1997) reported a stimulation of phototrophic nanoflagellates due to the addition of rainwater affected by Saharan dust and Herut et al. (2005) registered increases in small phototrophs and a decay of other phytoplankton cells – diatoms and coccolithophores – following Saharan dust enrichments. Higher additions of dust (DH) led to enhanced biological responses and a series of growth peaks could be distinguished. Inorganic nutrients and dissolved organic carbon released from the dust (Lekunberri et al., 2010) triggered bacterial growth; bacterial increases were immediately followed by a rise in heterotrophic nanoflagellates (HNF) feeding on them. A similar bacterial response and subsequent decay due to grazing has been previously reported for dust-amended waters (Herut et al., 2005; Pulido-Villena et al., 2008).

The rapid increase of bacteria in DH containers suggests that these organisms took advantage of DOM carried over with the dust and outcompeted phytoplankton cells in nutrient uptake (Thingstad et al., 2005). Several factors may have favored bacterial dominance: (1) the dissolution rate of silicate was much slower than the release of phosphate or ammonium (maximum concentrations of silicate occurred 2 days after the dust enrichments); (2) the initial phytoplanktonic community was dominated by large-sized decreasing diatoms, so their response to nutrient enrichment was slow; (3) the addition of dust decreased the available photosynthetically active radiation (PAR) inside the enclosures during a few hours, further limiting the phytoplankton response. Nevertheless, the whole dynamics was not straightforward. Coinciding with the decrease in bacterial abundance, chlorophyll concentrations started to increase and, by day 3, the initial concentration of autotrophic organisms was largely surpassed. Two features are noteworthy: firstly, nanoflagellates accounted for most of the chlorophyll increase; secondly, unlike in the rest of treatments, the concentration of diatoms increased.

A predominant response of bacterioplankton shortly after dust additions has also been recently reported by Marañón et al. (2010). Dust levels in their experiments were considerably lower than the ones used here and the authors found larger changes in metabolic rates than in total biomass values, particularly for bacterial production. This could also be observed in our experiment (see also Lekunberri et al., 2010). Despite this, after the initial bacterial response in dust-enriched treatments we observed an increase of autotrophic cells, and hence the predominant response of heterotrophic organisms described by Marañón et al. (2010) should be considered within the short time lag of their experiments, namely 72 h.

As diatom growth occurred only in DH treatments, this is possibly related to the amount of dust added and it can be explained in terms of silicate limitation. Egge and Aksnes (1992) suggested that when nutrients are in excess, the presence of diatoms is highly correlated to silicate concentrations, and if silicate exceeds a threshold of approx. 2 μmol L^{-1}, diatoms are likely to dominate the community. Egge (1998) refined this premise and pointed out that for diatom dominance to occur, silicate

Table 3
Particulate organic carbon and nitrogen, total living biomass (TB) and relative proportion of autotrophic biomass to total biomass (AutB:TB) for all experimental conditions at times 0 (initial), 3 (mid) and 7 (final). Note that the initial values are common for all treatments. Carbon biomass was estimated applying the conversion factors specified in the text. Total biomass is calculated by the addition of algae –derived from chlorophyll *a*–, bacteria and heterotrophic flagellates. Autotrophic biomass corresponds to the conversion of chlorophyll *a*. The values represent the average ± standard deviation of two replicates (when possible).

	POC (μmol C L^{-1})	PON (μmol N L^{-1})	TB (μmol C L^{-1})	AutB:TB
t0	24.18 ± 2.65	2.57 ± 0.14	16.59	0.66
CS t3	13.11 ± 0.34	1.41 ± 0.06	3.69	0.49
CS t7	14.23 ± 0.86	1.75 ± 0.18	12.43	0.13
CT t3	16.07 ± 2.40	1.87 ± 0.36	5.11	0.56
CT t7	19.03 ± 3.76	2.88 ± 0.32	9.60	0.20
DLS t3	24.23 ± 1.05	3.05 ± 0.00	7.86	0.61
DLS t7	15.86 ± 0.38	2.33 ± 0.21	17.49	0.18
DLT t3	27.31 ± 0.11	3.51 ± 0.10	10.05	0.57
DLT t7	23.00 ± 3.71	3.47 ± 0.79	19.90	0.22
DHS t3	57.61	10.25	40.77	0.44
DHS t7	113.77	15.48	77.71	0.57
DHT t3	69.41	12.14	65.28	0.37
DHT t7	105.81	14.42	72.09	0.49
PS t3	12.53	1.46	3.98	0.44
PS t7	20.13	2.71	22.31	0.26
PT t3	17.93	2.33	5.26	0.47
PT t7	21.51	3.20	19.39	0.42

concentration should be >2 μmol L^{-1} and phosphate should be in excess. Otherwise, diatom abundance varied widely and flagellates, less affected by the lack of phosphate, would take their place. This reasoning fits with our findings: silicate concentration surpassed the 2 μmol L^{-1} threshold only in the DH tanks, and within those, phosphate was largely consumed by bacteria during the first 48 h (assuming for bacteria C:P ≈ 50 (Fagerbakke et al., 1996), approx. 65–85% of the decrease of phosphate between day 0.5 and day 1 was due to bacterial growth). Only when bacteria decreased and sufficient phosphate was available, due to grazing and/or virus lysis and the consequent nutrient recycling, diatoms could grow and consume the inorganic silicate. At the end of the experiment dissolved silicate was exhausted, nanoflagellates dominated the phytoplanktonic community and no diatoms remained. This also explains why neither previous experiments with lower dust enrichments (Klein et al., 1997; Herut et al., 2005) nor our DL treatments allowed for the growth of diatoms and favored autotrophic flagellates instead.

The large addition of dust in DH treatments also induced a change within diatom species composition. *Pseudo-nitzschia* spp. and centric diatoms were replaced by *Nitzschia* sp., *Skeletonema costatum* and *Chaetoceros* spp. (among others) and, when the latter ones declined, small flagellates appeared. Jacobsen et al. (1995) observed a similar succession. When communities dominated by *S. costatum* were exposed only to nitrogen and phosphate enrichments, uncoupled from silicate increases, diatoms were systematically replaced by flagellates. It is of note that in our experiment the diatom sequence evolved from large-sized, silicate-rich organisms produced by a previous bloom to smaller cells which may have a higher growth capacity, and revealed a type of rapid species succession which allows the persistence of diatoms even when flagellates dominate the community, and which may potentially allow the blooms to last longer. Differences in the community composition of the primary producers also affect bacterial community composition (Puddu et al., 2003; Pinhassi et al., 2004), as also shown by our experimental simulation (Lekunberri et al., 2010).

A metabolic analysis of the system shows an initial POC:PON of 9.4, that is enriched in carbon with respect to nitrogen and presumably limited by nutrients. This agrees with the low initial nutrient concentrations and the diatoms in a seemingly late-exponential or early-stationary growth phase. The calculated ratio of autotrophic biomass to total living biomass also shows a high initial value of 66% (Table 3). This ratio decreases in all treatments over time as a consequence of the initial settlement of the senescent diatoms. At the end of the experiment, only the high dust input treatment shows values above 50% and close to initial ratios, indicating that this treatment was most successful for an overall stimulation of autotrophic growth. All biomass indicators (POC, PON and total living biomass) clearly increased in the DH treatment (Table 3) at times 3 and 7, showing an initial preferential stimulation of heterotrophic bacterial growth, and a later stimulation of autotrophs. The decrease in POC in the control treatment resulting from the senescent diatoms is of about 10 μmol C L^{-1} up to day 3. Assuming that all this carbon is used for bacterial growth at a high 50% carbon conversion efficiency, and that grazing and viral lysis of bacteria does not occur, it would result in ca. $3 \cdot 10^6$ bacteria mL^{-1}. This is almost an order of magnitude lower that the bacterial concentrations reached in DH, and implies not only an inorganic nutrient-based stimulation of the system, but also a use of the organic matter added with the dust amendment (Lekunberri et al., 2010). Bacterial recycling of nutrients then also aids phytoplankton growth stimulation, together with the dust amendment of phosphorus and silicate. The addition of phosphorus alone, if that is the phytoplankton's growth-limiting nutrient, rapidly results in the next limiting (co-limiting) nutrient to kick in and slows primary production, fueled only by organic matter recycling. Metabolic balances calculated with primary production and respiration rates instead of biomass result in similar interpretations (Lekunberri et al., 2010).

4.4. Effects of turbulence

Although fertilization was the principal factor controlling plankton dynamics, turbulence appeared to enhance the response of organisms whenever it was applied. The biomass parameters (especially POC and PON) were generally higher under turbulence, and some positive effects appeared on phytoplankton, notably in the concentrations of total and fractioned chlorophyll (Table 2). In addition to affecting cell sedimentation inside the enclosures, turbulence is regarded as favoring the uptake of nutrients in osmotrophic cells (Lazier and Mann, 1989; Karp-Boss et al., 1996; Peters et al., 2006) and alter encounter ratios between prey and predator (Rothschild and Osborn, 1988; Marrasé et al., 1990; Saiz et al., 1992). Some of these effects could explain the higher number of phytoplanktonic cells, whose nutrient uptake might be favored under turbulent conditions (Arin et al., 2002), or the time gap between the peaks of bacteria in DHS and DHT tanks due to altered predator–prey interactions (Peters et al., 2002). Arin et al. (2002) showed that turbulence increases production with respect to still water. When nutrient concentrations are low, the stimulation is rather low and primarily of heterotrophic carbon through feeding interactions. In contrast, when inorganic nutrients are present at higher concentrations, primary producers are stimulated and this is reflected in total carbon in the system. The addition of organic carbon with the dust, as opposed to just mineral nutrients, results in a slight confounding outcome in this respect, particularly for the high dust addition. According to our results, the concurrence of turbulence with dust pulses induced slightly larger and longer-lasting production peaks, and this should be taken into account when considering the impact of dust on marine planktonic communities.

4.5. Relevance to the natural environment

The main limiting nutrient for primary production in the Mediterranean is thought to be phosphorus (Berland et al., 1980; Krom et al., 1991; Thingstad et al., 1998; Moutin et al., 2002). Phosphorus also tends to be limiting in the Blanes coastal site (Vidal and Duarte, 2000; Lucea et al., 2005; Pinhassi et al., 2006), although a high variability of the N:P ratio is observed throughout the year (Guadayol et al., 2009b). This may reflect not only a certain seasonal dynamics in nutrient availability in oligotrophic environments, as is the case in open ocean waters, but a dependence on fertilizing episodes of a varied nature in coastal areas. Guadayol et al. (2009) have shown that storms and river discharge result in system stimulation in Blanes bay. Storms carrying a large load of Saharan dust are episodic, but normal, in the Northwest Mediterranean, with the potential to stimulate system production. The fact that the dust we used in our experimental simulation does not reflect the large nitrate to phosphorus concentrations of other aerosol collections (Markaki et al., 2008) may be a consequence of early leaching of nitrate with the rainwater, but is less important to the objectives of this study. The initial water had an N:P of 31, and we were most interested in assessing whether the dust amendment could alleviate this growth limitation. Consequently, of higher importance is the P content and less whether the amendment had an N:P even higher than the water.

In our simulation, dust-amended treatments – especially the DH – and the phosphate amendment treatment did not show

the same dynamics, emphasizing the importance of components of the dust other than inorganic macronutrients. It appears that micronutrients, such as iron, would be less important in a shallow coastal site where terrestrial discharges override trace metal inputs (Tovar-Sánchez et al., 2006), and even less near a populated coast (Palanques et al., 2008). Although the dust carried an amount of organic matter increasing the DOC in the DH treatment by 14 μmol L^{-1} (Lekunberri et al., 2010), it is not known whether this organic matter in the dust traveled from origin or was scavenged during deposition, but it certainly induced bacterial growth. After the first bacterial response and because of the addition of phosphorus and silicate with the dust, diatoms and other phytoplankton responded, probably as bacteria were becoming controlled by grazers.

The rapid response of bacteria to dust amendments has been observed by others (Pulido-Villena et al., 2008, Marañón et al., 2010) and also agrees with their theoretically favorable surface to volume ratio. Thus, as shown elsewhere, aerosols deposited during dust storm events have the potential to alter the metabolic dynamics of NW Mediterranean coastal systems, adding to the variability sources that determine these dynamics. The highest observed deposition events would correspond to our DL level and after considering a very shallow water column or mixing depth. This situation would be relevant to shallow littoral areas and highly stratified water columns. Dust deposition has not been constant in geological times (Maher et al., 2010) and increases in aridity in the North African and Mediterranean regions (Gao and Giorgi, 2008), together with a more intense land use, are likely to increase the atmospheric dust load. It is within such scenarios that our highest experimental dust load needs to be framed. The observed responses in this study are surely dependent on initial plankton population physiological states as well as on particular nutrient levels and stoichiometries, as pointed out by Marañón et al. (2010) for Atlantic waters. All these parameters have a large variability and in-combination possibilities in coastal systems that cannot be addressed in any single experiment or study. Non-unique nutrient-limiting elements (Sundareshwar et al., 2003; Zohary et al., 2005), especially in complex natural communities and under relatively low basal nutrient loads, are likely to be usual rather than the exception. Thus, it is most important to get information on as many situations as possible, and our study adds to this needed knowledge acquisition process.

5. Conclusions

We have shown that atmospheric dust pulses have the potential to induce shifts within the microbial community in relatively oligotrophic Mediterranean shallow coastal waters. Episodic dust pulses may lead to rapid growth events that, although short in time, add to the variability sources that fuel system production. Our experiment shows that dust pulses occurring after the spring bloom can regenerate the bloom and let the overall production last longer, as Bonnet et al. (2005) suggested before for open sea waters.

Because of the diversity in the chemical composition of atmospheric aerosols, dust has a non-unique path of alleviating possible nutrient limitations of marine plankton, as we showed in comparison to the phosphate-only addition. When in combination with a system situation where different planktonic components, such as heterotrophic bacteria, siliceous and non-siliceous phytoplankton, are present with different growth limitations, the response dynamics is variable and rather complex and may depend on the particular initial conditions, both in nutrients and in plankton biomass and physiological state. In this experiment, dust-amended treatments favored the growth of both autotrophic and heterotrophic cells. Finally, it appears that when dust inputs are accompanied by turbulence, i.e. dust storms which come with strong winds, the potential effects of dust on plankton, particularly on large phytoplankton, are likely to be magnified.

Predictions of future global changes foresee regions of increased drought and a consequent increase in aeolian transport of mineral sources (Prospero and Lamb, 2003; Gao and Giorgi, 2008). If so, the potential impact of these dust storms on marine organisms may also increase and the results of this paper can help to understand the mechanisms. Resulting shifts within the marine microbial community are crucial to consider, because energy and matter flows in the ocean depend on the structure and composition of the microbial compartments (Azam et al., 1983; Pomeroy and Wiebe, 1988; Karl, 2007). Overall, the potential impact of dust storms should be highest in relatively shallow coastal areas or in highly stratified water columns (Pulido-Villena et al., 2010), since nutrient inputs are introduced into a shallow water column and the temporary impact of storm-derived turbulence will be high.

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