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Response of East Mediterranean surface water to Saharan dust: On-board microcosm experiment and field observations

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Abstract

An on-board microcosm experiment was performed during the CYCLOPS May 2002 cruise to track the biogeochemical response of Eastern Mediterranean surface seawater to a gradient addition of fresh and pre-leached Saharan dust, mimicking the potential fertilization effect as opposed to the impact of adding particles alone. Response parameters examined were P-turnover time, bacterial production and abundance, chlorophyll *a*, other phytopigments, abundance of different pico and nanophytoplankton groups, primary production rates, abundance of heterotrophic nanoflagellates and ciliates. The addition of fresh Saharan dust (range: 0.2–4.9 $mg\,l^{-1}$) and the subsequent nutrient release triggered an increase in phytopigments and primary production, while no response was detected for pre-leached dust particles. Most responses were linearly related to the amount of fresh dust added. *Synechococcus* and prymnesiophytes increased in abundance along with cellular pigment content while *Prochlorococcus* disappeared, heterotrophic bacteria increased production rates, and ciliates showed a small increase in cell density. A less clear response was recorded by in situ measurements following a Saharan dust storm during a cruise in the Levantine Basin in May 2001. The calculated amount of nutrients and dust particles delivered by such an event to a 15-m thick mixed surface layer is low ($\sim$0.3 $nmol\,P\,l^{-1}$, $\sim$9 $nmol\,N\,l^{-1}$ and 0.06 $mg\,dust\,l^{-1}$), falling close to the lowest dust addition in our microcosm experiment. Even so, an enhancement of phosphate turnover time, a sharp decline of *Prochlorococcus* abundance, and slight increases in chlorophyll *a* and bacterial activity were observed in response to the dust storm. Considering the linear effect of fresh dust concentrations on the bacterial activity, primary production and pigment concentration (total and per cell), and the likely stimulation of grazing, it is not surprising that changes due to moderate strength dust storms are mostly close to detection limit of either field or remote sensing measurements.
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Keywords: Dust; Sahara; *Synechococcus*; *Prochlorococcus*; Nutrients; Mediterranean

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1. Introduction

The Eastern Mediterranean Basin is ultra-oligotrophic, nutrient depleted even in deep water where nitrate is ~20% and phosphate ~10% of the values measured at similar depths in N. Atlantic (Kress and Herut, 2001). Long-term (annual scale) measurements have been carried out to determine the importance of dry and wet atmospheric input as a source of new nitrogen and phosphorus to this basin (Herut et al., 1999a, 2002; Kouvarakis et al., 2001; Markaki et al., 2003; Krom et al., 2004). Although rainfall is moderate over the basin, it receives relatively high dust fluxes particularly from the adjacent Sahara Desert (Guerzoni et al., 1999). This dust has a relatively high content of bioavailable P (Herut et al., 2002). It also interacts with polluted air masses from Europe and scavenges NO_x and NH_3 resulting in an atmospheric input of high bioavailable N:P ratio (~100 : 1, Herut et al., 1999a, 2002; Markaki et al., 2003). These and other studies from the western basin (e.g., Bergametti et al., 1992; Guieu et al., 2002a,b; Migon and Sandroni, 1999; Migon et al., 2001; Ridame and Guieu, 2002) emphasize the unique importance of Sahara/desert type aerosols as suppliers of soluble nutrients to the system.

The Eastern Mediterranean basin is also unique in that it is depleted in phosphate relative to nitrogen. It has long been known that its deep water has unusually high $NO_3^- : PO_4^{3-}$ ratios (~27), significantly higher than the 'normal' oceanic Redfield ratio of 16:1 (Krom et al., 1991). The cause of this phenomenon is still unknown, and several processes have been hypothesized as potential contributors: (1) nitrogen fixation (Béthoux et al., 1998, 2002; Pantoja et al., 2002); (2) selective adsorption of phosphate and its removal from the water column by descending atmospheric particles (Krom et al., 1991); (3) input of atmospheric precipitates with relatively high $NO_3^- : PO_4^{3-}$ ratios (~100) (Herut et al., 1999a,b, 2002; Markaki et al., 2003); (4) relative enrichment of NO_3^- at areas of deep East Mediterranean water formation (Civitarese et al., 1998); (5) no significant denitrification in either the coastal sediments or intermediate water retaining a high $NO_3^- : PO_4^{3-}$ ratio, mainly from atmospheric sources (Krom et al., 2004). Several of the above hypotheses emphasize the possible important role of atmospheric inputs in this basin.

Atmospheric deposition of desert dust supplies soluble or bioavailable macro and trace nutrients, which may influence ocean biogeochemistry. Recent studies attempt to assess the dust impact through microcosm experiments. On-board experimental studies at the northeast Atlantic Ocean (in the core of a cyclonic eddy) has suggested that the supply of iron by Saharan dust (using Saharan soils as proxy) stimulates phytoplankton growth (Blain et al., 2004). Similar study in the Eastern tropical North Atlantic suggests that the supply of both iron and phosphorus together with Saharan dust promotes nitrogen fixation (Mills et al., 2004). A possible field implication was a *Trichodesmium* bloom observed on the West Florida shelf following a Saharan dust event (Lenes et al., 2001). Stimulation of phototrophic nanoflagellates was observed in an experimental study in which rainwater affected by polluted and Saharan sources was added to NW Mediterranean coastal waters (Klein et al., 1997).

While previous studies suggested that atmospheric input of nutrients make a significant contribution to export production (Krom et al., 2004), almost no studies have investigated the short-term response of live East Mediterranean surface seawater (SSW) to the addition of Saharan dust. It has been hypothesized that Saharan dust pulses can cause phytoplankton blooms in summer when there is no nutrient supply by water column mixing (Ridame and Guieu, 2002) or in events of daytime dust deposition in wet conditions (Saydam and Senyuva, 2002). In a series of radiolabel on-board microcosm experiments (using $^{32}PO_4^{-3}$), in which loess particles (as dust proxy) were added to live surface seawater, it was found that P was initially released and then biological activity and inorganic particles removed approximately similar amounts of the tracer (30–40%) (Herut et al., 1999b). It has been hypothesized that in actual surface waters (in situ), it would be likely for biological uptake to outcompete inorganic uptake because both the much lower concentrations of particles found under natural conditions than those used in the experiment and the known ability of the microbial community to extract available nutrients from surface waters.

Here we present new results from an on-board dust gradient microcosm experiment performed during a CYCLOPS cruise in May 2002. It aimed to track the biogeochemical responses of East Mediterranean SSW to a gradient addition of fresh and pre-leached Saharan dust, mimicking the potential fertilization effect of nutrients and possibly other constituents released from particles

compared with the impact of the particles alone. The response to dust additions is compared to results of a microcosm nutrient addition experiment conducted subsequently on-board (Zohary et al., 2005). We also present the chemical and biological observations made before, during and immediately after a dust storm event in the S.E. Levantine basin in May 2001.

2. Methods

Work presented here was conducted aboard the R.V. Aegaeo during two different cruises to the Cyprus Eddy, Eastern Mediterranean: the first in May 2001, during which a dust storm took place; the second in May 2002, when the on-deck microcosm experiment was conducted.

Experimental design and sampling—The on-board gradient microcosm experiment was set up to investigate the biogeochemical responses of Eastern Mediterranean SSW to the addition of different loads of unaltered (natural) and pre-leached Saharan dust (Table 1). A gradient design was chosen over replicating each treatment. This approach allows the relationship between the various parameters and the dust load to be quantified statistically since adjacent addition treatments verify each other. Having chosen the gradient strategy, the handling limitations restricted the number of replicates per treatment to two (extreme treatments: no addition and highest additions of fresh and pre-leached dust) or one (intermediate additions). The statistical correlations and tests for comparison between fresh and pre-leached dust treatments were carried out applying statistical procedures with XLSTAT software (e.g., Linear regression model, Pearson's correlation coefficient test, Mann–Whitney, ANOVA).

SSW was collected from Niskin bottles mounted on a rosette, on 15 May, 2002, on board R.V. Aegaeo from 5 m depth (station 2CYC23) at 33°24.85′N; 32°18.49′E. It was immediately pre-meshed through 200 μm, to exclude larger zooplankton, and was transferred into 12 pre-washed 8-l polycarbonate Nalgene bottles. The bottles were pre-washed by filling them with approximately 4 l of 10% HCl, intense mixing and remixing so that the caps were acid-washed as well, washing twice with Milli-Q water, and again twice with the sampled seawater. A concentration gradient of unaltered and pre-leached dust (collected at Beit Yannay, Israel, see hereafter) was added to the incubation bottles (Table 1). The bottles were immediately shaken and incubated in a 2-m^3 on-deck flow-through water bath, covered by a screen that reduced the incident light by ca. 50%. During approximately four days, each of the 12 incubation bottles was sampled for a suite of parameters at the

Table 1
Fresh and pre-leached Saharan dust additions (concentrations) to the microcosm experimental bottles (8 l volume)

Incubation bottle no.	Symbol used	Dust concentration ($mg\,l^{-1}$)	Estimated addition of leachable PO_4(nM)	Estimated addition of leachable NO_3+NH_4(nM)
Fresh dust (FD)				
1	CTRL 1	No dust–control	–	–
2	CTRL 2	No dust–control	–	–
3	FD3	4.88	16	750
4	FD4	4.88	16	750
5	FD5	2.0	7	307
6	FD6	0.7	2.5	108
7	FD7	0.2	1	31
Pre-leached dust (LD)				
8	LD8	4.94	nk	nk
9	LD9	4.75	nk	nk
10	LD10	1.95	nk	nk
11	LD11	0.69	nk	nk
12	LD12	0.21	nk	nk

The estimated addition of nutrients released from the dust was calculated based on data from Table 3 assuming linear relationship between dust concentration in seawater and the leachable fraction. The estimates contain an approximately 20% error. nk, not known.

following sampling times: T0 = 15 May 2002 at 16:45; Tl = 6 h, 15 May, 22:45; T2 = 19 h, 16 May, 11:45; T3 = 44 h, 17 May, 12:45; T4 = 90 h, 19 May, 10:45. Volume-consuming analyses (Chl *a*, HPLC-phytopigments, primary production, heterotrophic nanoflagellates (HNF), larger phytoplankton and ciliates) were conducted on samples taken at the start (T0) and the end of the experiment (T4), while bacterial counts and activity, P-turnover time and picophytoplankton (flow cytometry) were measured at all five sampling times during the four days.

Dust origin and treatments—Dust powder (dry deposited material) was collected during a major Saharan dust storm on 1 May 2001 from the top of a glass panel collector at Beit Yannay, Israel (located on the roof of a building 300 m from shoreline). Dust's origin was tracked by calculating three days back trajectories for 1000, 850, 700 and 500 hPa showing the transport of air masses was directly from the Sahara. Immediately after the event, dust powder was gently scrapped from the panel with a clean plastic knife, into pre-washed (10% hydrochloric acid) 20-ml scintillation vials. Sub-samples of fresh dust were weighed (see Table 1) into micro conic pre-cleaned Eppendorf plastic tubes. Additional sub-samples were pre-leached for 24 h in 40-ml centrifuge tubes in aged filtered (0.2 μm) SSW from the Cyprus Eddy collected in May 2001 (during the first CYCLOPS cruise). It was then centrifuged at 5000 rpm for 10 min, leached again for 6 h and centrifuged, followed by 1 h leach and centrifugation. The dust pellet with residual 1 ml of seawater was stored wet (at 4 °C in the dark). At the time of the microcosm experiment, the leached dust was rinsed into the 8-l incubation bottles. The fresh dust sub-samples were suspended in water from the incubation bottles, shaken and rinsed into the incubation bottle at the flow bath.

Total suspended particles (*TSP*) *in air and seawater*—During the May 2001 cruise to the Cyprus Eddy, atmospheric aerosol (TSP) samples were collected on 20 × 25 cm Whatman 41 filters by a high-volume sampler (Fig. 1) with a flow rate of 42 m^3 air h^{-1}. The sampling intervals are given in Table 2. By fortunate coincidence, two of the filters represent a significant dust storm that occurred during the cruise on 12–13 May. All Filters were analysed for leachable P and N, total P and Al concentrations, and their atmospheric fluxes were calculated, as described in Herut et al. (2002) and Carbo et al. (2005). SSW samples were collected

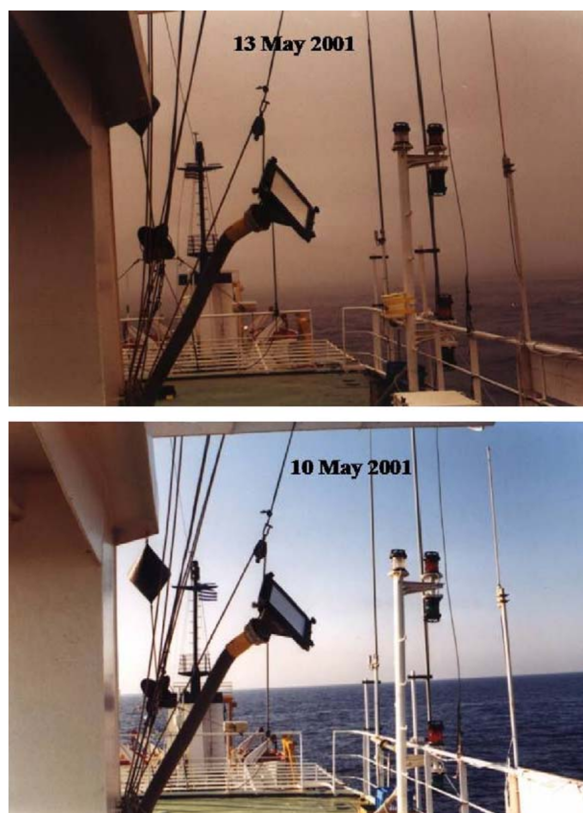

Fig. 1. Murky skies photographed during a dust storm (upper panel) that began the night between 12 and 13 May 2001, and lasted till about 11:00 h of 13 May, and the clear sky a few days earlier (lower panel). During the height of the storm visibility was limited to less than 200 m. The rectangular filter head of the high volume dust sampler is shown in the centre part of the pictures.

Table 2
Sampling intervals and location of atmospheric aerosol samples collected on Whatman 4-l filters by high-volume sampler on board R.V. Aegaeo, during CYCLOPS cruise in May 2001 (local time)

From		To		Longitude	Longitude
Date	Time	Date	Time		
7 May 01	6:58	8 May 01	19:10	32 16.89	33 09.44
8 May 01	19:20	10 May 01	9:20	32 59.81	33 14.87
10 May 01	9:30	12 May 01	8:05	32 49.86	33 15.86
12 May 01	8:10	13 May 01	8:12	32 45.64	33 23.73
13 May 01	8:19	13 May 01	21:10	32 57.93	33 24.13
13 May 01	21:20	15 May 01	8:20	33 07.35	33 18.83
15 May 01	8:29	16 May 01	8:35	34 00.05	32 39.98

The Saharan dust storm begun during the night between 12 and 13 May, and lasted till about 11:00 h of 13 May.

during and after the dust storm by Niskin bottles for P-turnover time, Chl *a*, bacterial counts, bacterial activity and picophytoplankton abundance.

Dust chemical composition—Experiments were performed to evaluate the amount of phosphate, nitrate + nitrite and ammonium leached from the dust collected at Beit Yannay by pre-filtered (0.2 μm) 30 ml SSW poisoned with 50 μl chloroform. Different amounts of sub-samples were shaken in pre-cleaned 50-ml centrifuge tubes for 30 h in dark conditions. After leaching, samples were centrifuged and sub-sampled into 15-ml pre-cleaned (10% HCl) plastic vials and stored frozen for subsequent nutrient analysis. Total Al, Fe and Mn in the dust were determined as detailed in Herut et al. (2001).

Nutrients—In the ambient water used for filling the experimental bottles, PO_4, NO_3, NO_2 (nanomolar technology), UV-labile dissolved organic phosphorus (DOP) and dissolved organic carbon (DOC) were determined as detailed in Krom et al. (2005). At the additional sampling times, nutrients in the microcosm were measured by conventional micromolar technology (using a segmented flow Skalar SAN^{plus} System) and were below the effective detection limits at all times. The leachable nutrients from the dust were determined by the methods described in Herut et al. (1999a). Total inorganic P was determined by adding 2 ml 1 N H_2SO_4 and 3 ml 1 N HCl to the weighed dust sample or by 3-ml 1 N HCl alone. The precision for nitrate + nitrite, phosphate and ammonium was 0.02, 0.003 and 0.007 μM, respectively. The bottle blanks were corrected and accounted for $<5\%$, $\sim 20\%$ and $\sim 30\%$ of the nitrate + nitrite, phosphate and ammonium, respectively.

P-turnover time—Carrier free $H_3{}^{33}PO_4$ was added to 12-ml samples in 15-ml Falcon® tubes to give a final radioactive concentration of ca. 10^6 DPM ml^{-1}. Amersham BF1003 $^{33}PO_4$ in dilute HCl solution was used. This has a specific activity of 92.5–129.5 TBq mmol^{-1}. With the additions used, this gives an addition of the order of ~0.1 nM phosphate. The samples were incubated at 24 ± 1 °C under subdued (laboratory) illumination for an incubation time of 0.5 h (except T4, 0.25 h) according to expected turnover time. Samples for subtraction of background and abiotic adsorption were fixed with 50 μl 25% glutaraldehyde per 12-ml sample before addition of the isotope. Incubations were stopped by a cold chase addition of 100 μmol KH_2PO_4 l^{-1} and within 1 h, 3-ml aliquots filtered in parallel on 25-mm polycarbonate (Poretics®) filters of 0.2-μm pore-size. Using a Millipore 12-place filter manifold, the polycarbonate filters where mounted on GF/C support filters pre-soaked in 10 mmol l^{-1} KH_2PO_4. The needle valve of the suction pump was kept at <0.2 bar until all water had passed the filters, then closed to increase the suction to >0.6 bar to remove any water remaining in the filters. No washing was performed. The ^{33}P on the filters was measured by scintillation counting and turnover time calculated from the formulae $T_t = -t/\ln(1-f)$, where f is the fraction of added isotope recovered on the 0.2-μm filter (corrected for background), and t is the incubation time. Replicate samplings were made six times. The average deviation was 2.5% of the mean.

Bacterial activity and production—Bacterial protein synthesis was determined in triplicates for each sample by the ^{14}C-leucine incorporation using a modified micro-tube technique (Smith and Azam, 1993) and as detailed in Zohary et al. (2005). Leucine uptake was converted to carbon uptake according to Simon and Azam (1989) with an isotope dilution factor of 1, which gives a minimal estimate of bacterial production.

Bacterial counts—The 30-ml samples were fixed with 4.2 ml of filtered 5% Formalin and kept refrigerated until analysis. DAPI-stained bacteria were counted with a fluorescent microscope (Porter and Feig, 1980). Bacterial counts were converted to C biomass assuming cellular C content of 20 fg C per bacterial cell (Lee and Fuhrman, 1987).

Chlorophyll a—Sample of 0.5–1 l was filtered in parallel through 0.2-μm polycarbonate filters (Poretics, ⌀47 mm). Filters were placed in −20 °C immediately after filtration and kept frozen for six weeks until laboratory analyses were performed. Chlorophyll *a* and phaeopigment concentrations were determined fluorometrically according to Yentsch and Menzel (1963) with the use of a TURNER 112 fluorometer. Filters were extracted in 90% acetone and phaeopigments were estimated by acidification with 0.1 N HCl.

Phytopigments by HPLC—GFF-filtered 2-1 samples were immediately frozen at −70 °C for high performance liquid chromatographic (HPLC) analyses of chlorophylls and carotenoids. Pigment analyses involved reversed phase RP-HPLC as described by Mantoura and Llewellyn (1983) and adapted by Barlow et al. (1999).

Primary production—Photosynthetic carbon fixation rates at T4 were estimated by means of the ^{14}C technique of Steemann-Nielsen (1952), as modified

for the ultra-oligotrophic water of the Eastern Mediterranean by Psarra et al. (2000) and Ignatiades et al. (2002). The 250-ml sub-samples from each experimental bottle were placed in transparent polyethylene bottles, inoculated with 5 μCi of $NaH^{14}CO_3$ tracer and incubated for ca. 2.5 h around midday, when the incident irradiance is maximum yielding maximum primary production rates. Dark bottles also were used with control samples and served as background that was subtracted from the light bottles' yield. At the end of the incubation samples were immediately stored in the dark until filtration. Samples were filtered onto 0.2-μm pore-size polycarbonate filters (Poretics) at <100 mm Hg vacuum pressure. Deionized water and pre-filtered (through 0.2 μm) seawater were also processed and used as blanks. Killing of samples and rinsing of the filters at the end of the filtration were avoided in order to minimize exudation losses of organic matter. All materials were acid-cleaned prior to use. To remove excess ^{14}C-bicarbonate, filters were soaked in 1 ml 0.5 N HCl and allowed to stand in uncapped polycarbonate 5-ml vials (Packard) overnight. Activity was measured using a Packard Tri-Card 4000 Liquid Scintillation Counter after the addition of 4 ml of BSF scintillation cocktail (Packard).

Picophytoplankton (flow cytometry)—Samples (1.8 ml) were preserved with 140 μl of 25% glutaraldehyde (Sigma G-5882), deep-frozen in liquid N_2, shipped on dry ice, kept at −80 °C until analysis about two months later using a FACScan (Becton Dickinson) flow cytometer. The samples were thawed for 1 min at 37 °C and analysed at room temperature (23 ± 2 °C), by excitation with Argon laser at 488 nm. The forward light scatter (FSC), side scatter (SSC), red (chlorophyll) fluorescence above 630 nm (FL3) and orange fluorescence at 585 ± 15 nm (FL2) were measured. Before running the sample, 0.93 μm beads (produced by Poly-Sciences) were added as an internal standard. The phytoplankton assemblages were composed of three groups, mainly *Synechococcus* sp., *Prochlorococcus* sp., and diverse picoeukaryotes, each characterized by its unique light scatter (size and granularity) and autofluorescence features.

Nanoflagellates (epifluorescent microscope counts)—Water samples were fixed with glutaraldehyde (final conc. 1%). Sub-samples (50–100 ml) were concentrated to ca. 10 ml on a 25-mm, 0.8-μm pore-size polycarbonate black filter, DAPI-stained for 10 min (final conc. 0.5 μg ml^{-1}), and filtered (Porter and Feig, 1980). HNF of 2–10 μm cell length were counted by epifluorescence microscopy.

Larger phytoplankton—Water samples of 100-ml preserved with acid Lugol's solution (final conc. 2%), stored at 4 °C were sedimented in settling chambers for 24 h and examined with an inverted microscope. All the dinoflagellates, coccolithophores and diatoms >7 μm were counted. For further details, see Psarra et al. (2005).

Ciliates—The 500-ml samples were preserved with borax-buffered formalin (final concentration 2% formaldehyde) and stored at 4 °C in the dark and counted with an inverted microscope as described by Pitta et al. (2005). Cell sizes were measured with an ocular micrometer and converted into cell volumes using appropriate geometric formulae.

3. Results

3.1. Microcosm

The nutrient concentrations in the surface water (5 m depth) used in the experiment as determined by nanomolar technology were extremely low (Krom et al., 2005) (PO_4^{-3} < 2 nM, NO_3^- < 1 nM, NO_2^- < 0.5 nM). The ammonium concentration was approximately 80 nM and the UV-labile DOP concentration was 50–70 nM. Measurements on ambient SSW in the region of the sampling site were for dissolved organic nitrogen 5–7 μM and DOC 60–70 μM (Krom et al., 2005). Silicate was nearly 1.4 μM.

The dust analysis showed 9.3% Al, 3.5% Fe and 590 ppm Mn, which is within the upper characteristic range of dust of Saharan origin (Guieu et al., 2002a). The amount of leachable phosphate from the dust was 3.2 ± 0.4 μmol P per g dust (Table 3), corresponding to 15.6 ± 1.8 nmol P l^{-1} in bottles 3 and 4, and lower amounts, respectively, in the other fresh dust treatments. The dust also contained significant amounts of seawater leachable nitrogen as presented in Table 3. The amount of dissolved inorganic N was in average 155 μmol N per g dust (Table 3), corresponding to 0.75 μmol N l^{-1} in bottles 3 and 4. The leachable N/P ratio is approximately 50, higher than Redfield ratio.

The P-turnover time prior to addition of dust was 3 h, a value typical of P deficiency in East Mediterranean water (Zohary and Robarts, 1998; Moutin et al., 2002; Flaten et al., 2005). Immediately after the highest addition of fresh dust the

Table 3
Seawater leachable phosphate (LPO_4), nitrate (LNO_3) and ammonium (LNH_4), and total inorganic P (total IP) in dust powder collected on 1 May 2001 at the northern Israeli Mediterranean coast (see Methods for details)

$\mu mol\,g^{-1}$ dust	LPO_4	Total IP	LNO_3	LNH_4
Average	3.2	31.7	114	41.2
Standard deviation	0.4	3.3	33.8	5.7
n	3	3	4	3

Fresh dust concentrations were 40–90 $mg\,l^{-1}$ per tube of leaching experiment.

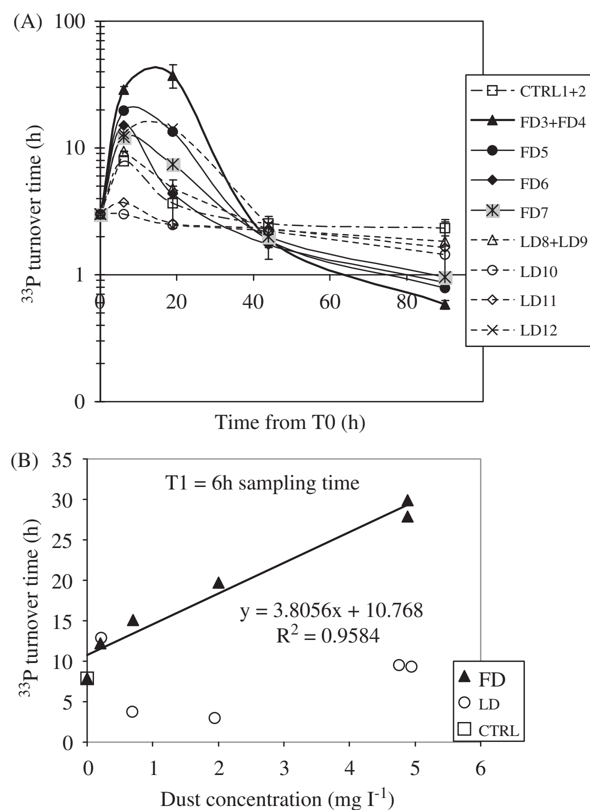

Fig. 2. Levels of P-turnover time (logarithmic scale) in the experimental bottles (see symbols in Table 1) at different sampling times (A) and versus different concentrations of fresh dust (FD) and leached dust (LD) at T1 (after 6 h) (B). The linear regression lines calculated from the data is included in (B).

turnover time increased to 29 h at T1 (6 h) and to 37 h at T2 (19 h) (Fig. 2A). However, by T3 (44 h) there was no significant difference between the dust addition and the pre-leached dust or the controls, all of which were similar to the initial values of P-turnover times. By contrast, the pre-leached dust showed similar behavior to the control (bottles 8, 9) or even had decrease turnover time (bottles 10, 11) possibly due to adsorption of phosphate on the particles. Bottle 12 was exceptional (turnover times of 13 h at T1 and 14 h at T2) for unknown reasons. By T4 (90 h) turnover time in all the fresh dust treatments declined below 1 h, probably due to its renewed uptake; in the pre-leached dust treatments the decline by T4 was more moderate.

A significant linear correlation (Fig. 2B; $r^2 = 0.96$; $p<0.01$) was calculated between the fresh dust concentration and the P-turnover times for the first two sampling times (data for T2 are not shown, $r^2 = 0.93$). This linear increase in P-turnover times with increasing dust concentration was probably attributed to the amount of phosphate released from the fresh dust, increasing the total bioavailable stock. The pre-leached loads showed no significant change (Fig. 2B).

3.2. Response of the autotrophic community

The water used in the microcosm was typical of surface water in the Cyprus Eddy (Table 4): *Synechococcus* (thousands of cells ml^{-1}) > picoeukaryotes (hundreds of cells ml^{-1}) > *Prochlorococcus* (tens of cells ml^{-1}) > larger phytoplankton taxa (coccolithophores, dinoflagellates, diatoms) with densities in the order of 0.1–1 cell from each taxonomic group per ml. The HPLC pigment analyses showed the prevalence of 19′-hexanoyl oxyfucoxanthin (19′-hexa), indicative of prymnesiophytes (including coccolithophores and probably some of the picoeukaryotes) and zeaxanthin, indicative of *Synechococcus* and *Prochlorococcus* (Fig. 3B, data not shown). Since the flow cytometry determinations showed that *Prochlorococcus* was relatively rare, the zeaxanthin is attributed mostly to *Synechococcus*.

Chl *a* increased linearly with fresh dust concentration, at a ratio of approximately 32 $ng\,l^{-1}$ per addition of 1 mg fresh dust l^{-1} (Fig. 3A; $r^2 = 0.99$; $p<0.01$). A similar pronounced linear increase was observed in 19′-hexanoyl-oxyfucoxanthin and less distinct though significant in zeaxanthin (Fig. 3B). By contrast, there was no significant response to pre-leached dust additions in Chl *a* or in the individual pigments when compared with the controls. When compared to the control bottles on T4 there was a significant increase of approximately fivefold in the Chl *a* of the highest fresh dust addition (Table 4). A similar increase was calculated

Table 4
Treatment average ±SD (in parentheses) of Chlorophyll *a* (Chl *a*) concentrations (determined by the fluorometric method and by HPLC), arbitrary units of Chl total fluorescence (Chl-Fluo, determined by flow cytometry), primary production (PP), bacterial counts (Bac #), bacterial production (Bac Prod) and the abundance of the major taxonomic groups of the phytoplankton, in the initial (T0, all treatments) and final (T4, average of treatments 1–2, 3–4 and 8–9) water

Water type	Chl *a* ($ng\,l^{-1}$)	Chl *a* (HPLC) ($ng\,l^{-1}$)	Chl Fluo (arbitrary units)	PP ($mgC\,m^{-3}\,h^{-1}$)	Bac # (10^3 cells ml^{-1})	Bac Prod (pmol Leu $l^{-1}\,h^{-1}$)	Syn (cells ml^{-1})	Euk (cells ml^{-1})	Prochlor (cells ml^{-1})
All treatments T0	17.2 (1.7) $n = 3$	17.3	274	0.11 (0.01) $n = 3$	106	16.6 (1.8)	3380	364 (62)	99
Control T4	36.4 (0)	35.2 (2.7)	628 (111)	0.10 (0.00)	111 (28)	41 (4)	5040 (276)	516 (17)	45 (2)
Fresh dust T4	124 (25)	190	3375 (1286)	0.55 (0.01)	136 (16)	350 (27)	10300 (3500)	430 (118)	15 (1.5)
Pre-leached dust T4	37.9 (2)	39.9 (7.6)	707 (199)	0.08 (0.01)	146 (7)	86 (30)	6570 (1870)	400 (50)	14 (6)

Water type	Cocco (cells ml^{-1})	Diatoms (cells ml^{-1})	Dino (cells ml^{-1})	Ciliates (cells l^{-1})	HNF (10^5 cells l^{-1})
All treatments T0	1.26	0.13	0.69	124	3.57
Control T4	0.45 (0.05)	0.24 (0.06)	0.43 (0.11)	109 (37)	2.98 (0.91)
Fresh dust T4	0.09 (0.12)	0.23 (0.13)	0.28 (0.03)	142 (18)	1.84 (0.31)
Pre-leached dust T4	0.09 (0.04)	0.18 (0.0)	0.28 (0.02)	85 (13)	2.06 (0.61)

Syn, *Synechococcus* sp.; Euk, picoeukaryotes; Prochlor, *Prochlorococcus*; Cocco, coccolithophores; Dino, dinoflagellates; HNF, heterotrophic nanoflagellates.

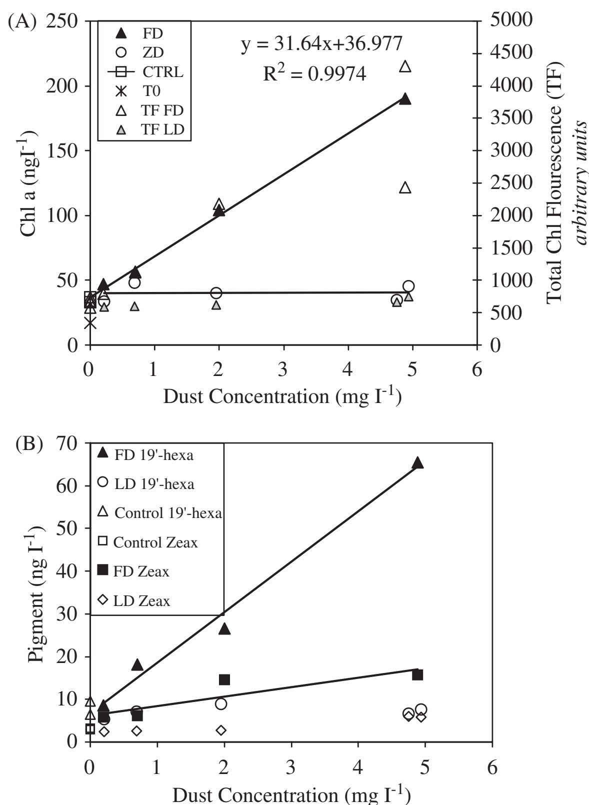

Fig. 3. Concentrations of extracted chlorophyll *a* and flow-cytometer determined total chlorophyll fluorescence, TF (A) and HPLC-determined pigments (B) at T0 and at the end of the experiment (T4, 90 h) vs. different concentrations of fresh dust (FD) and leached Sahara dust (LD). The pigment 19′-hexanoyl oxyfucoxanthin (19′-hexa) is indicative of prymnesiophytes and zeaxanthin (Zeax) is indicative of cyanobacteria, in this case of *Synechococcus*. The linear regression lines calculated from the data are included.

using the flow cytometry determined total chlorophyll (FL3) fluorescence (TF in Fig. 3A).

Similar behaviour was recorded for primary production, which at T4 also showed a linear increase as a function of fresh dust load resulting in approximately fivefold increase in the highest fresh dust addition (Fig. 4A) while the leached dust primary production remained similar to that of the controls and T0 values.

In the two control bottles, Chl *a* doubled from T0 to T4. This result was obtained using three independent methods, including fluorometric and HPLC determinations and flow-cytometric total chlorophyll fluorescence. The phytoplankton composition was slightly changed. The cell density of *Synechococcus* and picoeukaryotes increased by approximately 50% (Table 4). An additional >50% increase in picoeukaryote and *Synechococcus* cellular chlorophyll content, possibly a result of the partial light shading of the incubation tank, also contributed to the doubling of total chlorophyll. In contrast, the relatively rare *Prochlorococcus* cell density declined to about half the T0 values (Table 4).

The phytoplankton composition at T4 changed as follows (Table 4, Fig. 3B):

(1) The cell density of *Synechococcus* increased by approximately threefold (highest fresh dust addition vs. control) while pre-leached dust showed only a small increase of 1.4-fold relative to the control. There was a similar increase in zeaxanthin, indicative of *Synechoccocus*, by fivefold in the highest fresh dust addition relative to control. No difference from control was measured for the lower pre-leached dust additions and an approximate doubling in zeaxanthin in the highest pre-leached dust addition.

(2) Picoeukaryotes showed no significant response (relative to the controls) in any treatment.

(3) *Prochlorococcus* decreased relative to controls in the fresh dust treatments but not in the pre-leached dust treatments.

(4) Cell densities of the larger phytoplankton (coccolithophores, diatoms and dinoflagellates) remained low or declined to lower than the T0 values in all 12 bottles (Table 4). However, the low cell numbers do not allow statistically significant conclusions to be made although it is evident that none of these larger phytoplankton groups was able to grow substantially. It remains unclear which were the prymnesiophyte species that contributed to the increase in 19′-hexa in the fresh dust additions.

Synechococcus cell densities at T4 were dependent on fresh dust load up to an approximate threshold of $2\,\mathrm{mg\,l^{-1}}$ and only slightly dependent on pre-leached dust concentrations (Fig. 4B). The level of Chl pigment per cell was linearly correlated to the fresh dust gradient, while no such correlation was observed for the pre-leached treatments (Fig. 4C).

Picoeukaryote densities showed no significant difference between fresh and pre-leached dust treatments. However, at T4 a significant increase of approximately 1.5-fold of pigment per cell was observed in the fresh dust treatment (Fig. 4D).

Prochlorococcus cell concentrations were drastically decreased from T0 values upon the addition of dust particles but also in the controls (Table 4; Fig. 4F), which probably reflect the extreme sensitivity of these microorganisms to handling

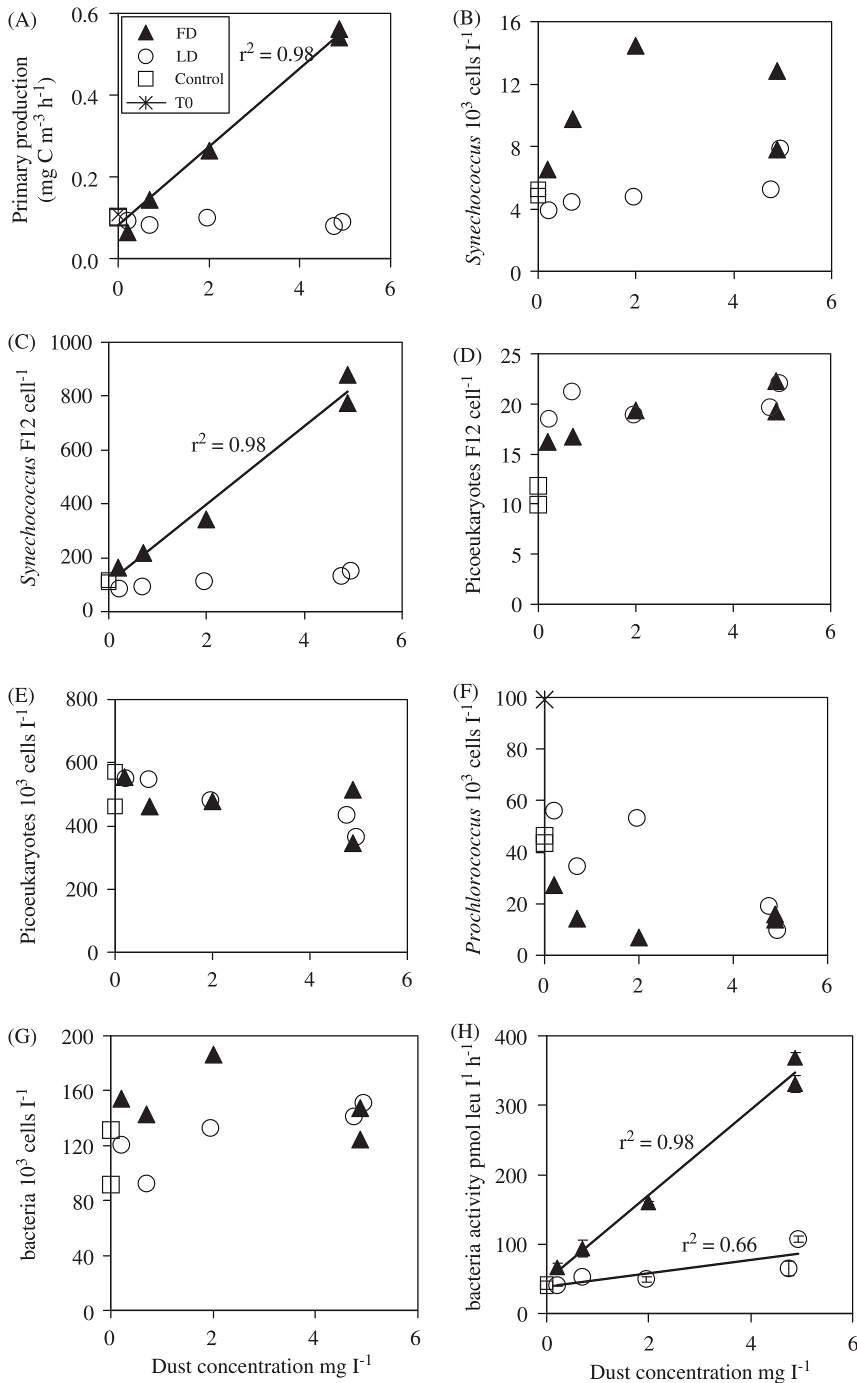

Fig. 4. Relationships between different concentrations of fresh dust (FD) and leached Saharan dust (LD) and primary production (A), *Synechococcus* density (B) and orange fluorescence (FL2-~585 nm) per cell (C), picoeukaryotes red fluorescence (Fl3->630 nm) per cell (D) and density (E), density of *Prochlorococcus* (F), bacteria abundance (G) and activity (H), at the end of the experiment (T4, 90 h).

(Partensky et al., 1999). In the fresh dust treatments they decreased by approximately an order of magnitude, in the pre-leached dust they decreased from twofold (low additions) to 10-fold (high additions) while in the controls the decline was ca. eightfold.

3.3. Response of the heterotrophic community

At T4 bacterial activity was higher than that at T0 by ~ eightfold in the highest load of fresh dust and by twofold in the highest pre-leached dust. The activity increased with dust load (Fig. 4H) and fluctuated with time (not shown). The effect increased with time from T0 to T3 and then declined somewhat to T4. This increase was due to the dynamics in the bottles: as bacteria grow and are grazed, nutrients are recycled and can induce a further increase in bacterial activity. This also is indicated by the oscillation over time of the turnover time of available *o*-phosphate (Fig. 2A). At T3 when bacterial activity was at its maximum in all experimental bottles, turnover time was low (= low P availability) followed by a decrease in bacterial activity at T4 with the further decline in turnover time on T4. The magnitude of oscillations of bacterial activity depended on the initial amount of fresh dust added. For the dust concentration range between 0.2 and 5 mg l^{-1} this effect was linear at T4. Bacterial cell concentrations show minor changes between T0 and T4 (Table 4) and across the dust load gradient (Fig. 4G). Cell numbers at T0 were ca. 1.0×10^5 ml^{-1} increasing up to ca. 1.6×10^5 ml^{-1} on T4 in different dust treatments (Fig. 4G). It is probable that bacterial species composition changed during the experiment and that their mean cell size increased but these parameters were not quantified.

The bacterivores, the HNF and ciliates, responded differently to the dust additions. From T0 to T4, a certain increase of ciliate abundance was measured in most fresh dust additions and a decline in most leached dust additions; however, due to large variability these changes could not be shown as significant (Table 4, partial data). Over the whole dust gradient the ciliate density was enhanced by the fresh dust additions as compared to the pre-leached ones. HNF declined from T0 to T4 in both dust treatments. The magnitude of decrease varied among the dust concentrations (Table 4, partial data).

By T4, the ciliate community structure changed in all treatments (fresh and pre-leached dust) as well as in the control bottles in a similar way (Table 4). The percentage of large aloricates contribution decreased and the one of tintinnids increased, whereas small aloricates did not show any change (data not shown). This change was more or less similar in the control bottles and in the fresh dust addition ones (on average, large aloricates decreased from 73% on T0 to 46% on T4) and it was more pronounced in the bottles with the pre-leached addition (large aloricates decreased from 73% on T0 to 31% on T4).

3.4. Nutrient fluxes and biological response to Saharan dust storm during May 2001 (CYCLOPS cruise)

A dust storm reached the Cyclops Eddy region (ca. 33°N and 33°E) where the R.V. Aegaeo was sampling during the night between 12 and 13 May 2001, and lasted till about 11:00 h of 13 May. At the height of the storm, in the early morning hours, the wind was strong, visibility was limited to less than 200 m, and the sky was brown (Fig. 1). At that time fluxes of Al, total P (Fig. 5B) and seawater leachable inorganic P (LIP) and N (LIN) reached maximum levels (Fig. 5A). Compared to the background daily fluxes for LIP and LIN there was a three- to fourfold increase in LIP input, and a smaller increase in LIN, during the storm. In spite of the lower LIN input, LIN:LIP contributed by atmospheric deposition was present at greater ratios than Redfield throughout the cruise (~30 during the dust storm and ~100 in background conditions).

This dust event triggered an enhancement of phosphate turnover time corresponding to the release of phosphate from the dust. ^{33}P-turnover time in surface water prior the event was 8 h (12 May 2001 morning), during the event (13 May 2001 morning) 18.7 h, and after the event (13 May 2001 evening) 9.2 h. In addition, in response to the dust event, a sharp decline of *Prochlorococcus* abundance in the top 25 m was noted (Fig. 6A), while their much higher abundance (by two orders of magnitude) at the deep chlorophyll maximum was not affected (data not shown). No such decline was noted for either *Synechococcus* or picoeukaryote abundance (not shown). A diminutive increase in Chl *a* concentrations (~5 ng l^{-1}, $p<0.05$ Student's *t* test and Mann–Whitney test) in the top 15-m mixed layer was observed by comparing values of two days prior the event to values measured during three days at and after the event. In addition, a certain increase in bacterial activity was noted after one-day lag-time (Fig. 6B).

4. Discussion

There was a clear response by the autotrophic community to the addition of fresh Saharan dust to

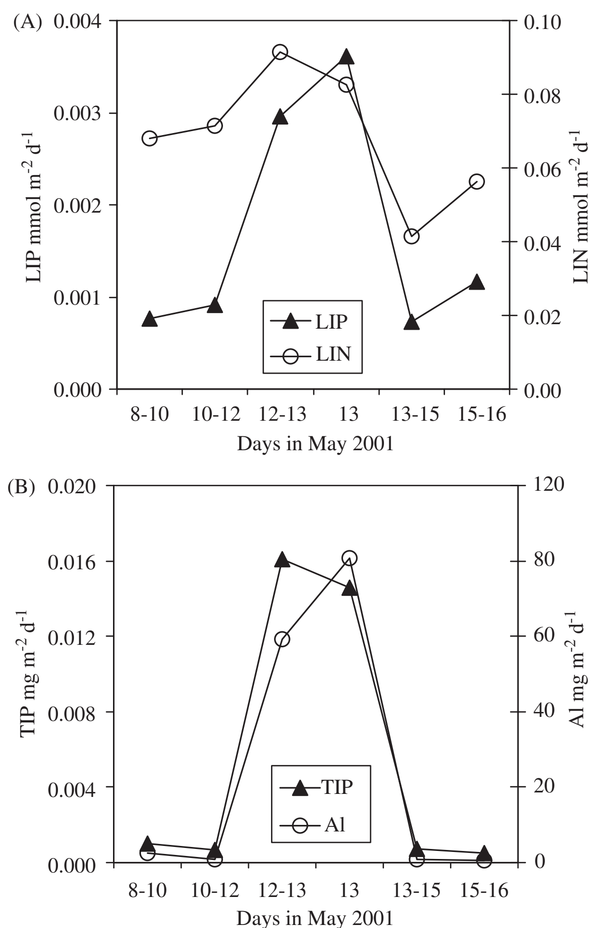

Fig. 5. Fluxes of atmospheric seawater leachable inorganic P (LIP) and N (LIN) (A) and of A1, total P (TIP) (B) in the Cyclops Eddy, Eastern Mediterranean during 8–16 May 2001. All fluxes reached a maximum level at the height of a dust storm (12–13 May 2001).

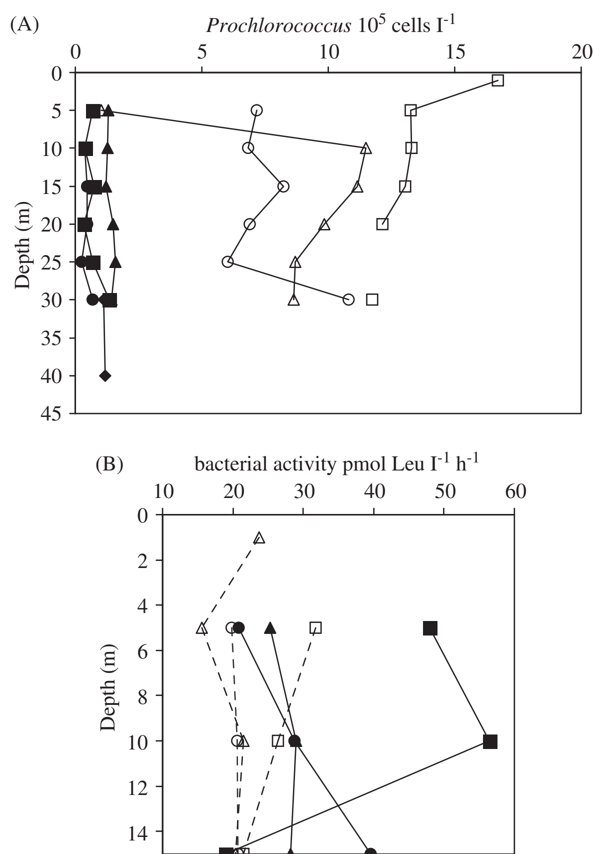

Fig. 6. Depth distribution of *Prochlorococcus* abundance (top 40 m) (A) and bacterial activity (top 15 m) (B) before (open symbols) and after (full symbols) a Saharan dust storm on 12–13 May 2001. The symbols represent different stations within the Cyprus Eddy area.

Levantine surface seawater, which resulted in a fivefold increase in Chl *a* and in primary productivity while leached dust particles resulted in no significant increase.

Compared to this study, in which 50 ng Chl $a\,l^{-1}\,mg^{-1}$ dust was developed in 90 h, a much larger response in Chl *a* (700 ng Chl $a\,l^{-1}\,mg^{-1}$ dust developed in 90 h) was observed by Blain et al. (2004) after addition of 1.34 mg of Saharan surface soils (as dust proxy) to 1 l of Northeast Atlantic SSW. The addition of 0.5 and 2 mg of the same Saharan surface soils to 1 l of tropical North Atlantic SSW resulted in a similar enhancement of Chl *a* (~200 ng Chl $a\,l^{-1}$ within 48 h) (Mills et al., 2004—correction in press).

Zohary and Robarts (1998) reported P-turnover times below 7 h in severely P-deficient regions of the Eastern Mediterranean, whereas P-replete areas like the Rhodes Gyre had P-turnover times longer than 100 h. In this experiment, P-turnover times never reached 100 h, suggesting that P-sufficiency was never obtained, hence contributing to the linear relationships between dust (i.e. P) addition and chlorophyll or primary production.

The amount of phosphate or dissolved inorganic nitrogen added to the system by leaching from the dust cannot be measured directly in the microcosm because of rapid uptake by the microbial community. However, it can be calculated from the dust seawater leachability and assessed by the dynamics of P-turnover times (Fig. 2A). The average amount of leachable P and N (16 and ~750 nM, respectively) corresponds to a potential increase of Chl *a* between 250–800 ng Chl $a\,l^{-1}$ by using P:C ratios of Redfiled (1:106) and C:Chl a = 23–79 (wt., Parsons

and Takahashi, 1975). The observed Chl *a* increase (Fig. 3A) is close to the lower estimate. Based on previous experiments (Herut et al., 1999b; Pan et al., 2002), it can be assumed that phosphate was released from the dust shortly after its addition, peaking before 2 h. By definition, the turnover time is equal to the amount of bioavailable phosphate divided by its consumption (or uptake) rate. This relationship can be used to assess the minimum input of bioavailable phosphate from dust at the first sampling (T1), as compared to T0, before dust addition. At T0, a concentration of ~0.2 nM free phosphate was calculated, using 3 h turnover time and assuming its uptake rate was $\sim 0.05\,\mathrm{nmol\,P\,l^{-1}\,h^{-1}}$, calculated from the bacterial production rate of $2.2\,\mathrm{nmol\,C\,l^{-1}\,h^{-1}}$ for the highest dust addition (bottles 3 and 4) using a C/P ratio of 50 for bacteria (Fagerbakke et al., 1996). This value would be higher considering that some of the P was consumed by phytoplankton. It is compatible with the phosphate measured using nanomolar technology at the start of the experiment, which was below the detection limit of 2 nM. Assuming that at T1, the uptake rate of phosphate in bottles 3 and 4 is mostly due to bacteria, i.e. $\sim 0.07\,\mathrm{nmol\,P\,l^{-1}\,h^{-1}}$, the calculated phosphate concentration is approximately 2 nM. Including certain uptake by phytoplankton, this value would get even closer to the amount of phosphate that could be released from the dust (~16 nM). Additional micronutrients (Fe, Zn) which probably have been delivered by the dust were not assessed in this study. Assuming that particulate Fe dissolution in seawater is ~0.06% (Blain et al., 2004) a maximum amount of $\sim 2\,\mathrm{nmol\,Fe\,l^{-1}}$ $(0.17\,\mathrm{mg\,Fe\,l^{-1}} \times 0.06\%)$ was released from the highest fresh dust addition. Although the bioavailability of this entire amount is not certain (Rue and Bruland, 1995), the amount is high enough to exclude possible Fe-limitation.

Most responses were linearly related to the fresh dust concentration gradient in the range of $0.2–4.9\,\mathrm{mg\,l^{-1}}$. By contrast, there was no response of the autotrophic community detected for pre-leached dust particles in chlorophyll or primary productivity or in most measures of group abundances, though there was a small increase in *Synechococcus* abundance. Thus, the response of the autotrophic community was due to nutrient addition supplied by leaching from the dust and not due to the particle effect.

In the autotrophic community, *Synechococcus* and prymnesiophytes were the main groups to immediately benefit from the released nutrients within the four-day experiment. The fivefold increase in Chl *a* was attributed to increases in both biomass and fluorescence per cell. In another set of incubation experiments, Klein et al. (1997) found that phototrophic nanoflagellates and not picocyanobacteria nor the larger phytoplankton appeared to benefit most from new nutrients added as rainwater.

Prochlorococcus on the other hand disappeared (relative to control) in fresh dust treatments but not in pre-leached dust treatments, suggesting that the added nutrients rather than the particles were responsible for the decline.

Both *Synchococcus* and *Prochlorococcus* have been shown to have higher than Redfield cellular C:P and N:P ratios, and more so under nutrient-depleted conditions (Bertilsson et al., 2003; Heldal et al., 2003), reflecting the low P content of these cells and giving them an advantage in low-P environments. Moutin et al. (2002) have shown that *Synechococcus* has a significantly higher maximum uptake rate and higher affinity for orthophosphate than heterotrophic bacteria or eukaryotic algae, which contribute to their success in P-depleted environments and to transient blooms of this species in the open ocean during episodic orthophosphate nanopulse events. Apparently, *Prochlorococcus*, which a priori is much more abundant at deeper strata and lower light intensities than at the surface water of the Eastern Mediterranean (Li et al., 1993; Zohary et al., 1998), was not able to take advantage of the added N+P while *Synechococcus* was. We do realize the wide existence of high-light adapted ecotypes of *Prochlorococcus* in the surface ocean as opposed to the low-light adapted ecotypes occupying the deeper waters (e.g., Post, 2005; Moore et al., 2002). Assuming that the *Prochlorococcus* in our experiment belonged to the high-light ecotype, the set of associated features did not prevent it from losing the competition. Atmospheric deposition may influence the picocyanobacteria through the release of potential toxic ions as free Cu^{2+}, to which *Prochlorococcus* is more sensitive than *Synechococcus* (Mann et al., 2002). Another interesting result was that diatoms that usually associated with injections of new nutrients (Goldman, 1993) were not the ones to respond to dust.

A similar response was observed in a nutrient addition microcosm experiment performed at sea a few days after this experiment, in which N

Table 5
Differences in nutrient (N, P) concentrations, Chl *a* concentrations, bacterial activity (BacAct.), *Synechococcus* sp. (Syn.) abundance and arbitrary units of red fluorescence (FL3, >630 nm) per *Synechococcus* cell, and ciliate abundance during four days on-board microcosm experiment of different nutrient addition treatments (modified after Zohary et al., 2005)

Treatment	N removed nM	P removed nM	Chl *a* ($ng\,l^{-1}$)	BacAct.* ($pmol\,Leu\,l^{-1}\,h^{-1}$)	Syn. ($cells\,ml^{-1}$)	Syn. ($FL3\,cell^{-1}$)	Ciliates ($cells\,ml^{-1}$)
No addition	~40	(<1.3)	18^{a}	100^{a}	354^{a}	21^{a}	-0.03^{a}
N addition	165	(<1.3)	36^{a}	96^{a}	963^{a}	71^{b}	-0.08^{a}
P addition	~40	~20	19^{a}	323^{b}	598^{a}	13^{a}	0^{a}
N + P addition	570	~20	162^{b}	1759^{c}	8554^{b}	338^{c}	0.33^{b}

Differences were calculated between mean values of triplicates (day 4–day 0). Treatment means were compared using one-way ANOVA. Within each column, values with the same letter are not significantly different.
*Due to bottle effects, the bacterial activity represents differences between day 3 and day 0.

(as ammonium), P or both were added to SSW (Table 5, modified after Zohary et al., 2005). The responses measured in the nutrient addition experiment (detailed below and in Table 5) confirm that the responses measured in the dust microcosm experiment can be attributed to the release of both N and P from the dust. In the Zohary et al. (2005) experiment, the addition of N alone resulted in a minor Chl *a* increase, not significantly different from the control (no addition) or P alone addition treatments, whereas the addition of both N and P resulted in a significant increase of 162 ng Chl $a\,l^{-1}$ within four days (Table 5), similar to the increase observed in the largest fresh dust addition treatment of this present experiment ($\sim 124-190\,ng\,l^{-1}$).

The response to the N and P addition was an enhancement of *Synechococcus* and prymnesiophytes, disappearance of *Prochlorococcus*, and an increase in bacterial activity (with no change in cell density) and an abundance of ciliate cell (Table 5, not all data shown). All these changes did not take place in three other treatments: control, N alone, P alone (Table 5). Nevertheless, while N addition alone did not support significant new growth, some luxury uptake did take place by the *Synechococcus* (Table 5) representing an opportunistic qualification in such oligotrophic environment (Palenik et al., 2003).

The change in Chl *a* (enhancement of $162\,ng\,l^{-1}$) in the treatment of N and P addition corresponded to a decrease (uptake) of 570 nM N or a ΔChl a:ΔN ratio of -0.28. Similar associations were calculated from the dust incubation experiment of Blain et al. (2004) in which ΔChl a:ΔN are approximately -0.36 ($1700\,ng\,Chl\,a\,l^{-1}$ vs $-4700\,nmol\,N\,l^{-1}$). Using this relationship of $\Delta Chl\ a:\Delta N \approx 0.3$, it is possible to calculate that an increase of Chl a to $\sim 124-190\,ng\,l^{-1}$ in bottles 3 and 4 (Table 4) corresponds to a maximum release of approximately 375–630 nM N. Assuming that this amount was released by 4.88 mg dust particles per liter, it corresponds to 77–129 μmol N leached from 1 g of Saharan dust. This value is within the measured leachable range presented in Table 3 ($\sim 155\,\mu mol\,N\,g^{-1}$ dust).

The response of the heterotrophic community to additions of fresh dust and hence a pulse of nutrient release (and perhaps DOC, not measured) was a fast increase in bacterial activity though not in biomass and an increase in ciliate abundance as compared to pre-leached treatments ($p<0.05$, Mann–Whitney test). This was similar to the response observed in the nutrient microcosm (Table 5) and in the CYCLOPS Lagrangian addition (Flaten et al., 2005; Pitta et al., 2005). It suggests that the micrograzers had a major and rapid role in controlling the bacterial biomass. According to Pitta et al. (2001) tintinnids ingest more prey than aloricates by a factor of 5 and, on the other hand, both tintinnids and aloricates show a selection for small cells (<3 μm) and for algal cells. In the fresh dust addition bottles, the lack of increase in picoeukaryote abundance could be attributed to increased grazing on these phytoplankters by ciliates (slight increase) and particularly by tintinnids.

The SSW in the Eastern Mediterranean is low-nutrient low-chlorophyll (LNLC) acting as P-limited for bacteria and N and P-limited for phytoplankton (Flaten et al., 2005; Zohary et al., 2005). In the CYCLOPS P-addition experiment, where only phosphate was added in situ, there was an increase in bacterial activity but not in bacterial biomass. This was interpreted as the heterotrophic

bacterial community being able to access DON or recycled N more efficiently than phytoplankton and increased activity, which was immediately grazed by micrograzers, thus keeping the biomass constant. It was similar to the response of the bacteria observed in this study though it is unknown here whether the N used by the bacterial community came from DON or DIN leached from the dust.

In the CYCLOPS P-addition experiment we also found an unexpected no change in Chl *a*. This was interpreted as the phytoplankton did not have rapid access to N and yet was subject to increased grazing pressure (Psarra et al., 2005). The response was channelled up the food web reaching the mesozooplankton in the form of increased gut content and egg numbers. By contrast, in this study chlorophyll increased. This was due to both N and P being supplied by the dust and to the reduced grazing pressure because the mesozooplankton community was removed.

In May 2001, we were able to sample the effects of a dust storm in situ. Air mass back trajectories and crustal element composition indicated that the Sahara was the source area of this dust event. The dust storm is reflected by the changes in the calculated atmospheric fluxes of Al, total phosphorus, leachable phosphate and inorganic nitrogen (Fig. 5A,B). This dust storm delivered bioavailable nutrients that correspond to addition of approximately 0.3 nmol P l^{-1} and ~9 nmol N l^{-1} to a 15-m surface mixed layer. Even such a small nutrient (both N and P) injection triggered an enhancement of phosphate turnover time corresponding to the release of phosphate from the dust, a sharp decline of *Prochlorococcus* abundance in the top 25 m (Fig. 6A), a small increase in bacterial activity after one-day lag-time (Fig. 6B) and a minute increase of ~5 ng l^{-1} Chl *a* in the top 15-m mixed layer. This minute increase in Chl *a* is similar to a calculated ~7 ng Chl *a* l^{-1} increase from the calculated addition of bioavailable ~0.3 nmol P l^{-1} by the dust event, using P:C ratios of Redfiled (1:106) and C : Chl $a = \sim 50$ (wt., Parsons and Takahashi, 1975). No detectable change was measured either in bacterial abundance.

This less obvious response recorded by the in situ measurements following the Saharan dust storm is not surprising considering the relatively low (though important) amount of nutrients released per event and the relatively low dust particle input. Given an average Al flux of 70 mg m^{-2} per 36-h event (Fig. 5B) and a concentration of 9% (dry wt.) of Al in Saharan dust, the event enriched a 15-m surface mixed layer by approximately 0.06 mg dust l^{-1}. This dust concentration falls at the lower tail of the dust concentration gradient used in this study. Thus, an addition of approximately 0.06 mg dust l^{-1} would correspond to a change of few ng Chl *a* l^{-1}, which would be close, anyway, to detection limits for a change in chlorophyll using remote sensing observations.

The Levantine basin is characterized by low-nutrient surface waters and a high N:P ratio (~27) in the deep water. It is noted here that the principal supply of nutrients to the system is atmospheric (dust and rainfall), which has a bioavailable N:P ratio above Redfield (70, Herut et al., 2002; Krom et al., 2004). The surface waters are also dominated by *Synechococcus* and Prochlorococcus probably containing bio-elemental N:P stoichiometry in excess of the Redfield ratios (20–30, Bertilsson et al., 2003; Heldal et al., 2003) especially under P-limited conditions (>60, Bertilsson et al., 2003). This relationship may be an important component in the unusual nutrient ratios and recycling observed in the East Mediterranean.

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