frontiers in Marine Science

ORIGINAL RESEARCH
published: 21 July 2016
doi: 10.3389/fmars.2016.00127

The Impact of Atmospheric Dry Deposition Associated Microbes on the Southeastern Mediterranean Sea Surface Water following an Intense Dust Storm

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Specialty section:
This article was submitted to Marine Ecosystem Ecology, a section of the journal Frontiers in Marine Science

Received: 27 March 2016
Accepted: 07 July 2016
Published: 21 July 2016

Citation:
Rahav E, Paytan A, Chien C-T, Ovadia G, Katz T and Herut B (2016) The Impact of Atmospheric Dry Deposition Associated Microbes on the Southeastern Mediterranean Sea Surface Water following an Intense Dust Storm. Front. Mar. Sci. 3:127. doi: 10.3389/fmars.2016.00127

This study explores the potential impacts of microbes deposited into the surface seawater of the southeastern Mediterranean Sea (SEMS) along with atmospheric particles on marine autotrophic and heterotrophic production. We compared *in situ* changes in autotrophic and heterotrophic microbial abundance and production rates before and during an intense dust storm event in early September 2015. Additionally, we measured the activity of microbes associated with atmospheric dry deposition (also referred to as airborne microbes) in sterile SEMS water using the same particles collected during the dust storm. A high diversity of prokaryotes and a low diversity of autotrophic eukaryotic algae were delivered to surface SEMS waters by the storm. Autotrophic airborne microbial abundance and activity were low, contributing ~1% of natural abundance in SEMS water and accounting for 1–4% to primary production. Airborne heterotrophic bacteria comprised 30–50% of the cells and accounted for 13–42% of bacterial production. Our results demonstrate that atmospheric dry deposition may supply not only chemical constitutes but also microbes that can affect ambient microbial populations and their activity in the surface ocean. Airborne microbes may play a greater role in ocean biogeochemistry in the future in light of the expected enhancement of dust storm durations and frequencies due to climate change and desertification processes.

Keywords: dust storm, southeastern Mediterranean Sea, atmospheric dry deposition associated microbes, primary production, bacterial production

INTRODUCTION

Aerosols, including mineral-dust, are regularly transported across marine systems, supplying nutrients and trace metals to the surface water (Prospero et al., 2005). Aerosols may also contain a wide array of microorganisms (reviewed in Griffin, 2007; Després et al., 2012; Polymenakou, 2012), which can be transported thousands of kilometers from their place of origin within a few days (Prospero et al., 2005; Kellogg and Griffin, 2006). These aerosol-associated (airborne) microbes may include heterotrophic bacteria (e.g., Seifried et al., 2015), fungi (e.g., Dannemiller et al., 2014), cyanobacteria, chemolitoptophic bacteria, and other autotrophic algae

(e.g., Marshall and Chalmers, 1997; Lang-Yona et al., 2014; Gat et al., 2016), as well as viruses (e.g., Chow and Suttle, 2015). The diversity and viability of airborne microbes depends on the aerosol's route prior deposition (Rahav et al., 2016a).

Several studies have examined the effect desert dust and aerosols have on ocean productivity and microbial biomass, via on-board microcosm or mesocosm experiments that simulated atmospheric nutrient addition (e.g., Mills et al., 2004; Herut et al., 2005; Mackey et al., 2007; Pulido-Villena et al., 2008; Christaki et al., 2011). Overall, the impacts observed following desert dust or aerosol additions are diverse and cannot all be explained by the inducement of a "fertilization response" (Guieu et al., 2014). Although variability in aerosol composition and changes in ocean hydrography and ecosystem structure at the time of deposition have been invoked in order to explain the diverse responses (Paytan et al., 2009), another possible explanation is the impact of the airborne microbes delivered with the added dust/dry aerosol deposition. Such microbes, if viable, may interact with ambient microbial populations in the receiving environment. A recent study conducted across the North Atlantic Ocean measured the abundance of microbes in the lower atmosphere and estimated that airborne microbes cross over 10,000 Km in several days and that millions of microbes are being exchanged on a daily basis between the atmosphere and the ocean's surface layer (Mayol et al., 2014). Further, studies performed in freshwater (Reche et al., 2009; Peter et al., 2014) and marine (Rahav et al., 2016a) environments suggest that airborne microorganisms may remain viable after deposition and thus may play an important role in the receiving aquatic system. For example, Peter et al. (2014) reported viable airborne bacteria following dust deposition into sterile lake water, and Rahav et al. (2016a) showed activity of heterotrophic airborne bacteria in sterile seawater and measured both carbon and nitrogen fixation by these microbes. Airborne microbes can remain viable for decades (Gorbushina et al., 2007), and yet, the full extent of this "biological" addition and the ecological importance of airborne microbes in natural environments are unclear (Hervas et al., 2009; Rahav et al., 2016a). This is because our knowledge about the viability and functionality of airborne microorganisms upon deposition in the ocean is scant (Polymenakou et al., 2008).

The southeastern Mediterranean Sea (SEMS) is an ideal marine environment for studying the role of aerosols and associated microbes on surface ocean microbial production for multiple reasons. First, it is subjected to relatively high aerosol deposition throughout the year (Guerzoni et al., 1999; Ganor et al., 2010). Secondly, it is an oligotrophic environment with low inorganic nutrients (Herut et al., 2000; Kress and Herut, 2001; Kress et al., 2014) and low autotrophic and heterotrophic activity (Raveh et al., 2015). Thus, any external input of micro/macronutrients, along with aerosols-associate microbiota, can have a substantial effect upon interaction with the ambient microbial populations.

In this study, we followed the *in situ* temporal dynamics of autotrophic and heterotrophic microbial abundances and production rates in the SEMS surface waters during an intense natural dust storm event that lasted a few days. Specifically, we evaluated the role that the autotrophic and heterotrophic microbial communities associated with atmospheric dry deposition particles play in the SEMS surface water following this event.

MATERIALS AND METHODS

Sampling Strategy

Surface SEMS water (∼1 m depth) was sampled every 12 h at a coastal station near the National Institute of Oceanography (Haifa, Israel, Lat. 32.28N, Lon. 34.95E), from the 8th to the 13th of September 2015, during an intense storm event (**Figures 1A,B**). Seawater temperatures were measured using an *in situ* HOBO Pendant Temperature data logger (model UA-002-64, Onset Computer Corporation) mounted on the rocky bottom at a depth of ∼4 m. Salinity was measured using a Yellow Spring Instruments YSI-6000. In order to quantify dry deposition during the dust storm event, atmospheric suspended particles were collected on a Whatman 41 filter (125 mm, ∼20 μm pore size) using a high volume total suspended particles (TSP) sampler (located on a headland pointing into the sea, 22 m above sea level) at a flow rate of 60 m^3 h^{-1} for 24 h (**Figure 1**), as described in Herut et al. (2002). Dry deposition rates were calculated based on Al concentration in the collected aerosol (measured by XRF, 7.6% dry wt. Table S1), a settling velocity of 1.8 cm s^{-1} (Kocak et al., 2005), and the particles weight collected on the filter for the volume pumped during the collection time (1.77 mg m^{-3} air). This yielded a deposition of 1.05 mg of dry deposition L^{-1} in seawater when integrated over the upper 5 m mixed layer, similar to values reported for other intense dust storm events in this area (Herut et al., 2005). Seawater was sampled twice a day for chlorophyll-*a* (acetone extraction), cyanobacterial abundance, pico-eukaryotic abundance and heterotrophic bacterial abundance (flow-cytometry), primary production ($NaH^{14}CO_3$ incorporation), and bacterial production (^{3}H-Leucine incorporation) measurements.

Aerosol Collection and Bioassay Experiment

Dry deposited material was collected on September 8th 2015 during a major dust storm event using a pre-cleaned glass deposition plate. The deposited particles were collected from the plate using a clean plastic knife, transferred into prewashed (10% hydrochloric acid) sterile 2 ml plastic tubes and stored at −20°C until further analyses. Three-day back trajectories arriving at 500 and 1000 m altitude levels were calculated, commencing at 10.00 UTC using the HYSPLIT model from the Air-Resources Laboratory, NOAA (**Figure 1C**). A few days after the aerosol deposition event (between the 16th and 20th of September 2015), an aerosol-enrichment microcosm bioassay experiment was carried out in triplicate using 4.6-L acid-washed polycarbonate Nalgene bottles and sterile (0.2 μm filtered and autoclaved-killed) surface SEMS water. The collected aerosol was added to each of the bottles (∼1.5 mg dust L^{-1} of sterile surface seawater), and the bottles were incubated in an outdoor pool with seawater flow-through in order to maintain ambient temperatures. The pool was covered with a neutral density screening mesh to simulate ambient light and the experiment

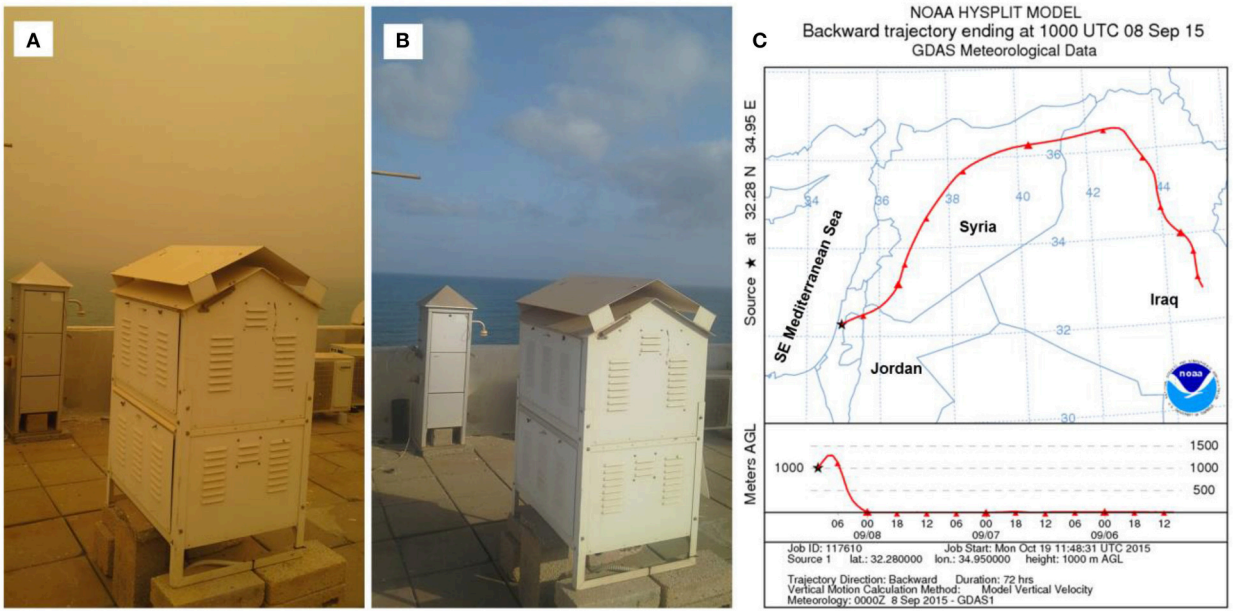

FIGURE 1 | Dusty (A) and clear (B) skies off the SE Mediterranean coast between the 8th (A) and 13th (B) of September 2015. Air mass back trajectory analysis shows the dust's origin **(C)**.

lasted for 4 days. Blank treatments of sterile SEMS water without added aerosol were carried out in parallel and sampled at the beginning (0.5 h) and at the end of the experiment (96 h). Subsamples of seawater from each incubation bottle were collected for chlorophyll-*a*, cyanobacterial abundance, pico-eukaryote abundance, heterotrophic bacteria abundance, primary production, and bacterial production measurements, at 0.5, 9, 24, 48, 57, 72, and 96 h after aerosol addition. The differences between *in situ* values (measured during September 8–13, 2015, and representing the ambient community's response to the dust storm event) and those measured during the enrichment experiments (September 16–20, 2015) performed in sterile seawater using the same particles that were collected during the dust storm, were used to estimate the potential contribution of the autotrophic and heterotrophic microbes associated with the event (hereafter airborne microbes) to the overall *in situ* microbial abundance and production rates following aerosol deposition during the storm.

Inorganic Nutrients and Trace Metals Leached from the Aerosol

These micro- and macro-nutrients from the aerosol particles were extracted according to Buck et al. (2012) and analyzed using a flow injection autoanalyzer (FIA, Lachat Instruments model QuickChem 8000) as describe in Chen et al. (2006). A detailed description of the method can be found in the supporting information.

X-Ray Fluorescence (XRF)

An elemental analysis of the collected aerosol particles was carried out using an ED-XRF spectrometer (SPECTROSCOUT) in a vacuum chamber. A detailed description of this method can be found in the supporting information.

DNA Extractions and High-Throughput Phylogenetic and Sequence Analyses

DNA was extracted from the aerosol particles that were collected on the clean glass deposition plates during the atmospheric deposition event. The DNA was extracted using the phenol–chloroform method, modified from Massana et al. (1997). A detailed description of this method can be found in the supporting information.

Chlorophyll-*a* Extraction

Autotrophic biomass was determined using the non-acidification method (Welschmeyer, 1994). A detailed description of this method can be found in the supporting information.

Pico-Phytoplankton and Bacterial Abundance

Water samples (1.8 mL) were analyzed using an Attune® Acoustic Focusing Flow Cytometer (Applied Biosystems) equipped with a syringe-based fluidic system and 488 and 405 nm lasers (Vaulot and Marie, 1999). A detailed description of this method can be found in the supporting information.

Primary Production

Photosynthetic carbon fixation rates were estimated using the ^{14}C incorporation method (Steemann-Nielsen, 1952). A detailed description of this method can be found in the supporting information.

Bacterial Production

Rates were estimated using the ^{3}H-leucine (Amersham, specific activity: 160 Ci mmol^{-1}) incorporation method (Simon et al., 1990). A detailed description of this method can be found in the supporting information.

Statistical Analyses

The different variables presented in the figures and tables are averages and standard deviation (biological replicates, $n = 3$). Changes in chl-*a*, production rates, and abundance of cyanobacteria, pico-eukaryotes, and bacteria throughout each of the experiments (4–5 days) were evaluated using a one-way analysis of variance (ANOVA), followed by a Fisher LSD multiple comparison *post-hoc* test with a confidence level of 95% ($\alpha = 0.05$). The difference between samples collected *in situ* at the SEMS during the dust storm event (8–13 September 2015) and those from the sterile seawater bioassay experiments (16–20 September 2015) were evaluated using a student *t*-test with a confidence level of 95% ($\alpha = 0.05$). These statistical analyses were carried out using the XLSTAT software. The Shannon-Weiner diversity index (Margalef, 1958) was calculated using the primer software.

RESULTS

The initial pre-storm physiochemical characteristics of the surface SEMS are shown in **Table 1**. The ambient surface seawater depicts a high temperature (∼30°C) and high salinity (39.8). The algal biomass, derived from chl-*a* levels, was low overall (0.17 ± 0.02 mg m^{-3}), as were the cyanobacterial and picophytoplankton abundances (1.9×10^4 and 8.0×10^2 cells mL^{-1}, respectively). Concurrently, the primary production rates were low (1.99 ± 0.41 μg C L^{-1} d^{-1}). In contrary to the low autotrophic biomass, bacterial heterotrophs were more abundant (8.5×10^5 cells mL^{-1}), and active (5.18 ± 1.51 μg C L^{-1} d^{-1}).

The aerosols collected during early September 2015 had a very high fraction of Ca (20%) and were rich in Mg (4.3%), Fe (6.3%), Mn (945 ppm), Sr (450 ppm), Al (∼67 ng mg^{-1}), and Cu (∼25 ng mg^{-1}; **Table 2**, Table S1). They also had significant amounts of soluble $NO_3^- + NO_2^-$ (∼176 nmol mg^{-1}) and relatively less NH_4^+ (∼5.4 nmol mg^{-1}) and PO_4^{3-} (∼1.5 nmol mg^{-1}), resulting in a high N:P ratio of ∼120:1 (**Table 2**, Table S1).

Aerosol-derived autotrophic and heterotrophic microorganisms were also transported with the atmospheric particles (**Figure 2**). These included a wide array of prokaryotes (>100 families in 23 different phylum, ∼650 species, Shannon-Weiner diversity index = 3.88) and a small number of autotrophic eukaryotic microbes (4 families in 2 phyla, 4 species, Shannon-Weiner diversity index = 1.03). Among the prokaryotes, the most dominant families (as relative operational taxonomic units, OTUs) were Cytophagaceae (10.3%), Chloroflexaceae (7.8%), Frankiales and Rhodobacteraceae (6.4% each), and Bacillaceae (4.3%), as well as other bacteria (**Figure 2A**). The autotrophic eukaryotic microorganisms contained within the aerosol particles belonged to Tracheophyta (61.5%), Chlorodendraceae (23.1%), Bryophyta (8.9%), and Pedinomonadaceae (6.5%) taxa (**Figure 2B**). Despite the low number of the different eukaryotic-autotrophic families, ∼30% were of marine or freshwater origin (i.e., green algae).

TABLE 1 | The initial characteristics of the SE Mediterranean seawater 3 days prior to the dust storm event (5th September 2015).

Variable	Unit	Value
Temperature	°C	30.1
Salinity	–	39.8
Chl-*a*	mg m^{-3}	0.17 ± 0.02
Cyanobacteria	Cells mL^{-1}	1.9×10^4
Picoeukaryotes	Cells mL^{-1}	8.0×10^2
Heterotrophic bacteria	Cells mL^{-1}	8.5×10^5
Primary production	μg C L^{-1} d^{-1}	1.99 ± 0.41
Bacterial production	μg C L^{-1} d^{-1}	5.18 ± 1.51

TABLE 2 | The trace metals derived from the aerosols collected in September 8, 2015 and the subsequent values following the dust storm in the SEMS water.

Variable	Leached element conc. (ng mg^{-1})[a]	Element conc. (ng mg^{-1})[b]	Leachable fraction (%)	Amount deposited (nM)[c]	Amount added in bioassay (nM)[d]
Pb	0.34	34	1.0	0.36	0.51
Al	66.8	76000	0.09	70.14	100.20
Mn	83.4	945	8.8	87.57	125.10
Fe	20.6	63000	0.03	21.63	30.90
Ni	2.69	250	1.1	2.82	4.04
Zn	1.40	377	0.4	1.47	2.10
Mg	NA	43000	NA	NA	NA
Ca	NA	200000	NA	NA	NA
Sr	NA	4.5×10^{-4}	NA	NA	NA
Cu	25.4	105	24.2	26.67	38.10

[a] *Leaching experiments were performed as described in Chen et al. (2006, 2007).*
[b] *Measured by XRF.*
[c] *Assuming a 1.05 mg L^{-1} dust deposition in the upper mixed layer (5 m).*
[d] *Addition of 1.5 mg L^{-1} dust.*
NA, not available.

The *In situ* Temporal Dynamics of Autotrophic and Heterotrophic Microbial Communities during the Dust Storm Event

The *in situ* chl-*a* concentrations gradually increased from its background pre-storm levels (**Table 1**) to 0.24 mg m^{-3} within 55 h, corresponding to ∼40% change, and decreased back to background levels at day 5 following the dust storm (0.19 mg m^{-3}, **Figure 3A**, Figure S1). Contrary to the chl-*a* levels, cyanobacterial abundance exhibited a different yet insignificant temporal trend ($P > 0.05$), with an immediate 20% decrease in cell numbers (∼1.3×10^4 cells mL^{-1}), an increase back to the initial levels after 48 h (∼1.7×10^4 cells mL^{-1}), which was followed by another decrease (∼1.3×10^4 cells mL^{-1}; **Figure 3B**, Figure S1). The picoeukaryotes remained unchanged (∼8.2×10^2 cells mL^{-1}, $P > 0.05$; **Figure 3C**, Figure S1). Heterotrophic bacterial abundance increased by 30% within 10 h (8.7×10^5 cells mL^{-1}, $P = 0.05$), an increase that lasted for 3 days (**Figure 3D**,

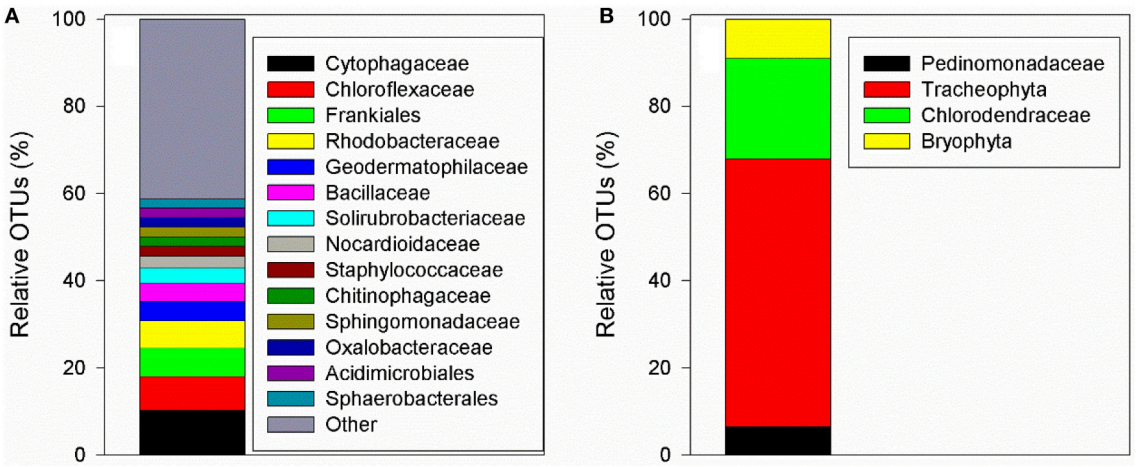

FIGURE 2 | Distributions of bacterial 16S rRNA (A) and 18S rRNA (B) gene reads at a family level, retrieved from a dry deposition particles sample collected on September 8th 2015 off the SE Mediterranean Sea coast.

Figure S1, $P < 0.05$). *In situ* primary production rates reached maximal values 48 h after deposition (a 25% increase, $P > 0.05$) and then decreased to background levels over the course of 5 days (**Figure 4A**, Figure S2). Bacterial production increased slightly (∼15%, $P > 0.05$), however this increase lasted for only 48 h (**Figure 4B**, Figure S2).

The Impact of Airborne Autotrophic and Heterotrophic Microorganisms

Airborne autotroph abundance (measured in the sterile seawater after aerosol addition) constituted only a small fraction of the overall photosynthetic biomass observed *in situ* (**Figures 3A–C**). Airborne cyanobacteria and picoeukaryotes comprised <1% of the autotrophic microbial abundance (**Figures 3B,C**, Figure S1). Airborne heterotrophic bacteria were more significant (Figure S1), comprising 30–50% (abundance per gram of aerosol added) of the total heterotrophic bacteria in the SEMS water during the dust storm (**Figure 3D**).

Concurrent with the low airborne contribution to autotrophic biomass, the airborne primary production was low (Figure S2), comprising 1–4% of the rates measured *in situ* (activity per gram aerosol added) during the dust storm event (**Figure 4A**). The airborne bacterial production rates were higher (Figure S2), corresponding to 13–42% of the rates measured *in situ* during the dust storm event (**Figure 4B**). Taken together, the airborne heterotrophic cell specific activity (bacterial production per cell) was not different from the activity measured in the seawater during the dust storm event (∼0.01 fg C d^{-1} $cell^{-1}$, $n = 6$, $P = 0.67$). The airborne autotrophic cell specific activity (primary production per cell) was three-fold lower than in seawater (∼19 vs. 6 μg C μg chl-a^{-1} d^{-1}, $n = 6$, $P < 0.001$).

DISCUSSION

The SEMS is constantly exposed to high levels of atmospheric deposition derived primarily from surrounding deserts and land sources (Herut et al., 2002; Lawrence and Neff, 2009). These atmospheric inputs provide a variety of nutrients and trace metals (Table S1 and reviewed in Guieu et al., 2014), which are required for microbial cellular metabolism, enzymatic activity and growth (e.g., Cvetkovic et al., 2010; Huertas et al., 2014). In addition to nutrients and trace metals, atmospheric deposition may also introduce a wide array of airborne microorganisms to surface seawater (reviewed in Griffin, 2007; Polymenakou, 2012). Some of these microbes can remain viable and fix carbon (C) and dinitrogen (N_2) upon deposition in seawater (Rahav et al., 2016a).

The aerosol deposition event into the SEMS water in early September 2015 was an exceptional regional event. Previous works linked dust fallout over the Levantine Basin to Saharan origins (Ganor and Mamane, 1982; Herut et al., 1999, 2005), whereas the studied event originated from drylands in Eastern Syria (**Figure 1C**). This difference in origin is evident in the chemical composition of the Syrian aerosol particles when compared to the reported composition of Saharan dust particles (**Table 2**, Table S1). The most prominent difference was in Ca, which was much higher than the reported fraction in Saharan aerosols (Krom et al., 1999; Goudie and Middleton, 2001; Herut et al., 2001). This high Ca content in the Syrian aerosols likely reflects a source origin of calciorthid soils, which covers large areas in Syria (Ilaiwi, 1985). The Syrian aerosol was also richer in Mg, Fe, Mn, and Sr (normalized to Al) when compared to the reported concentrations in Saharan samples (Table S1, Krom et al., 1999; Goudie and Middleton, 2001; Herut et al., 2001). When calculating the soluble fraction of trace metals that were leached from the aerosols and added to seawater during this event (**Table 2**) concentrations were below the threshold for toxicity for phytoplankton in seawater (e.g., Sunda, 2012). In fact, some of the added trace metals, such as Fe or Zn, are key cofactors for many enzymatic reactions in the marine environment, including photosynthesis and N_2 fixation (Falkowski, 1997; Sohm et al., 2011), and may contribute to enhancing production.

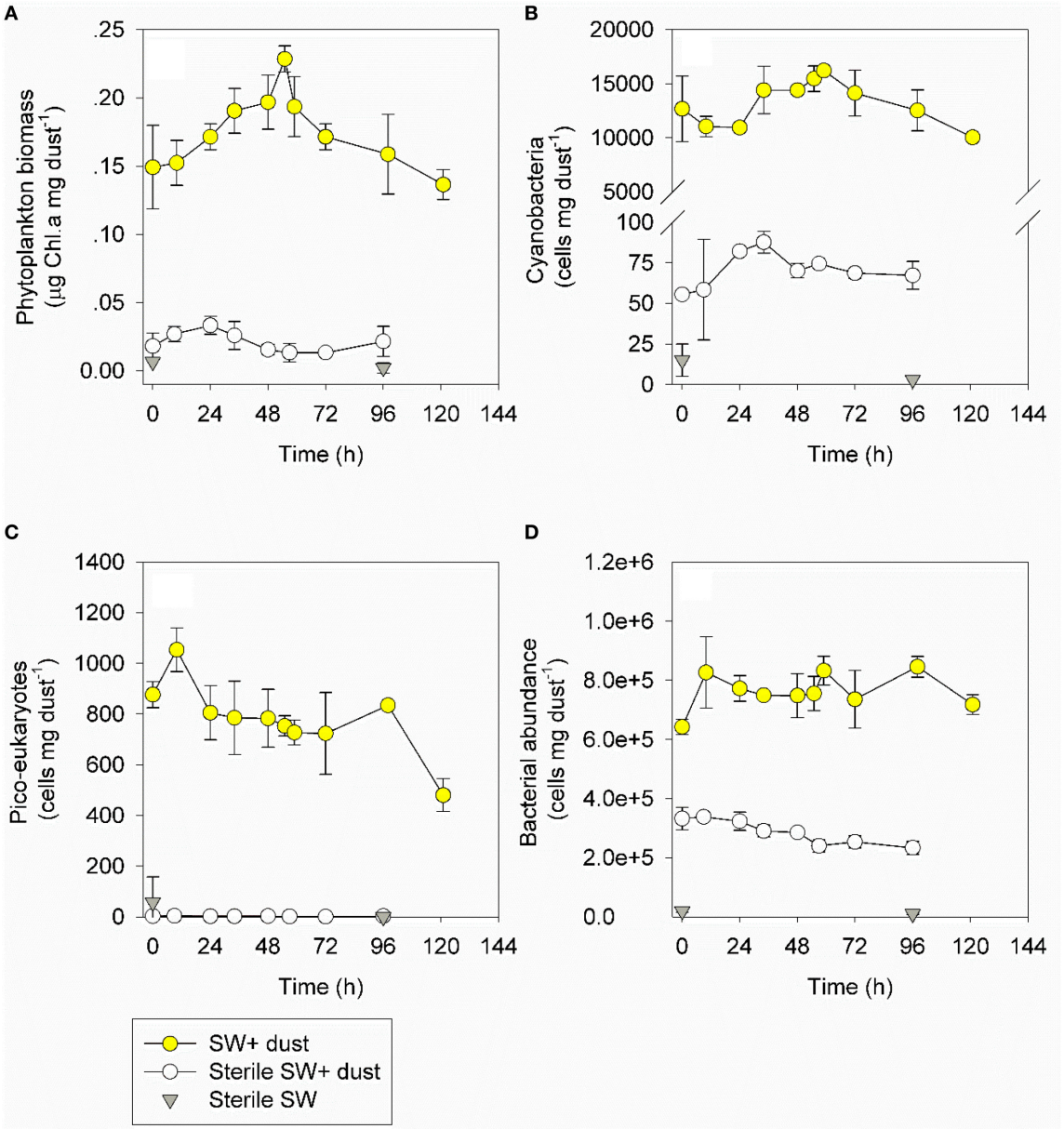

FIGURE 3 | The temporal dynamics of chl-*a* (A), cyanobacterial abundance (B), pico-eukaryotes abundance (C), and heterotrophic bacterial abundance (D) during a dust storm event (*in situ* measurements, 1.05 mg L^{-1}, yellow) off the SEMS between the 8th and 13th of September 2015. The contribution of airborne microbes was tested between the 16th and 20th of September 2015 in sterile seawater, either supplemented with 1.5 mg L^{-1} of the same atmospheric particles deposited the previous week (white) or without any addition (gray). Values (as averages and standard deviations, $n = 3$) are normalized to the amount of dust added. The un-normalized values are presented in Figure S1.

The studied Syrian aerosol particles released soluble $NO_3^- + NO_2^-$ and PO_4^{3-} (**Table 3**, Table S1), which may relieve nutrient stress for autotrophic and heterotrophic microbial biomass and activity in the surface SEMS (i.e., Kress et al., 2005; Zohary et al., 2005; Pitta et al., 2016). Assuming 1.05 mg L^{-1} of dust deposition into the upper SEMS 5 m mixed layer (see Materials and Methods), ~185 nM of $NO_3^- + NO_2^-$ and ~1.5 nM PO_4^{3-} were actually added into this water layer (**Table 3**), which constitutes ~50 and 5–10% of the nutrient concentration typically reported for this system during summer, respectively (Kress et al., 2014; Raveh et al., 2015). Due to the extremely oligotrophic nature of the SEMS, any amendment might prove to be important and may alter microbial dynamics via the release of scarce, key-limiting nutrients. For example, several authors showed that inorganic nitrogen (N) and phosphorus (P) may enhance algae biomass and growth rates in the SEMS water (Kress et al., 2005; Lagaria et al., 2011; Pitta et al., 2016), whereas P (Thingstad et al., 2005; Zohary et al., 2005) or dissolved organic

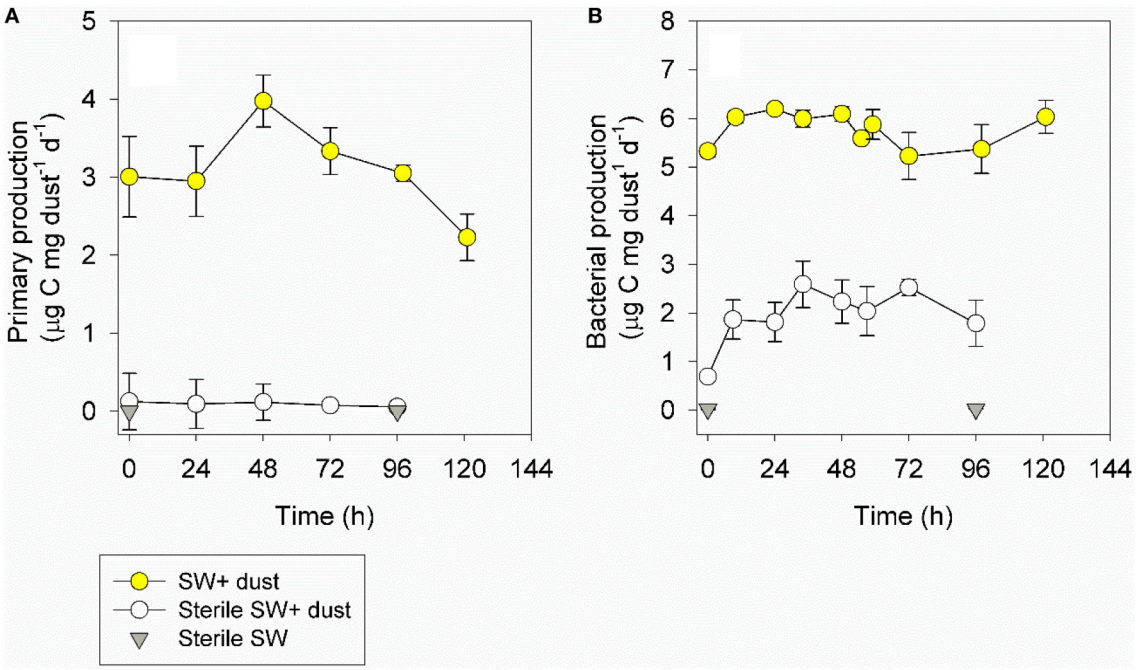

FIGURE 4 | The temporal dynamics of primary production (A) and bacterial production (B) during a dust storm event (*in situ* measurements, 1.05 mg L^{-1}, yellow) off the SEMS between the 8th and 13th of September 2015. The contribution of airborne microbes was tested between the 16th and 20th of September 2015 in sterile seawater, either supplemented with 1.5 mg L^{-1} of the same particles deposited the previous week (white) or without any aerosol addition (gray). Values (as averages and standard deviations, $n = 3$) are normalized to the amount of aerosols added. The un-normalized values are presented in Figure S2.

TABLE 3 | Leached nutrients derived from the aerosols collected in September 8, 2015 and the subsequent values following the dust storm in the SEMS water.

Variable	Leached element conc. (nmole mg^{-1})[a]	Amount deposited (nM)[b]	Amount added in bioassay (nM)[c]
NO_3+NO_2	175.95	184.75	263.93
NH_4	5.37	5.64	8.06
PO_4	1.46	1.53	2.19
$Si(OH)_4$	2.05	2.15	3.08

[a] *Leaching experiments were performed as described in Chen et al. (2006, 2007).*
[b] *Assuming a 1.05 mg L^{-1} dust deposition in the upper mixed layer (5 m).*
[c] *Addition of 1.5 mg L^{-1} dust.*

carbon (Rahav et al., 2016b) can also stimulate heterotrophic bacterial activity. Thus, assuming a C to chl-*a* ratio of ~80 (e.g., Behrenfeld et al., 2005; Wang et al., 2009) and a 106:1 C:P ratio (Redfield, 1934), the addition of the dust-derived P could explain a chl-*a* enhancement of ~0.05 mg m^{-3} above the ambient levels. The chl-*a* enhancement calculated based on the added P is lower than the overall chl-*a* change measured following the dust examined here (~0.08 mg m^{-3}, Figure S1 and see Discussion below). One of the possible explanations for this difference between the actual increase in chl-*a* (~0.08 mg m^{-3}) and the dust-P derived chl-*a* (~0.05 mg m^{-3}) may be chl-*a* associated with airborne microbes (algae and cyanobacteria).

Indeed, both autotrophic and heterotrophic microbes were delivered with the Syrian aerosol studied here (**Figure 2**). These include commonly isolated bacteria from marine, freshwater, and terrestrial environments (e.g., Hervas and Casamayor, 2009; Cho and Hwang, 2011; Seifried et al., 2015), as well as from the surroundings of the SEMS (Katra et al., 2014; Rahav et al., 2016a). It should be noted, that based on the 16S rRNA gene, we cannot rule out that in addition to heterotrophic microbes, chemolithotrophic bacteria were also part of the aerosol collection (Gat et al., 2016). More specific assays should be carried out in future studies to fully understand whether these chemolithotrophic microbes were actually transported with the aerosol particles. Such chemolithotrophic bacteria may play an important role e in the biogeochemistry of nitrogen, sulfur, and iron (e.g., Saeed and Sun, 2012). In contrast to this broad airborne microbial heterotroph biodiversity, only few algal families associated with the aerosol particles were observed based on the 18S rRNA gene. This may be due to the high settling velocities of large eukaryotic particles (such as those of microphytoplankton). Most of the large-size algae and other terrestrial plants were probably deposited along the dust's route (above land) rather than being suspended over long distances and, therefore, were rarely found in our sample. It is possible, however, that aerosols from different origins would contain different amounts of marine/freshwater autotrophic organisms, and particularly small-size cyanobacteria (Cho and Hwang, 2011; Lang-Yona et al., 2014; Seifried et al., 2015). Thus, a more typical atmospheric deposition event coming from the southwest (e.g., Herut et al., 2005) rather than from the northeast (**Figure 1**) would potentially carry more algae or small-size cyanobacteria,

and, therefore, airborne autotrophs could be more abundant than what we have observed in this study.

In situ Dynamics of Autotrophic and Heterotrophic Microbial Populations Following Aerosol Deposition and the Relative Contribution of Airborne Microbes

A moderate change in the *in situ* chl-*a* level and picophytoplankton abundance was observed following the aerosol deposition event of early September 2015 (**Figures 3A–C**). This is consistent with the expected change derived from the PO_4^{3-} addition (∼1.5 nM) and its subsequent carbon addition based on the C to chl-*a* ratio (see above). The relatively limited change in picophytoplankton abundance implies a possible top-down control of small-size autotrophs by grazers (Billen, 1990), dominance of larger-size algae such as microphytoplankton that utilized most of the leached nutrients/trace metals and compete with the picophytoplankton (Duarte et al., 2000), or toxicity of small-size autotrophs (Mann et al., 2002; Paytan et al., 2009). It may also hint at interactions between the ambient population and the airborne microbes that affect the abundance of small-size autotrophs. In contrast, the heterotrophic bacterial abundance was immediately enhanced (**Figure 3D**), suggesting that the leached nutrients and trace metals, and possibly the addition of airborne microbes, favored heterotrophy. A similar response was recorded by Herut et al. (2005) in the SEMS water following a desert-dust storm event that triggered a slight increase in the chl-*a* and heterotrophic bacterial abundance and a decrease in cyanobacterial abundance (*Prochlorococcus* sp.). The similarity in trends observed during these two distinct events lends credibility to the observations.

The temporal dynamics of the *in situ* primary and bacterial production (**Figure 4**, Figure S2) are consistent with observed autotrophic and heterotrophic bacterial abundances (**Figure 3**, Figure S1). The overall low impact of the dust on autotrophic biomass and production is similar to the response reported from an onboard microcosm experiment in the open SEMS (Herut et al., 2005), and was most likely a result of the relatively low nutrient and trace metal amounts added from the dust (**Tables 2, 3**). It may also suggest the likely control of grazing pressure, and/or possible toxicity effects of the dust (Paytan et al., 2009). Alternatively, it is possible that airborne microbes delivered with the dust interacted with the ambient microbial populations and, in some circumstances, outcompeted them, resulting in the decline of abundance and production rates.

The airborne chl-*a* (up to 0.03 mg m^{-3}) measured in sterile SEMS water reached 5–30% (biomass per gram of dry deposition particles added) of the total chl-*a* measured *in situ* during the event (**Figure 3A**, Figure S1). This airborne contribution to the total chl-*a* (∼0.03 mg m^{-3}), along with the increase in the chl-*a* level calculated based on that expected from the uptake of the leached P (∼0.05 mg m^{-3}, see above), is consistent with the overall increase measured *in situ* 55 h post-deposition (∼0.08 mg m^{-3}, Figure S1). The contribution of airborne heterotrophic bacteria measured here (abundance per gram of aerosol added) to the total bacterial abundance in the water is lower than the values recently reported for aerosols collected in the SEMS during 2006–2015, representing different source origins and seasons (Rahav et al., 2016a). This highlights the importance of biogeographical aspects in introducing not only a different diversity of airborne microbes but possibly also different quantities of cells with potentially different activities and functions. However, it should be noted that the presence of autotrophic and heterotrophic bacteria, regardless of their fraction of the total abundance measured *in situ*, is no evidence for their viability in the receiving seawater. It is possible that inactive/dormant cells were leached off the aerosol particles along with viable microbes and were counted using flow cytometry. This issue necessitates additional studies implementing techniques designed to estimate the microbial abundance of active cells.

Another method for estimating whether the retrieved cells are viable upon deposition in seawater is to measure metabolic parameters, such as primary production and bacterial production of the airborne microbes. Our results suggest that airborne primary production was low overall (**Figure 4**, Figure S2), which is consistent with the low contribution of airborne chl-*a* and the negligible fraction of small-size airborne photosynthetic microorganisms (**Figures 3A–C**). On the other hand, airborne bacterial production was more important and immediately responded to the aerosol addition, suggesting that airborne heterotrophs can rapidly interact with the ambient populations. The nature of such interactions can be diverse, depending on the species of the microbes that are associated with the aerosol particles (Rahav et al., 2016a). It is possible that under some circumstances airborne microbes can negatively affect certain microbial groups in seawater (competition, allelopathic affects, cell lysis, etc.), or that they can affect certain ambient populations positively (serving as unique food, relieving N-stress via N_2 fixation, etc.). Rahav et al. (2016a) reported airborne heterotrophic bacterial production rates similar to changes observed following dry deposition aerosol amendments in seawater, potentially accounting for 100% of the change. In this study, however, the contribution of airborne heterotrophic bacterial production rates was lower than that reported by Rahav et al. (2016a) and accounted for a maximum of 42% of the ambient-typical production levels in the SEMS (e.g., Raveh et al., 2015), once again highlighting the importance of the aerosol's origin and associated numbers and taxa of airborne microbes.

To the best of our knowledge, this is one of only few attempts to estimate the role of airborne microbes in seawater following a major dust storm. If the results from this dust storm event are representative, the small contribution of airborne autotrophs (in terms of both abundance and C fixation) may suggest that the increase in primary production and chl-*a* usually observed following dust events (e.g., Herut et al., 2005; Ternon et al., 2011; Gallisai et al., 2014) results from the beneficial impacts of nutrient and/or trace metal additions from the aerosols. However, we postulate that the contribution of airborne microbes to the ambient autotrophic community's chl-*a* in the SEMS water may occasionally be higher if the dust's route prior to deposition went over marine areas of higher productivity rather than over land, which would be more likely to contain a higher abundance of

viable autotrophic organisms that will be viable upon deposition in seawater.

CONCLUSIONS

We determine the role of autotrophic and heterotrophic airborne microbes in seawater during a specific dust storm event. Our results demonstrate that in this case, where the dust arrived from an atypical continental source (**Figure 1**), only a few groups of eukaryotic-autotrophic microbes were transported (**Figure 2B**) and their overall impact in the surface ocean was thus negligible (**Figure 4**). In contrast, a higher diversity of prokaryotes (both heterotrophs and possibly autotrophs such as cyanobacteria and chemolitotrophs) was contained within the dry deposition particles (**Figure 2A**), and at least some of these microbes exhibited immediate activity upon deposition (**Figure 4**). It should be noted that the open SEMS is an ultra-oligotrophic environment (Kress et al., 2014), much more than our coastal study site (Bar-Zeev and Rahav, 2015; Raveh et al., 2015). We postulate that airborne microbes (along with aerosol-derived nutrients) are likely to have a more profound affect in such oligotrophic provinces.

To date, we cannot say what mechanisms and strategies are used by airborne organisms once deposited in seawater to successfully compete with ambient microbes that are already acclimated in their habitat. It is possible that some chemical components derived from aerosols are toxic to specific groups of organisms (Paytan et al., 2009) or have negative biologically impacts via viral lysis (Vardi et al., 2012; Sharoni et al., 2015), allelopathy, or other mechanisms that may be at play. It is also possible that airborne microbes will synergistically interact with ambient populations. Dedicated studies aimed at filling these knowledge gaps are needed, including investigations of dust-derived allelopathic affects and a comparison between the nutrient uptake rates of airborne bacteria and those of *in situ* communities. Addressing these aspects will be particularly important in the near future, since climate and anthropogenic changes may increase aerosol deposition (including mineral dust). This, in turn, will also upsurge airborne microbes transfer and deposition in seawater and could, subsequently, impact surface ocean carbon and nitrogen cycles (Rahav et al., 2016a) as well as other biochemical and ecological aspects.

AUTHOR CONTRIBUTIONS

Conceived and designed the experiment: ER and BH. Performed the experiment: ER, GO, CC, TK, and AP. Analyzed the data: ER, AP, TK, and BH. Contributed reagents/materials/analysis tools: ER, TK, and AP. Wrote the paper: ER, CC, AP, TK, and BH.

ACKNOWLEDGMENTS

We would like to thank Lilach Baumer and Kimberley Bitterwolf for English editing, Dr. Yana Yudkovsky for the XRF analysis and four reviewers that greatly improved the manuscript. This study was supported by a grants awarded by the Ministry of National infrastructures, Energy and Water Resources (grant 3-11519) to ER, by the Ministry of environmental Protection (145–1–2) to ER, by the PERSEUS project's (EC contract 287600) contribution to BH, partially by the ENVIMED MERMEX TRACOMED project's contribution to BH and by the NSF-OCE (grant 0850467) to AP. The authors gratefully acknowledge the NOAA Air Resources Laboratory (ARL) for the provision of the HYSPLIT transport and dispersion model used in this publication.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fmars.2016.00127

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The reviewer CP and handling Editor declared their shared affiliation, and the handling Editor states that the process nevertheless met the standards of a fair and objective review.