

THE IMPACT OF SAHARAN DUST DEPOSITION ON BACTERIOPLANKTON IN
MARINE SURFACE WATER

by

TRACE BORCHARDT

(Under the Direction of Elizabeth Ottesen)

ABSTRACT

Within the last 30 years, dust deposition has been identified as a key contributor of nutrients to the open ocean. While most research in this field has been conducted using mesocosms with artificial additions, we have collected a 21-day *in situ* time series of the microbial structure and chemical concentration changes during elevated atmospheric dust levels. An increase in microbial abundance and diversity, and shifts in dominant taxa like *Synechococcus* and *Prochlorococcus* occurred after dust entered our study site. Along with biological changes, delayed increases in chemical parameters like iron and phosphorus were observed. Using experimental incubations we confirmed many changes that happened *in situ* also occurred after incubation, indicating the changes seen were not due to disparate bodies of water, supporting previously published work using mesocosm experiments. As research continues, more *in situ* events should be investigated to more fully understand the effect dust deposition has on marine environments.

INDEX WORDS: Microbial ecology; Saharan dust; marine biogeochemistry; bacterial community structure; 16s rRNA sequencing

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DEDICATION

This is dedicated to my future wife and family. Their unwavering support, encouragement, and love over the past three years have made this difficult journey manageable and at times, even enjoyable. Thank you, and I love you all.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Each year approximately 1700 Tg of desert dust is blown into the atmosphere by high winds where it is transported across the globe (Mahowald et al. 2005). Globally, there are many atmospheric dust source regions including the Middle East, North-China, Australia and Africa. One of the largest source regions is the Sahel and Saharan Desert in North Africa, contributing ~69% of all atmospheric dust (Muhammad Akhlaq et al. 2012). The dust is deposited in both terrestrial and aquatic environments (Swap et al. 1992) contributing biologically important nutrients and trace elements (Swap et al. 1992; Mahowald et al. 2005, 2010). Of this atmospherically transported dust, approximately 477 Tg yr⁻¹ settles in marine systems (Mahowald et al. 2010).

Within the last 30 years, scientists have begun to understand that atmospheric deposition, along with riverine addition, is a key source of nutrient input to the open ocean (Duce and Tindale 1991; Duce et al. 1991; Arimoto et al. 1992). The dust contains large amounts of nutrients including nitrogen (Loÿe-Pilot et al. 1990), phosphorus (Mills et al. 2004), carbon (Pulido-Villena et al. 2008; Lekunberri et al. 2010), iron (Duce and Tindale 1991; Duce et al. 1991; Lenes et al. 2001; Bonnet and Guieu 2006) and other trace metals (Duarte et al. 2006; Moore et al. 2013; Wuttig et al. 2013). Due in part to the formative work of Redfield (1934), nitrogen or phosphorus were often believed to be the key limiting nutrients in marine systems. While this is true for many areas (Thingstad and Rassoulzadegan 1995; Thingstad et al. 1998; Mills et al. 2004), iron (Martin and Fitzwater 1988; Martin and Michael Gordon 1988; Blain et

al. 2004), or a combination of multiple nutrients have been identified as limiting in many marine systems (Moore et al. 2013).

While dust contains high amounts of nutrients, they become more bioavailable after atmospheric transport (Baker and Croot 2010; Guieu et al. 2014a). During transport, nutrients contained in dust become more bioavailable from both UV irradiation and dissolution by anthropogenic acids in the atmosphere (Stockdale et al. 2016). Although this is generally true, bioavailability can vary widely based upon the origin of the source material and the particulate size (Baker and Jickells 2006; Baker et al. 2006; Stockdale et al. 2016). While dust events have been widely studied, there is still much to be learned about what impact they have on biological and chemical components in the marine systems into which they settle.

One limitation to studying dust events is their episodic and infrequent nature. This has led to few *in situ* investigations of Saharan dust deposition as it naturally occurs (Bonnet and Guieu 2006; Hill et al. 2010). To understand what is happening to the marine system during a dust event, most studies have relied on experimental incubations with dust or dust proxies (Mills et al. 2004; Herut et al. 2005; Duarte et al. 2006; Davey et al. 2008; Lekunberri et al. 2010; Guieu et al. 2010, 2014a; Hill et al. 2010; Laghdass et al. 2011; Langlois et al. 2012; Pulido-Villena et al. 2014; Westrich et al. 2016; Guo et al. 2016; Marín et al. 2017; Tsiola et al. 2017; Lagaria et al. 2017). Experimental mesocosms allow for control of many aspects, including the conditions before, during, and after a dust addition is made, and the exact amount of dust added.

The high nutrient content of desert dust has been shown to cause changes in microbial community structure and function (Mills et al. 2004; Herut et al. 2005; Davey et al. 2008; Pulido-Villena et al. 2008, 2014; Laghdass et al. 2011; Langlois et al. 2012; Guieu et al. 2014a; Westrich et al. 2016; Marín et al. 2017). Studies have found changes in the autotrophic (Lenes et

al. 2001; Mills et al. 2004; Davey et al. 2008; Langlois et al. 2012), heterotrophic (Laghdass et al. 2011; Westrich et al. 2016), and viral communities (Guieu et al. 2014a; b; Pulido-Villena et al. 2014) along with both increases and decreases of individual taxa. While results differ due to the location of the study and the amount or form of dust added, there seem to be groups that benefit and are hindered by dust addition. The Atlantic Ocean receives the highest percent of Saharan dust at around 42% (202 Tg yr⁻¹), and the Mediterranean Sea receives around 8% (40 Tg yr⁻¹) (Guerzoni et al. 1999; Jickells 2005; Guieu et al. 2014a). Due to this, most incubation experiments have taken place in these two areas. This review discusses the changes in the biotic and abiotic factors in *in situ* and mesocosms based studies in the North Atlantic Ocean and Mediterranean Sea.

NORTH ATLANTIC OCEAN

Nutrient Limitation:

Although the Atlantic Ocean receives the highest annual dust deposition, the area over which it settles is vast. Various studies have demonstrated differing nutrient limitations throughout different regions of the North Atlantic Ocean. The eastern coast of Florida is likely iron limited, at least for the heterotrophic community (Westrich et al. 2016), the western coast of Florida is limited by iron (Lenes et al. 2001), and the Sargasso Sea is likely limited by a combination of nitrogen, phosphorus, or iron (Menzel and Ryther 1961; Wu et al. 2000; Moore et al. 2008). The region closest to the western coast of Africa has been shown to experience nitrogen, phosphorus, or iron limitation depending upon the organism and precise location (Mills et al. 2004; Davey et al. 2008). Coastal anthropogenic input and upwelling events can also change the nature and degree of nutrient limitation in the areas where they occur (Duarte et al. 2006; Lin et al. 2016).

North Atlantic Studies:

While no studies have reported the changes seen to the whole bacterial community, individual members have been investigated. These groups include cyanobacteria like *Prochlorococcus* and *Trichodesmium*, and heterotrophs like SAR-11 and the *Vibrio* community (Lenes et al. 2001; Mills et al. 2004; Duarte et al. 2006; Davey et al. 2008; Hill et al. 2010; Langlois et al. 2012; Westrich et al. 2016). Lenes and Westrich focused on the waters around Florida, and the remaining five studies focused off of western Africa.

A recent study investigated the effects of Saharan dust deposition in the Florida Keys (Westrich et al. 2016). The study focused on the heterotrophic population, more specifically, the genus *Vibrio*. Some *Vibrio* species are also well known pathogens, and human infections from *Vibrio* have been on the rise for past 20 years, but many are non-pathogenic members of the global aquatic environment (Grimes et al. 2009; Shaw et al. 2011; Newton et al. 2012). *Vibrio* is normally a small fraction of the bacterial community (0.1%-2.2%) (Oberbeckmann et al. 2012), but increased to more than 20% of identified 16S rRNA sequence reads after an *in situ* dust event in the Florida Keys (Westrich et al. 2016). *Vibrio* has also been identified as a conditionally rare taxon in certain circumstances (Shade et al. 2014). Conditionally rare taxa are groups of organisms that contribute disproportionately to bacterial diversity after a disturbance event, which causes them to dramatically increase. These researchers hypothesized the change seen in *Vibrio* was due to iron in the dust, rather than nitrogen like previous studies in the Atlantic had shown (Mills et al. 2004). The researchers confirmed iron was the limiting nutrient through microcosm experiments where *Vibrio* increased to similar levels (50x-600x) as seen with iron additions.

Iron was also found to be the limiting nutrient for *Trichodesmium* off the western coast of Florida (Lenes et al. 2001). *Trichodesmium* is a well-known nitrogen fixing bacterium, and has a

large impact on the amount of bioavailable nitrogen in marine systems (Capone 1997). Nitrogen fixation also requires high iron due to the high number of iron-sulfur clusters nitrogenase contains (Raven 1988; Rueter 1988). Baseline iron levels were <0.1 nM, but following Saharan dust events increased to an average of 3 nM, reaching up to 16 nM. Post-dust deposition *Trichodesmium* increased up to ten-fold in multiple cases. During the same blooms the researchers saw a marked decrease in both inorganic and organic forms of phosphorus. This indicated that phosphorus was not the limiting nutrient prior to the dust deposition, but the excess phosphorus became available for utilization after iron needs were met.

Off the western coast of Africa, nitrogen was determined as the limiting nutrient for bacterial abundance and carbon fixation, but a combination of iron and phosphorus limited *Trichodesmium* nitrogen fixation (Mills et al. 2004; Davey et al. 2008). When 2 nM iron and 0.2 μ M phosphorus were added in conjunction, between a 2 and 12-fold increase in nitrogen fixation was seen. Neither iron nor phosphorus alone was able to stimulate the same increase. A similar increase in nitrogen fixation was seen when particulate dust additions were made, indicating it supplied both phosphorus and iron. Nitrogen limitation was confirmed for the phytoplankton community when additions of phosphorus, iron, or both did not increase carbon fixation nor chlorophyll *a* (used to measure biomass). When nitrogen was added alone or in conjunction with these other nutrients there was a statistically significant increase in both carbon fixation and chlorophyll *a*.

Finally, other groups discovered changes in the microbial community off the western coast of Africa after dust additions to experimental microcosms. One group found that atmospheric inputs increased the productivity of autotrophic communities much more than heterotrophic communities, and saw little change in bacterial abundance or production (Duarte et

al. 2006). Another group saw that when dust or dust leachate was added to a microcosm there was a decrease in the SAR-11 group and *Prochlorococcus* (Hill et al. 2010).

MEDITERRANEAN SEA

Nutrient Limitation:

Through the use of incubation studies, microbial growth in the Mediterranean Sea is identified to be limited by phosphorus, nitrogen or a combination of both (Krom et al. 1991; Thingstad et al. 2005; Tanaka et al. 2011; Moore et al. 2013). The southeastern Mediterranean Sea has been documented to have phosphorus limitation (Krom et al. 1991; Thingstad et al. 2005). Another study that investigated the Western, Ionian and Levantine basins of the Mediterranean found various limitations (Tanaka et al. 2011). These include nitrogen limitation for the autotrophic community, a combination of nitrogen and phosphorus limitation in the Levantine basin, nitrogen limitation in the Ionian Basin, and limitation by an uninvestigated nutrient in the Western basin. Similar to the North Atlantic, nutrient limitation is variable for different regions and can be limited by multiple factors (Tanaka et al. 2011).

Mediterranean Sea Studies:

While the majority of Saharan dust deposition occurs in the North Atlantic the Mediterranean Sea also receives a heavy dust loading of about 40 Tg yr⁻¹ (Mahowald et al. 2010). Due to the heavy dust load in this area a large number of studies have been focused on the impacts to this marine system. Research has shown effects on members of the autotrophic (Ridame and Guieu 2002; Herut et al. 2005), heterotrophic (Laghdass et al. 2011; Marín et al. 2017), and viral members (Pulido-Villena et al. 2008) of the microbial community. It also has strong effects on the structure and function of the overall microbial community including

makeup, abundance and production (Ridame and Guieu 2002; Laghdass et al. 2011; Pulido-Villena et al. 2014; Tsiola et al. 2017).

One study noted similar changes in both an *in situ* dust event and mesocosm based experiments (Herut et al. 2005). The *in situ* event led to a large increase in the phosphorus turnover time. *Prochlorococcus* decreased in the upper 25 m of the water column, but no decrease was seen in *Synechococcus*. Adding particulate dust to the mesocosm experiments increased phosphorus turnover times by ~10-fold, but this quickly returned to base levels. Adding dust leachate however, did not stimulate the same effect, indicating that the particulate dust plays a role in the response seen. The response of *Synechococcus* and *Prochlorococcus* was similar, but not identical, between the mesocosm experiments and *in situ*. An increase was seen in *Synechococcus* alongside a decrease in *Prochlorococcus*, but particulate dust increased *Synechococcus* by 3-fold, but only 1.4-fold with leached dust. *Prochlorococcus* became undetectable with particulate dust, but was unchanged in the leached experiment, again supporting the idea that the particulate form of dust is important.

Other studies have been run in the Mediterranean investigating abundance and respiration of the bacterial community. A group comparing the differences between anthropogenic input vs. mineral dust input found that mineral dust increased bacterial abundance greater than anthropogenic input, but bacterial respiration was amplified more by anthropogenic input (Marín et al. 2017). Another group saw increases in both bacterial abundance and respiration after Saharan dust and mixed dust deposition, but also found there was an increase in viral and flagellate lysis (Tsiola et al. 2017).

One particular study site that has been commissioned twice to investigate Saharan dust deposition is the Scandola Nature Reserve. It is a remote, coastal, low-nutrient, low-chlorophyll

area with no rivers for runoff, very little boat traffic, and no large industrial inputs from surrounding areas, making it a pristine site to perform these experiments (Guieu et al. 2014a). The DUNE (a DUst experiment in a low-Nutrient, low-chlorophyll Ecosystem) (Guieu et al. 2010, 2014a) project was a large undertaking by multiple universities in Europe utilizing large, 2.3 m in diameter, 12.5 m deep mesocosms that held 52 m³ of water, and had many published papers documenting aspects of change in the mesocosms. The setup consisted of three containers as control mesocosms (no additions) and three as experimental dust mesocosms. Due to the complications of collecting large amounts of atmospheric dust, the group used a protocol to age sand collected directly from the Saharan Desert (Guieu et al. 2014a), which aimed to mimic the atmospheric transport that natural dust experiences while traveling in the upper atmosphere. The studies investigated a single dry (DUNE-1-Q) and single wet (DUNE-1-P) deposition during the first round of experiments, and two successional wet deposition events in the second round (DUNE-2-R). Sampling and analysis was performed daily for the entire length of both experiments with multiple sampling events taking place on days when dust was added.

The results show that dust deposition had many effects on the system, including effects on both the macro- and micronutrients present (Ye et al. 2011; Wuttig et al. 2013; Guieu et al. 2014b; Ridame et al. 2014) and the activity and composition of the microbial community (Laghdass et al. 2011; Pulido-Villena et al. 2014; Ridame et al. 2014). During DUNE-1-Q (dry deposition) there was little to no change seen in the chlorophyll-*a* concentrations, nitrogen measurements, nor primary productivity (Ridame et al. 2014), but there was almost an immediate, long-lasting increase seen in DUNE-1-P and DUNE-2-R (wet depositions) in these three measurements and in phosphate. The researchers believe this result is due to the wet

deposition dissolving the nutrients that are present allowing for more change to occur in the system.

Iron levels had unexpected changes after dust addition was made. An initial decrease was noted in both DUNE-1-P (Ye et al. 2011) and DUNE-2-R (Wuttig et al. 2013), but after a second seeding event in DUNE-2-R the dissolved iron increased. Researchers believed the decrease was due to scavenging of dissolved iron from the particulate dust from the first event, which took iron out of the system. They believe the second dust addition caused an increase in dissolved iron due to more iron binding ligands produced by the bacterial community after the first addition. Aluminum and manganese both increased after the both wet depositions (Wuttig et al. 2013).

Dust also impacted the biological community. All three experiments saw shifts in the microbial population with changing abundances across many different groups. Some of the groups that saw increases include members of the *Gammaproteobacteria* and *Synechococcus*, while members of the *Bacteroidetes* decreased (Laghdass et al. 2011). During DUNE-2-R (wet deposition) a small increase in bacterial abundance was seen during the first seeding event, but the second seeding did not lead to increased bacterial abundance, although an increase in viral abundance was seen after the second seeding (Pulido-Villena et al. 2008). The researchers also saw a change in the bacterial community composition after the first seeding although a diminished impact was noted after the second addition.

Overall, atmospheric transport and deposition of desert dust-derived aerosols impact many biotic and abiotic factors of marine systems. Dust deposition in marine surface waters are thought to cause changes in both macro- and micronutrients, as well as substantial shifts in both viral and bacterial abundance, and alterations in microbial community composition.

Due to practical consideration, many of the studies conducted to date that investigate the effects of dust deposition have utilized mesocosms and simulated dust deposition events. While these incubation-based studies are informative, questions remain regarding the extent to which these simulated dust deposition events accurately represent *in situ* responses to natural dust deposition events. The study presented herein represents a time series of physical, chemical, and biological measurements of marine surface waters impacted by Saharan dust deposition. The *in situ* investigation is complemented with incubation studies in an attempt to evaluate alterations in nutrient limitation and to disentangle microbial community responses due to dust from observed changes due to hydrological dynamics. Together, these efforts are shedding new light on the role of Saharan dust in structuring marine microbial communities and shaping global biogeochemical cycles.

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CHAPTER 2

THE IMPACT OF SAHARAN DUST DEPOSITION ON BACTERIOPLANKTON IN MARINE SURFACE WATER¹

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ABSTRACT

Particulate dust is regularly blown into the atmosphere by high winds where it is then globally transported by atmospheric circulation. Work using experimental microcosms and simulated dust events has suggested that deposition of this dust has large impacts on marine microbial community structure and function. However, few studies have captured community responses to dust storms *in situ*. In the summer of 2016, our group collected 21 samples over a 26-day time series at Looe Key Marine Sanctuary, in Florida. Within this time series, we identified a period of elevated atmospheric dust content that corresponded with changes in microbial community composition as measured by 16S rRNA gene amplicon sequencing. Following dust deposition events, we observed changes in bacterial abundance and the relative abundance of major marine bacterial lineages such as *Prochlorococcus*, *Synechococcus*, and *Pelagibacteraceae*. In addition, less abundant, opportunistic taxa such as *Vibrionales*, *Cryomorpaceae*, and members of the *Rhodobacteraceae* and *Flavobacteriaceae* showed significant relative increases in abundance post-deposition. Experimental incubations of unamended seawater collected immediately following a dust deposition event showed similar shifts in the microbial community as seen in samples collected *in situ*. However, incubations of seawater with nutrients found in dust did not lead to an increase in bacterial abundance. Together, these results suggest that 1.) Saharan dust deposition events drive large shifts in marine surface water microbial communities, and 2.) these responses are not easily simulated through the addition of individual dust constituents.

INTRODUCTION

Every year mass desert dust transport and deposition occurs across the planet, 69% of which originates in the Saharan desert region (Muhammad Akhlaq et al. 2012). In marine waters, desert dust deposition has been demonstrated to provide key nutrients including, but not limited to carbon (Pulido-Villena et al. 2008; Lekunberri et al. 2010), nitrogen (Loÿe-Pilot et al. 1990), phosphorus (Mills et al. 2004), and trace metals like iron, copper, and aluminum (Duce and Tindale 1991; Duce et al. 1991; Lenés et al. 2001; Bonnet and Guieu 2006; Duarte et al. 2006; Moore et al. 2013; Wuttig et al. 2013). The added nutrients from dust alter marine microbial community structure and function in surface waters in the North Atlantic (Lenés et al. 2001; Mills et al. 2004; Hill et al. 2010; Langlois et al. 2012; Westrich et al. 2016) and in the Mediterranean Sea (Lekunberri et al. 2010; Guieu et al. 2014c; Guo et al. 2016a).

A number of studies have used mesocosms to explore the impact of dust on marine microbial communities (Mills et al. 2004; Duarte et al. 2006; Davey et al. 2008; Pulido-Villena et al. 2008, 2014, Guieu et al. 2010, 2014c; Hill et al. 2010; Laghdass et al. 2011; Langlois et al. 2012). Results from various mesocosm studies in the North Atlantic indicate that the addition of particulate desert dust, or dust leachate could relieve various nutrient limitations, especially iron, phosphorus, or a combination of the two (Mills et al. 2004; Davey et al. 2008; Langlois et al. 2012; Westrich et al. 2016). Relief of this limitation via dust leads to an increase in *Vibrio* growth (Westrich et al. 2016) or an increase in nitrogen fixation (Lenés et al. 2001; Mills et al. 2004; Davey et al. 2008). Experiments based in the Mediterranean showed shifts in the microbial community (Laghdass et al. 2011; Pulido-Villena et al. 2014), increases in dissolved nutrients (Wuttig et al. 2013), and an increase in both heterotrophic and autotrophic communities (Lekunberri et al. 2010; Marín et al. 2017).

Most *in situ* studies of marine microbial community responses to desert dust deposition have focused on changes in specific bacterial groups after dust deposition. Four Saharan dust events were studied off the western coast of Florida, and up to a 100-fold increase in *Trichodesmium* was seen, thus leading to an increase in nitrogen fixation (Lenes et al. 2001). The increase in *Trichodesmium* was attributed to relief in iron limitation. Similar increases in *Trichodesmium* results were seen by Langlois (2012) off the western coast of Africa, but this environment was limited by both iron and phosphorus. Finally, Westrich (2016) showed a large bloom of *Vibrio* both *in situ* and in a microcosm incubation, potentially due to relief of iron limitation.

To examine generalized microbial community responses to dust deposition, we have collected a daily time series of surface water samples at Looe Key reef in the Florida Keys National Marine Sanctuary (Florida, USA). The tropical northeast Atlantic Ocean is a well-documented oligotrophic area often limited by nitrogen, phosphorus, and iron (Lenes et al. 2001; Moore et al. 2013; Westrich et al. 2016). Due to the oligotrophic nature of this area, we determined this would be a fruitful location for the study of the marine microbial community to atmospherically transported desert dust.

This study focuses specifically on the microbial community of the ocean and its composition before, immediately following, and the days after a period of elevated atmospheric dust. To complement this approach, we incubated water collected from our sample site to ensure the incubated community changes observed mimicked those seen *in situ*. This showed that changes in community composition were due to dust events and not shifting bodies of water bringing in new communities. To our knowledge, this represents the first in-depth analysis of *in*

situ changes in the composition of marine surface water bacterioplankton community following dust deposition.

MATERIALS AND METHODS

***In situ* sample collection and filtration**

Between July 12th and August 6th, 2016 water samples were collected at <0.5 m depth at Looe Key Reef (N24° 32'41.42", W81°24'33.098") in 1 L sterile polypropylene bottles, after rinsing (3 x), and stored immediately on ice. No samples were collected on July 17th – 21st or August 2nd due to adverse weather conditions, and all samples were collected between 10:45 and 14:00 (Table S2.1). Aerosol collection and measurement was conducted on Big Pine Key (N24°38'4.16", W81°21'17.02"). Samples were collected approximately every 24 hr between 18:00 and 22:00 at ground level with a high-volume air sampler (model 5170-VBL, Tisch Environmental, Cleves, OH), which pulls air at approximately 1.2 m³ min⁻¹ through 12 replicate acid washed 47 mm nitrocellulose filter disks (Whatman 41, GE Healthcare Bio-Sciences, Pittsburgh, PA). Filters were frozen until analysis (Figure S2.1).

Instantaneous current speed and direction was measured every 10 min using a Marotte HS current meter (Marine Geophysics Lab, James Cook University, Queensland, Australia), which was attached to an anchor point on the reef at ~8 m deep sampling. The salinity was measured with a DS5X multiparameter Sonde (Hach, Loveland, CO) attached to a fixed location ~1 m deep and sampled every 20 min. A HOBO data logger UA-002-08 was attached ~8 m deep to measure the temperature every 10 min (Onset, Bourne, MA). Aerosol optical thickness was tracked using satellite and modeling products from NASA (<https://worldview.earthdata.nasa.gov/>), and the Naval Research Laboratory (www.nrlmry.navy.mil/aerosol/) (Westphal et al. 2009; Lynch et al. 2016).

Particulate and dissolved Fe measurement in seawater samples

Seawater samples were processed for dissolved Fe by the Mg-Fe coprecipitation isotope dilution method described in Saito and Schneider (2008). Briefly, 15 mL subsamples of acidified seawater were spiked with an Fe standard enriched in Fe^{57} over natural abundance. The samples were then buffered with 7.25 M ammonium hydroxide, resulting in the precipitation of Mg to $Mg(OH)_2(s)$ as well as the pre-concentration of Fe with the $Mg(OH)_2(s)$. The samples were centrifuged for 1 min and then decanted, leaving a pellet in the centrifuge tube. The pellet was re-dissolved in 1 mL of 0.32 M HNO_3 and analyzed using the Thermo Scientific Element 2 (E2) HR-ICP-MS. The concentration of Fe was calculated using a standard isotope dilution equation. For measurement of dissolved Fe in blanks and nutrient stocks, samples were acidified to 0.32 M with HNO_3 and run on the E2 HR-ICP-MS. Particulate Fe was digested using microwave digestion with concentrated (15.8 M) HNO_3 and concentrated (28 M) HF to dissolve the particulate matter. Samples were analyzed using the E2 ICP-MS. Fe concentrations were calculated using an external standard calibration.

Total and dissolved Fe in aerosols

Particulate matter captured on the high volume air sampler filters was leached. Instantaneous aerosol leaches (a.k.a. ultra-high purity (UHP)-soluble) were conducted using the method described in Buck et al. (2010) which uses UHP deionized water ($>18 M\Omega \cdot cm$; $pH = 6.0$). Total Fe concentrations were digested using a microwave digestion scheme with concentrated HNO_3 (15.8 M) and concentrated HF (28.9 M) proposed in Morton et al. (2013). All samples were analyzed using the E2 ICP-MS. Fe concentrations were calculated using an external standard calibration (0 ppb, 0.1 ppb, 1 ppb, 10 ppb, 20 ppb, 100 ppb), (High-Purity Standards, Charleston, SC).

Seawater nutrient measurement

Seawater samples were hand dipped and stored in shade. Inorganic nutrients were determined using filtrates that were passed through a 25 mm GF/F filter and stored frozen (-20°C) until analysis. After thawing to room temperature, samples were analyzed on a Seal QuAAtro autoanalyzer at Texas A&M- Corpus Christi. Standard curves with five different concentrations were run daily at the beginning of each run. Fresh standards were made prior to each run by diluting a primary standard with low nutrient surface seawater. Deionized water (DIW) was used as a blank, and DIW blanks were run at the beginning and end of each run, as well as after every 8-10 samples to correct for baseline shifts.

Nutrient addition experiment

Microbial growth responses to nutrient additions were evaluated daily using small-scale experimental incubations. Seawater samples were collected by submerging a closed, trace metal free bottle, removing the cap underwater, filling the bottle, rinsing three times, and on the final fill recapping to prevent contamination from the air-water interface. Samples were stored in shade until the experiment could be started, within 3 hr of collection.

Incubations were performed in trace metal free 15 mL polypropylene tubes (VWR, Radnor, PA). 12 mL of collected water were decanted into six tubes using trace metal clean techniques. 2 mL of the preaddition sample was immediately fixed in glutaraldehyde at a final concentration of 1% (v/v), inverted multiple times, and placed at -80°C. The remaining 10 mL sample was spun at 5400 x g for 20 min, supernatant fluid decanted, and the pellet was stored at -80°C. Four of the remaining tubes had single substrate or nutrients added in the following concentrations, acetate (+30 µM), phosphate (+0.2 µM KH₂PO₄), iron (+2 nM FeCl₃), and nitrate (+1.0 µM NaNO₃); the final tube was used as a negative control with no addition. After addition,

tubes were incubated shaking for 24 hr (~30°C). After incubation, microbial samples were collected and fixed as described above.

Cell counting

Glutaraldehyde fixed cells were stored at -80°C. Samples were thawed at room temperature and stained following Tripp (2008) with one alteration, that samples were incubated for 30 min before measurement rather than for 1 hr. Staining was done, and samples were counted in triplicate on a Beckman Coulter CytoFLEX (Beckman Coulter Inc., Indianapolis, IN) for 30 seconds with a 15 sec back flush between each sample to ensure cells were removed from the flow cell. Gates were chosen based upon blank sample patterns, size, and fluorescence pattern.

Water filtration and community DNA extraction for microbial community analysis

Seawater samples were filtered ~1 hr after collection. Water was filtered in-line using Masterflex L/S Precision Modular Drive peristaltic pump (Cole-Parmer, Vernon Hills, IL) with L/S 15 Masterflex tubing through a 5.0 µm Durapore prefilter (EDM Millipore, Darmstadt, Germany) (to capture debris and eukaryotic cells) followed by a final filter through a 25 mm 0.22 µm pore size Durapore membrane to collect bacterial fraction. Filters were immediately frozen and stored at -80°C until DNA extraction.

Total microbial community DNA was extracted from these filters using a modified version of the Omega Bio-tek EZNA Bacterial DNA kit (Omega Bio-tek, Inc., Norcross, GA) (Manual Rev. January 2016). The filters were cut into quarters using a flame sterilized forceps and scissors. These pieces were placed into a single tube for digestion in 20 µl of kit-supplied lysozyme (50 mg/mL) with 200 µL of 1X TE buffer, and incubated for 30 min with shaking (1000 RPM), at 37°C in eppendorf Thermomixer (eppendorf, Hauppauge, NY). After lysozyme

treatment, 100 mg sterilized glass beads were added, after which the samples were shaken at 3000 RPM on a bench-top vortex (Fisher Scientific, Hampton, NH) for 5 min. 200 μ L of TL buffer and 40 μ L of kit-supplied Proteinase K (20 mg/mL) were then added, and the tubes were incubated at 55°C for 1 hr shaking at 600 RPM. Following this incubation, samples were processed as the kit suggests from step 13, with volumes scaled proportionally to the previously increased volumes added. After elution with 50 μ l of 10 mM Tris HCl pH 8.5, DNA concentration and quality was measured using a NanoDrop lite (Thermo Fisher Scientific). Purified DNA was stored at -20°C until PCR amplification.

24-hour incubations of marine surface water for microbial community analysis

Water for experimental incubations was also collected off Looe Key Reef with a peristaltic pump and acid washed, trace metal free silicone tubing. Tubing inlet was ~2 m upcurrent from the boat at ~1 m depth. A 200 μ m acid washed Nitex mesh was placed over the end of the tubing to exclude collection of large debris and clumps of *Trichodesmium* cells. To minimize bottle-to-bottle variability, the water for all experiments was pumped into two acid-washed 50 L carboys simultaneously. Incubation experiments were started within 3 hr of collection.

The incubation experiments were repeated five times on July 16th, 21st, 26th, 29th, and 31st, and run in triplicate. 1 L samples were collected from each 50 L carboy for starting microbial community analyses. For each experiment, seawater was distributed into 3 different acid-washed 4 L Cubitainers (VWR, Radnor, PA). Samples were incubated using an outdoor, groundwater fed, flow-through incubator with 50% light attenuation. After incubation, samples were dispensed into clean bottles from acid-washed spigots on the cubitainer. 1 L from each

incubation was filtered, stored, and subjected to 16S rRNA gene amplicon library and preparation using the same methods as the *in situ* samples.

Library preparation and sequencing

The V4 region of the 16S rRNA gene was amplified for each extracted filter using a two-step PCR method as described by Tinker and Ottesen (2016). In brief, DNA was first amplified using un-barcoded 515F and 806R primers (15 cycles), followed by a second PCR amplification (10 cycles) using extended primers for incorporation of barcodes and Illumina adaptors. Following the second amplification, products were purified using a slightly modified protocol of the Omega E.Z.N.A. Cycle-Pure Kit (2014 version) with the following modifications: 5 volumes of kit-supplied CP buffer were added to the amplicons (step 1), only 500 μ L of DNA Wash Buffer was used for the second wash (step 13), and purified product was eluted in 30 μ L of elution buffer (step 16). PCR reaction success was verified via gel electrophoresis, and product concentration was measured using a NanoDrop lite.

For Illumina sequencing, PCR products from all samples were pooled to equimolar concentrations. These pooled libraries were submitted to the Georgia Genomics Facility for sequencing with custom primers (Caporaso et al. 2011) via manufacturer protocols (Illumina Miseq 250 x 250 base pairs; Illumina Inc., San Diego, CA).

Data analysis and visualization

Analysis of the sequence data was done using a combination of bioinformatic software and packages. Raw sequence data were processed using the mothur software package (Schloss et al. 2009). The MiSeq standard operating procedure was used with minor modifications: 1) Version 123 of the Silva database (Quast et al. 2013) was used to align the sequences. 2) Chimeras were removed using UCHIME (Edgar et al. 2011), 3) the Wang taxonomic

classification method was used, and 4) the sequences were classified using the Green Genes database (DeSantis et al. 2006). The number of sequences was brought from 5,253,049 raw sequences down to 3,207,059 filtered and classified sequences per sample (Table S2.2).

Using mothur, sequences were binned into either 97 percent identity OTUs, which yielded 49,240 different OTUs, or by genus, which yielded 1350 different putative genera. Sequence data was analyzed using R version 3.3.1 (R Core Team 2016), R Studio version 1.0.136 (RStudio 2012), vegan version 2.4-2 (Oksanen et al. 2017) and DESeq2 (Love et al. 2014) packages, to generate ordination plots and analyze significantly changing bacterial groups.

Statistical analyses

DESeq2 was used to investigate changing bacterial taxa from sequence data. As replicates were not available for time series data, biological replicates from the experimental incubations (two replicates of each time zero point) were used for estimation of dispersion for use in DESeq2-based identification of significantly changing groups. P adjusted values use the Benjamini-Hochberg adjustment.

NMDS and PCA plots were generated using the vegan package (Oksanen et al. 2017) in R (R Core Team 2016). NMDS used weighted Bray-Curtis dissimilarity without autotransformation. The NMDS plots were generated using either OTU level classification or genus-level classification in mothur (Schloss et al. 2009). Vector fitting for environmental data to NMDS and PCA were done using the EnvFit algorithm in the vegan package (Oksanen et al. 2017). P-values are based on 10,000 random permutations of sample labels. The environmental variables were shifted one day. P-values (<0.01 reported) are calculated as the proportion of times a randomized R^2 value is equal to or greater than the observed R^2 value (Table S2.3).

Spearman's ranks were calculated using R (R Core Team 2016). Correlations with biological and chemical parameters of the water were made using the average dust aerosol optical thickness (AOT) for 24 hr from 12:00 - 12:00 each day as water samples were collected closest to this time. Correlations with filter iron concentrations were made using the average dust AOT from 18:00 - 18:00 as filters were collected closest to this time. Comparison of dust AOT measurement periods was done using an unpaired, heteroscedastic, two-tailed Student's t-Test.

RESULTS AND DISCUSSION

Atmospheric and surface aerosol dust content and composition

Atmospheric dust was evaluated through two methods. First, the Navy Aerosol Analysis and Prediction System (NAAPS) estimated the aerosol optical thickness (AOT) through satellite measurements of the natural logarithm of the ratio of incident to transmitted radiant power through the atmosphere (Lynch et al. 2016). The dust component of optical thickness was modeled as described by Westphal et al. (2009). Both total and dust AOT showed a small peak prior to our sample collection, followed by a period of relatively low dust AOT (average of 0.051 from July 15th - 27th) and followed by increased AOT for the remaining sampling period (average of 0.105 from July 28th - August 6th). This represents significant elevation over baseline (p value <0.001). Atmospheric dust content (Figure 2.1) over our study site began to increase late on July 27th, peaked at 0.17 at ~00:00 on the 28th, and remained above at or above 0.06 until sampling finished on August 6th (Figure 2.1, Table S2.1). Dust AOT fell to 0.06 at 06:00 on the 31st, which was then followed by a period when dust content was variable, but remained elevated compared to the previously baseline at 0.097. This was followed by followed by an additional peak of 0.17 at 00:00 on August 4th.

The arrival of a significant dust event was also indicated through high volume air sample collection, which exhibited visible colorization of filters beginning July 28th (collected at 16:43 and representing ~24 hr of collection) (Figure S2.1). Filter leachates showed increases in dissolved (dFe) and total (tFe) iron coinciding with elevated dust AOT measurements and colored filters (Figure 2.1). Particulate matter captured on the high volume air sampler filters was evaluated for tFe. tFe was measured as the amount of iron that could be leached from filters through suspension in acidified H₂O. Iron on the filters increased after dust entered the area on July 27th, and exhibited strong peaks on July 29th and August 1st and 4th. Both tFe and dFe in aerosols were significantly associated with modeled dust AOT with a Spearman's rho of 0.924 (p-value <0.001) and 0.895 (p-value <0.001), respectively. The increased dust AOT from very early in our study period could not be confirmed via aerosol collection as it began after the dust AOT increase occurred.

It is interesting to note that these correlations between aerosol iron content and modeled atmospheric dust content were not exact. In particular, there appears to be a lag between the peak dust as seen in the AOT (early on July 28th) and peak aerosol iron content (collected during the July 28th - 29th 24hr period) (Figure 2.1). This may be in part because the atmospheric model contains data integrated across all altitudes, whereas aerosols were collected near the surface. Alternatively, others have noted that the iron content of dust can vary depending on the source location of the dust, which was not modeled for this study (Baker et al. 2006).

Temporal trends in surface water biological and chemical characteristics

When *in situ* biological and chemical parameters were compared to the NAAPS dust AOT, tFe, or dFe there were no significant correlations found (Table S2.4), including if the data was shifted one or two days (data not shown). A sharp increase of dissolved organic carbon

(DOC) and chlorophyll-*a* occurred on August 1st, five days after initial peak dust content, and one day after peak aerosol iron content. An increase of ortho-phosphate followed on August 5th. Minimal change occurred in other forms of nitrogen measured including dissolved organic nitrogen, ammonium, and nitrite.

Due to the high iron found in the aerosol filters we hypothesized there would be an immediate increase in both particulate (pFe) and dissolved (dFe) *in situ* iron. pFe varied from 5-25 nM early in the study period, and saw a large increase from the 29th to the 30th after dust entered the study site, and then stayed between 10-15 nM from July 31st to August 6th. While a slight increase in dFe was observed from the 27th to the 28th, this was followed by a 24 hr decrease in *in situ* dissolved iron (which coincided with peak aerosol iron content). After this initial dip, *in situ* dissolved iron began to increase, peaking on July 31, four days after the initial increase in atmospheric dust. Results similar to this pattern were previously observed in mesocosm experiments in the Mediterranean Sea (Wuttig et al. 2013). This group hypothesized this observation was due to dust particles scavenging the dissolved iron from the system. They found that after a second seeding event, an increase in iron was seen. The researchers suggested that this pattern is seen because ligands produced by microbes during the first deposition were available during the second deposition, which bound the iron and kept it in solution. The increase in iron days after July 28th could have been due to an increase in ligands because of the length of time dust AOT was elevated. Another piece of evidence supporting this hypothesis is that after peak dust AOT on August 4th there was an immediate increase in the *in situ* iron. This increase may have also been due to elevated ligands, which was spurred by the first dust event. Alternatively, another group noted that iron can take multiple days to dissolve in seawater

(Mackey et al. 2015), so the delay of iron could also be due to slow dissolution of iron into the system.

***in situ* changes in bacterial abundance**

Total bacterial abundance varied widely over the time series. It dropped from 1.26×10^6 cells/ml to 6.52×10^5 cells/ml from the 21st to the 28th of July (Figure 2.1). From the 28th, the day dust AOT peaked, to the 29th, there is a steep drop to 1.69×10^5 cells/ml. After July 29th, we observed a steady increase in bacterial abundance to 1.31×10^6 cells/ml until August 1st. While no data is available for August 2nd, similar bacterial abundances were observed on August 3rd-6th.

The cause of the initial decrease in bacterial abundance is unknown. It could be a direct response to dust, as individual components of dust, like copper, can be toxic to members of the bacterial community (Paytan et al. 2009). Alternatively, it may be the result of an increase in bacterial lysis due to viral activity or predation, protozoan grazing, or another unknown cause. Bacterial lysis could further explain subsequent increases in iron, dissolved organic carbon, ortho-phosphate, or chlorophyll-*a* seen in the days after the initial dust event (Figure 2.1). Extensive research suggests that the contents of lysed cells are readily taken up by other cells and used for growth (Proctor and Fuhrman 1990), and that cellular lysis can release a substantial amount of dissolved organic carbon, nitrogen, and phosphorus (Proctor and Fuhrman 1991).

While viral counts were not taken in the course of this study, researchers have previously reported an increase in viral abundance alongside a decrease in the bacterial abundance after dust addition (Pulido-Villena et al. 2014). In addition, we observed evidence of an increase in bacterial predation. A 9.51-fold increase (p adjusted < 0.001) in *Bdellovibrionales* was seen from the 28th to the 29th (Table S2.5). This bacterium is a well-known bacterial predator that invades and lyses other Gram-negative bacteria (Stolp and Starr 1963; Rendulic 2004). Formative studies

on this bacterium found that it had the ability to decrease viable cells 9×10^9 -fold after a 40 hr culture incubation, indicating that it has the potential to greatly affect bacterial cellular lysis (Stolp and Starr 1963).

Small-scale incubations show little bacterial responses to nutrient additions

To investigate the limiting nutrient(s) during our study period, we performed daily 24 hr experimental incubations to determine microbial growth responses to nitrate, phosphate, iron, or acetate additions (Figure 2.2). Previous studies suggested that bacterial growth in this area may be limited by either iron (Lenes et al. 2001; Westrich et al. 2016) or nitrogen (Mills et al. 2004). However, none of the nutrients led to a consistent increase in bacterial abundance as compared to the negative control. 24 hr growth responses were small, with change in total bacterial abundance compared to the negative control ranging from 0.85 to 1.36-fold. The maximum growth response to any one nutrient (vs. negative control) was the iron incubation on August 3rd, which had a 1.36-fold increase.

Overall, the addition of select dust components in purified, chemical forms, did not stimulate growth responses of a scale with those observed *in situ* following dust events. This indicates that either the exact chemical composition or form of nutrients present in dust is key to its impact on microbial growth, or that the limiting nutrients supplied by dust were not among the chemicals added to incubation experiments.

Bacterial community shifts

To identify shifts in the bacterial community composition over the time series, a non-metric multidimensional scaling (NMDS) plot was generated using genus-level classification (Figure 2.3). Bacterial community composition appeared to cluster based on time of collection. Samples collected between the 12th and 16th of July cluster on the bottom left portion of both

plots, indicating they are similar to one another. A large shift is seen between the 16th and the 21st (no samples were collected between these dates due to inclement weather), with the samples collected from 21st to the 24th again clustering together. The community shifts again over the 25th, and settles between the 26th and 28th. After dust entered the system on the 28th there is a large shift in the community, and during the period of elevated dust after the initial increase the daily bacterial communities begin shifting more rapidly, indicating that the overall communities are more dissimilar from one another. A second peak in atmospheric dust content was observed on August 4th. This resulted in a large shift in the community in the genus level NMDS plot.

EnvFit was used to identify environmental variables that may have been influencing the bacterial community. Three different environmental measurements taken showed a correlation with both NMDS plots (p value <0.01). The arrow refers to the gradient of the variable, the length shows the strength of the relationship, while the direction of the arrow indicates those points where the gradient is highest. The water temperature arrow is pointing toward the bottom of the plot, indicating that higher temperatures were seen earlier in the study period (1-2 C°) (Table S2.1). Average current speed of the 24 hr preceding sample collection is pointing toward the right side of the plot. Dust AOT points to the upper portion of the plot, showing that these points had higher dust AOT at the time of their collection.

Following increases in atmospheric dust, a large shift in overall community composition was observed. While no consistent trends are present after this, most points after the 28th trend in the upper portion of the plot, when dust AOT was at its highest. A PCA of the genus based analysis showed similar results, but no environmental variables were significantly correlated (p value <0.01) (Figure S2.2).

Dust deposition impact on bacterial diversity and individual microbial taxa

To identify individual bacterial groups that were affected by dust, OTUs were binned to genus level classifications to simplify presentation and increase statistical power. An overview of microbial responses is presented in Figure 2.4, while changes in the relative abundance of selected groups are presented in Figure 2.5. Fold-change and p adjusted values represent change in genus-level abundance between pairs of dates specified as calculated using DESeq2 (Love et al. 2014) (Table S2.5).

Prior to dust deposition on July 28th, an unclassified *Pelagibacteraceae* and *Prochlorococcus* were the dominant taxa present in the upper water column, comprising between 20%-30% of the overall bacterial community (Figure 2.4 & 2.5). Due to an unknown cause, *Pelagibacteraceae* began declining on the 25th, and between July 24th and the 1st of August, saw a 24-fold decrease (p adjusted = <0.001) and became <1% of the entire microbial community. This initial decrease corresponded with a slight increase in *Prochlorococcus*, which was the dominant phototroph identified in this period. After dust entered our study site on the 28th, *Prochlorococcus* began to decrease, dropping to <1% of the bacterial community from the 28th to the 1st of August experiencing a 23-fold decrease (p adjusted = <0.001) over this period. Both *Pelagibacteraceae* and *Prochlorococcus* are well known for their ability to thrive in oligotrophic environments (Partensky et al. 1999; Giovannoni et al. 2005), and during the period these groups were dominant, nutrients were at their lowest levels. While the cause of the initial *Pelagibacteraceae* decrease is unknown, both groups experienced continued decreases after the initial increase in AOT (Table S2.5). Other scientists have also seen decreases in abundance and metabolic responses in these two taxa after particulate dust addition both *in situ* (Herut et al.

2005) after 90 hr, and in experimental microcosm incubations after 2 day incubations (Hill et al. 2010; Marín et al. 2017).

Synechococcus, which prefers higher nutrient environments to *Prochlorococcus* (Partensky et al. 1999), was approximately 5% of the community from the 21st through the 29th. From the 29th to the 30th, two days after elevated AOT measurements, it increased 4.12-fold (p adjusted <0.001). *Synechococcus* sequences constituted 15-25% of 16S rRNA gene amplicons detected between July 30th and August 6th, with the exception of August 3rd (Table S2.5). On the 3rd it dropped to ~8% of the community, but after a second sharp increase of dust AOT and aerosol iron content on the 4th, it increased 3.37-fold (p adjusted <0.001) to ~25% relative abundance on the 4th and 5th. *Synechococcus* growth following dust addition has been previously reported (Herut et al. 2005; Ridame et al. 2014; Lagaria et al. 2017), although other studies have reported decreases as well (Paytan et al. 2009; Marín et al. 2017).

In addition to the above changes in the dominant taxa, less abundant taxa showed strong shifts over the course of the time series. The decrease in overall bacterial abundance observed on July 29 was accompanied by a large increase in bacterial diversity. On this date, the number of OTUs increased to 7657 from a pre-dust (July 12th-28th) average of 1870. During the pre-dust period the proportion of rare taxa (taxa observed at a relative abundance of < 5% in all samples) comprised an average of 27% of the total bacterial community. This increased to 44% of the community on the 29th, then decreased to an average of 24% from July 29th to August 6th. The increase in relative abundance of rare taxa translated to an increase in Shannon diversity from an average of 4.07 to 5.39 on the 29th, and back down to 3.91 after, but no response was seen to the second period of high dust AOT. It is unclear currently whether this increase in diversity is due to a growth response of “conditionally rare taxa” (Shade et al. 2014), a decrease in the abundance

of previously dominant taxa due to predation or viral lysis, or both. Alternatively, the influx of microbial species could be the direct result of deposition of microbial “hitchhikers” present on aerosol dust (Griffin et al. 2003).

Recent studies have reported that “conditionally rare taxa” play key roles in ocean biogeochemical cycles and responses to disturbance (Shade et al. 2014). Within this group lies the majority of the diversity that occurs in the marine environment. This group includes many heterotrophic organisms like *Vibrio*, which are of particular interest due to their fast doubling time, siderophore production, and ability to quickly scavenge and process nutrients like iron in the environment (Tortell et al. 1999; Maida et al. 2013; Westrich et al. 2016). *Vibrio* species have also been suggested as one of the first responders to Saharan dust input (Westrich et al. 2016). Results from DESeq2 showed a relative increase in the unclassified members of the *Vibrionales* order increased 9.41-fold (p adjusted 0.013) from the 28th to the 29th (Table S2.5).

Along with the initial bloom in rare taxa and changes in the dominant phototrophs discussed above, the increase in atmospheric dust deposition was followed by a succession of blooms among heterotrophic microbial taxa. The first group to increase after the rare taxa was *Cryomorpaceae*, a member of the *Flavobacteriales*. After a 2.83-fold decrease (p adjusted 0.013) on the 28th, *Cryomorpaceae* increased by 5.51-fold (p adjusted <0.001) from the 29th to the 30th. While this is, to our knowledge, the first report of a bloom in *Cryomorpaceae* following dust deposition, a previous study saw a decrease in *Flavobacteriales* members within 3 hr after dust addition (Guo et al. 2016b), while another group saw mixed results after 8 days (Laghdass et al. 2011).

On July 31st *Rhodobacteraceae* increased to its highest level of the study period. DESeq2 showed a 3.72-fold increase (p adjusted = <0.001) from July 30th. Members of the

Rhodobacteraceae like *Roseobacter* were previously shown to increase in microcosm experiments after atmospheric dust input (Guo et al. 2016b), although the response reported in that study was immediate (3 hr). The *Rhodobacteraceae* family are well-known for their ability to acquire and use a wide variety of substrates for growth (Moran et al. 2007), including bacterial lysates.

Finally, an unclassified member of the *Flavobacteriaceae* family increased 2.63-fold (p adjusted = 0.0018) on August 1st causing it to become the most abundant bacterial taxon identified on that day. Members of the *Flavobacteriaceae* are well-known for their ability to digest macromolecules like proteins and polysaccharides (McBride 2014). This increase coincided with the spike of DOC, and chlorophyll-*a* in the water column, which as discussed above may have been a product of increase primary production and/or lysis.

24 hr incubation experiments

To help determine whether changes in the microbial community were due to shifting bodies of water or other extraneous factors like dust input, we collected and incubated water to track the changes that occurred. Water was collected on July 16th, 21st, 26th, 29th, and 31st and microbial community composition was determined prior to and following 24 hr incubation (Figure 2.6, Table S2.6). Two technical replicates of the pre-incubation and three biological replicates of 24 hr incubation communities were sequenced and compared using DESeq2 (Love et al. 2014).

Water collected on July 16th, 26th and 31st showed very few changes from the starting microbial communities. In the incubations on these three days 1, 2, and 4 microbial taxa exhibited statistically significant changes in abundance, respectively. The only changing group on July 16th was *Prochlorococcus*, which had a 2.74-fold (p adjusted 0.02) increase over the 24

hr incubation period. The incubation on July 26th showed a decrease in *Myxococcales* and an increase in *Phycisphaerales*. Finally, the 31st showed a decrease in *Thermoplasmata* and an increase in three *Gammaproteobacteria*.

The other two incubation experiments saw much larger changes in the microbial community. Twenty-nine genera changed during the incubation of the water collected on the 21st. Due to a sampling gap very few biological and chemical parameters were measured leading up to the water collection on the 21st, but 17 of the 29 genera that changed were members of the *Proteobacteria*.

Incubations collected on the 29th (one day after increased dust AOT was measured at our study site), exhibited 51 significantly changing genera. 6 of the 8 genera that significantly changed in the *in situ* time series from the 29th to the 30th (Table S2.5), and 4 of the groups highlighted in Figure 2.5 in the microbial succession dataset, also changed in the experimental incubation from the water collected on the 29th. *Synechococcus*, *Cryomorpaceae*, and *Rhodobacteraceae* all increased after 24 hr of incubation, and *Prochlorococcus* also decreased, mirroring the *in situ* results. While these responses cannot be definitively confirmed to be a dust response, the similarities between changes observed *in situ* and in incubations suggest that the observed changes in microbial abundance were driven by changes in the local abiotic and/or biotic environment rather than the result of hydrological mixing. Furthermore, while similar microbial groups were identified as significantly changing in abundance in both incubations and *in situ*, many groups exhibited larger responses in the incubation. The most notable increase happened in *Cryomorpaceae*, which went from ~3% of the total starting bacterial community to ~21% of the community post-incubation. Unclassified members of the *Rhodobacteraceae* also increased from ~1.5% of the starting community to approximately 10% of the post-incubation

community. This finding suggests that hydrological mixing and/or predation may have limited and/or diluted the intensity of the growth responses observed *in situ*.

CONCLUSIONS

Overall, our results show that after Saharan dust deposition in our study area there were changes in bacterial abundance, community structure, and diversity. Increased atmospheric dust aerosol content as measured via remote sensing corresponded with an increase in the iron content of atmospheric aerosols collected at surface altitudes. However, the concentration of dissolved iron in surface waters did not increase immediately. Instead, an initial decline in dissolved iron in surface waters was followed by an increase ~24 hr later. These data suggest that chemical or microbial transformation of iron contained in dust resulted in a delayed pulse of free, soluble iron in marine surface waters.

The initial decrease in soluble Fe in seawater also corresponded with a decrease in bacterial abundance, increased bacterial diversity, and an increase in the abundance of many low-abundance, opportunistic taxa such as *Vibrionales*. Following this initial response, a succession of community shifts were observed, including a decrease in *Prochlorococcus* and an increase in the relative abundance of *Synechococcus*, *Cryomorphaceae*, *Rhodobacteraceae* and *Flavobacteriaceae*. 24 hr incubation of surface waters resulted in similar microbial community structure shifts, suggesting that these changes were responses to alterations in the local abiotic or biotic environment rather than mixing between disparate water masses. However, addition of individual dust constituents to seawater, including iron, carbon, nitrogen, and phosphorus, failed to stimulate bacterial growth responses either prior to, or concurrent with the increase in atmospheric dust content or changes in community composition. This observation suggests that bacterial growth was not limited by any of the tested nutrients alone, and/or that bacterial

community responses to dust may be in part dependent on the complex chemistry and physical structure of dust aerosols rather than a response to any individual chemical constituent. Taken together, our results suggest that more *in situ* observations of marine surface waters during and following atmospheric dust deposition events will be critical to understanding how atmospheric transport of dust impacts marine biogeochemical cycles.

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FIGURES

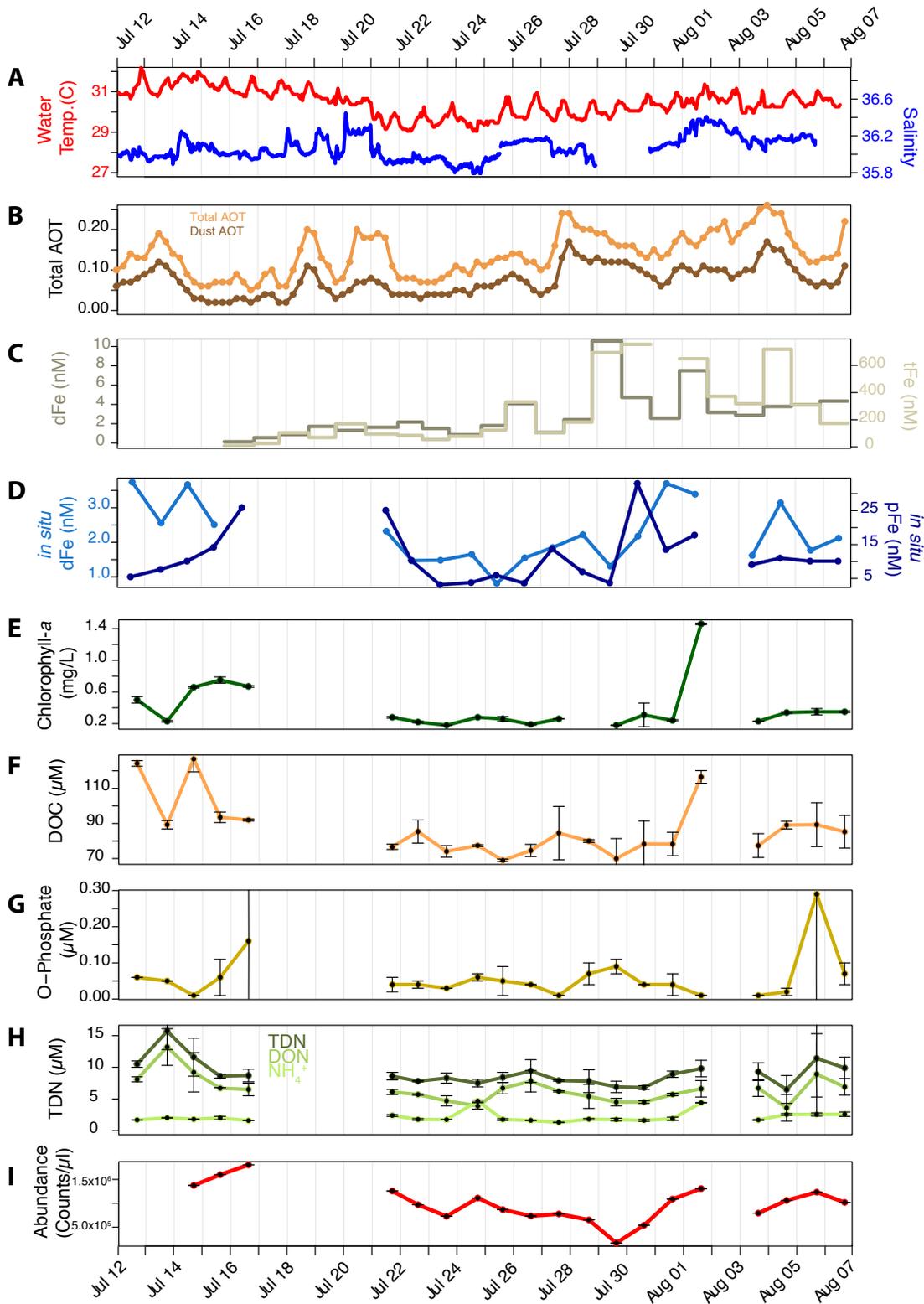


Figure 2.1: Measurements of environmental and biological factors during time series.

Environmental measurements of water and air collected from July 12th through August 6th, 2016. All times are shown in Coordinated Universal Time. Measurements without error bars were collected in singleton. Error bars represent the standard deviation of samples. A) Salinity and temperature were continually measured at Looe Key Reef, apart from a gap due to instrument failure. B) Total and dust AOT are aerosol optical thickness based on NAAPS model using NASA satellite data. C) tFe and dFe: total and dissolved Fe collected in 24 hr integrated samples in filter leachates. D-H) dissolved and particulate iron, chlorophyll, dissolved organic carbon, ortho-phosphate, and three forms of nitrogen (total dissolved nitrogen, dissolved organic nitrogen, and ammonium) from daily *in situ* seawater samples collected over Looe Key Reef. I) Total bacterial abundance (counts/ml) from water collected over Looe Key measured using flow cytometry. Error bars represent technical replicate measurements.

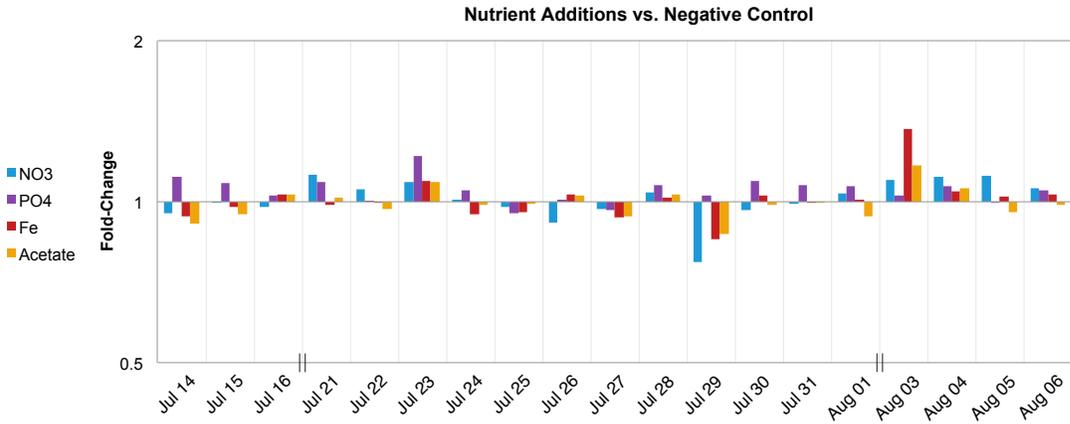


Figure 2.2: Measures of microbial abundance in nutrient addition experiment. Daily incubations to investigate growth responses to nutrient additions. Natural seawater samples were collected daily. 12 mL samples were incubated for 24 hr with 1.) no addition (Neg. control) 2.) +1.0 μM NaNO_3 , 3.) +0.2 μM KH_2PO_4 , 4.) +2 nM FeCl_3 , and +30 μM Acetate. Bacterial abundance was determined at the beginning of the experiment and following 24 hr incubation using flow cytometry.

Looe Genus NMDS EnvFit Shifted One Day P-Value 0.01 Dust AOT

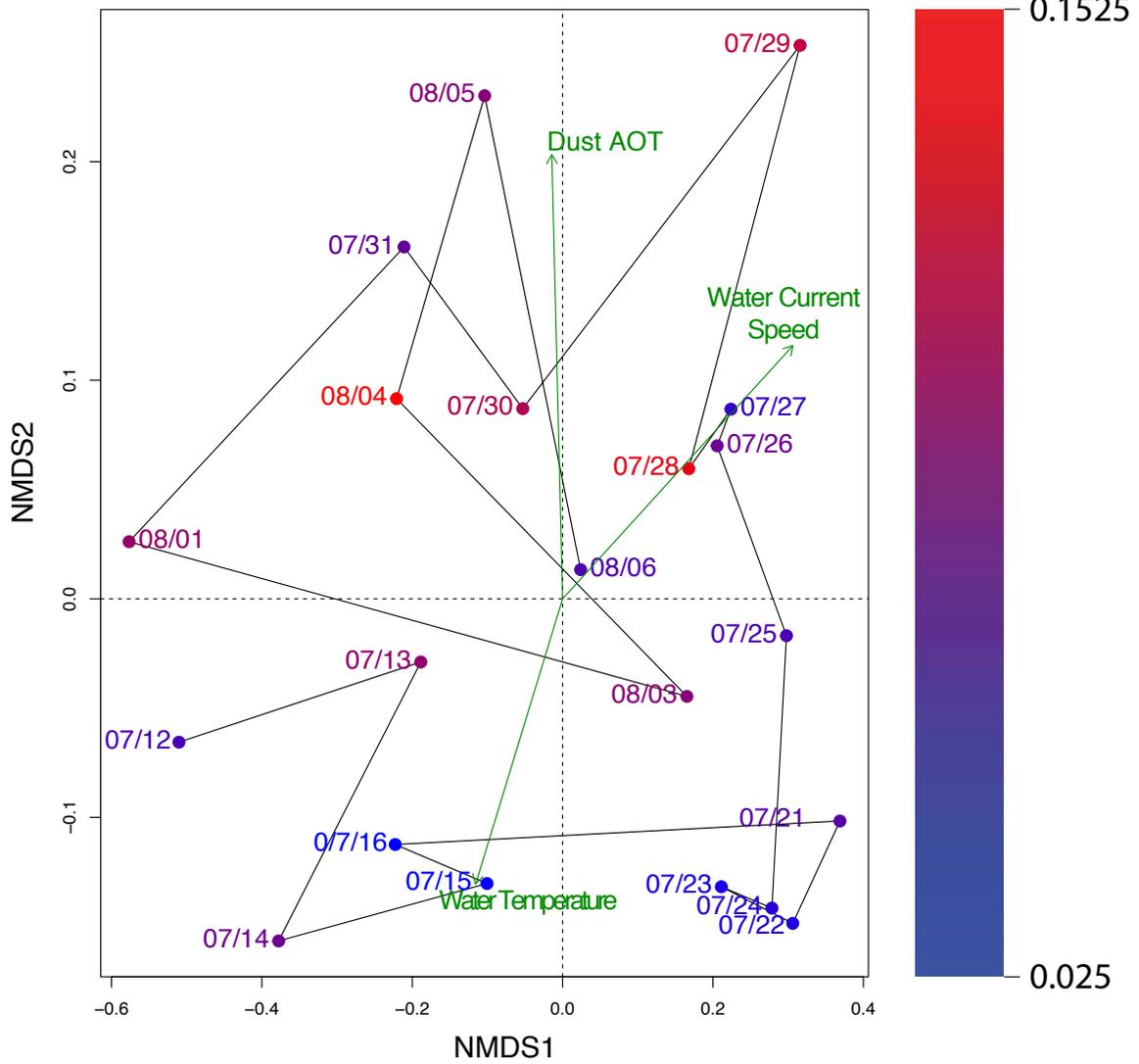


Figure 2.3: NMDS plot of genus level classification with correlated environmental measurements shifted one day. NMDS plot showing changes in bacterial and archaeal community composition. The plot was generated using the vegan package (Oksanen et al. 2017) in R using weighted Bray-Curtis dissimilarity without autotransformation, using genus level classification. Color of points/dates indicates the dust aerosol optical thickness modeled on that day by NAAPS scaled from the lowest thickness to the highest thickness measured during sampling. The more dust measured in the atmosphere, the redder the color of the point. Overlaid green arrows are environmental factors that are strongly correlated with community shifts ($P=0.01$) after being shifted one day using the EnvFit function in vegan package. The environmental variables that did not significantly correlate (p value <0.01) include: total AOT, DOC, TDN, DON, ammonia, nitrite, o-phosphate, silicate, chlorophyll-*a*, dFe, pFe, light intensity, filter dFe or tFe. The environmental variables that correlated <0.05 include: light intensity, filter dFe and tFe, total and dust AOT, average current speed, dissolved *in situ* iron, total dissolved nitrogen and water temperature.

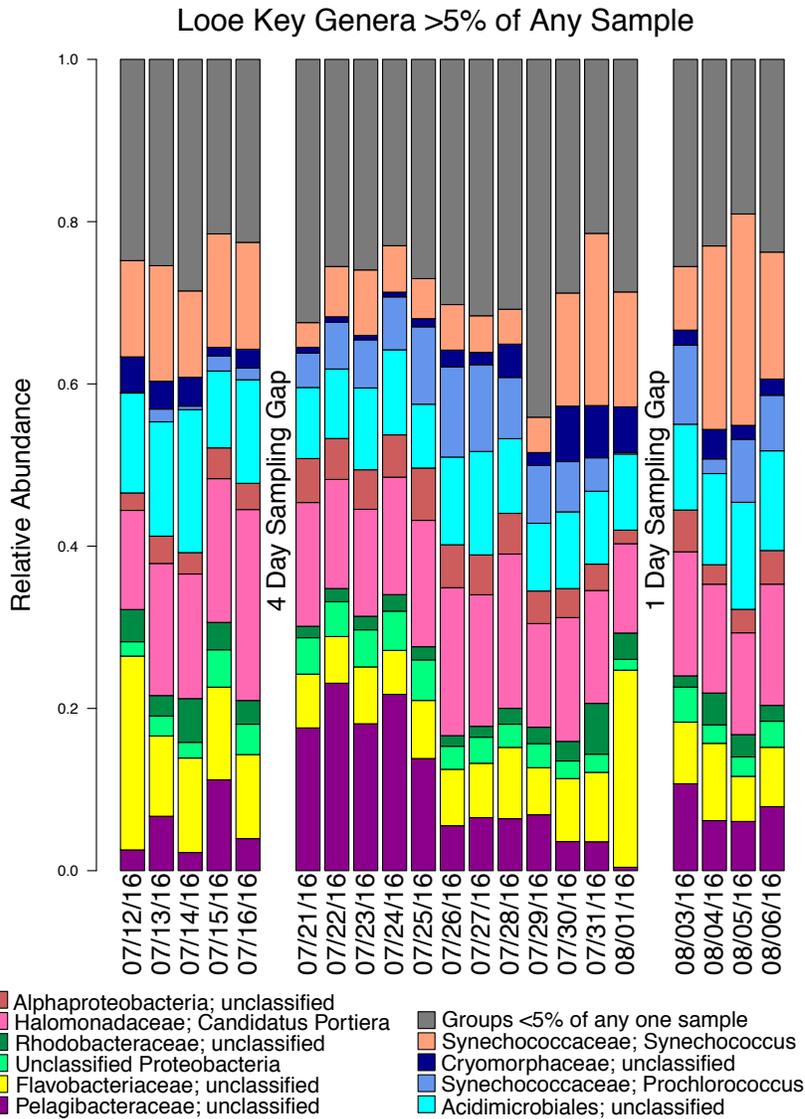


Figure 2.4: Relative abundance of *in situ* microbial taxa >5% of any one sample. Daily water samples over Looe Key Reef were collected and total community DNA was extracted. Bacterial and archaeal 16S rRNA genes were then amplified and sequenced from each daily sample. Colored bars represent the relative abundance of any bacterial genus that is >5% of any one sample, with taxa <5% of samples combined into gray portion. Dust began entering our study site on July 28th and increased aerosol optical thickness continued until study period ended.

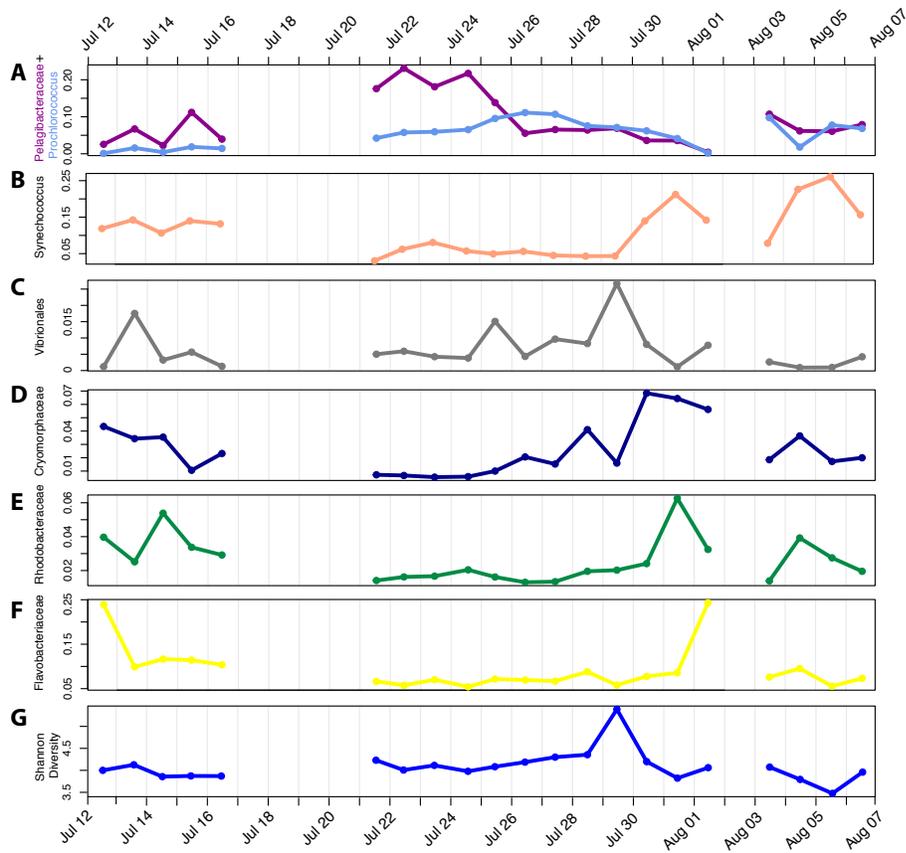


Figure 2.5: Relative abundance changes of individual microbial taxa and Shannon Diversity.

Individual taxa from daily *in situ* bacterial community sequence results that seem to be impacted by dust deposition. A) Relative abundance of *Prochlorococcus* and *Pelagibacteraceae* decrease prior to, and after initial dust deposition B) Relative abundance of *Synechococcus*, which increases after dust deposition. C) *Vibrionales*, a member of the “rare” taxa increased the day after dust deposition began. D-F) *Cryomorphaceae*, *Rhodobacteraceae* and *Flavobacteriaceae* increased the days following initial dust deposition to their highest relative abundance of time series. G) Shannon Diversity during time series, which increased the day after dust entered study site.

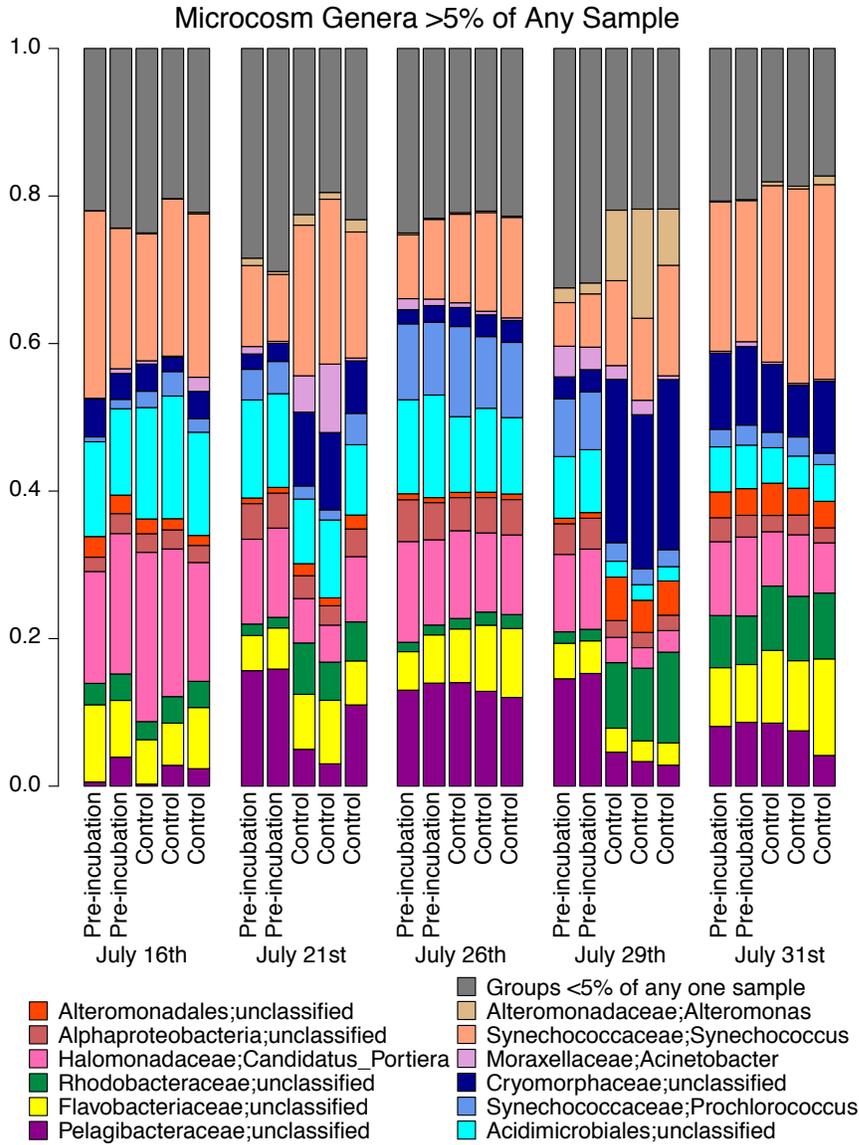


Figure 2.6: Relative abundance of microbial taxa in incubation experiments. Relative abundances of microbial genera representing >5% of any one sample of the microbial community in marine surface water incubation experiments. Incubations used water collected on July 16th, 21st, 26th, 29th, 31st. Two samples were collected pre-incubation, and three control incubations were held for 24 hr. Large shifts occurred in the microbial community after incubation of water collected on July 21st and 29th, but few changes were seen in water collected on July 16th, 26th, and 31st.

SUPPLEMENT

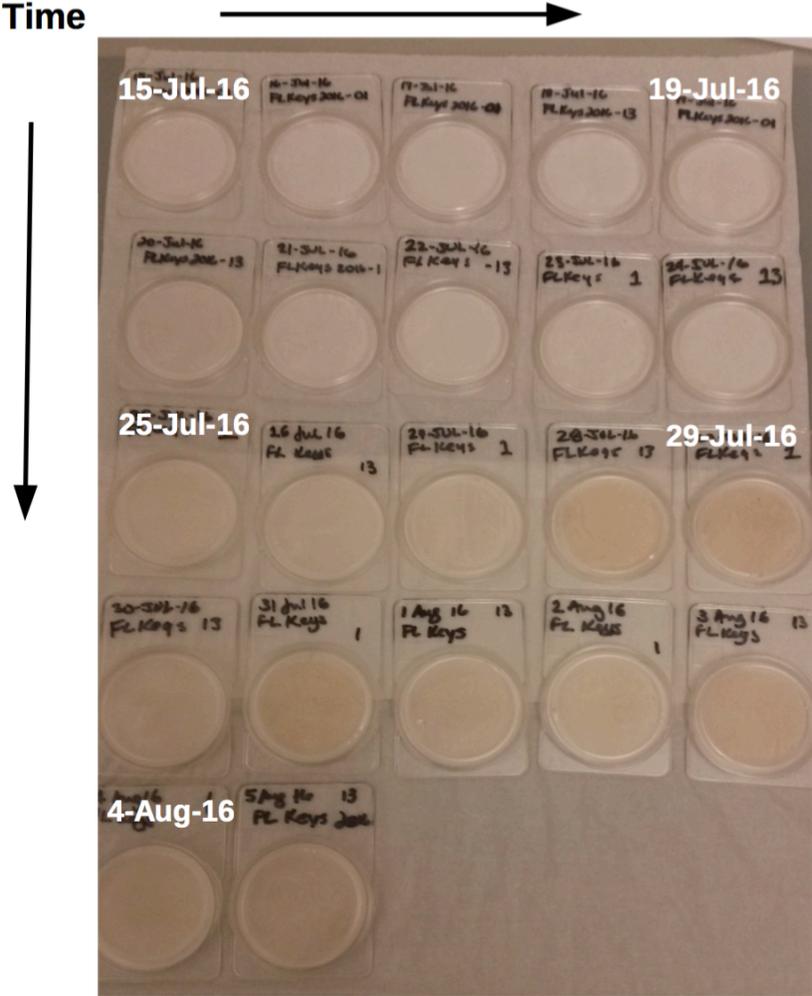


Figure S2.1: Aerosol dust captured on Whatman filters. Whatman filters used to collect aerosol particulate matter on high volume air sampler over a 24 hr period. Samples were collected on Big Pine Key. Dust aerosol optical thickness measurements showed an increase at 00:00 on July 28th, which is when filters begin appearing colored.

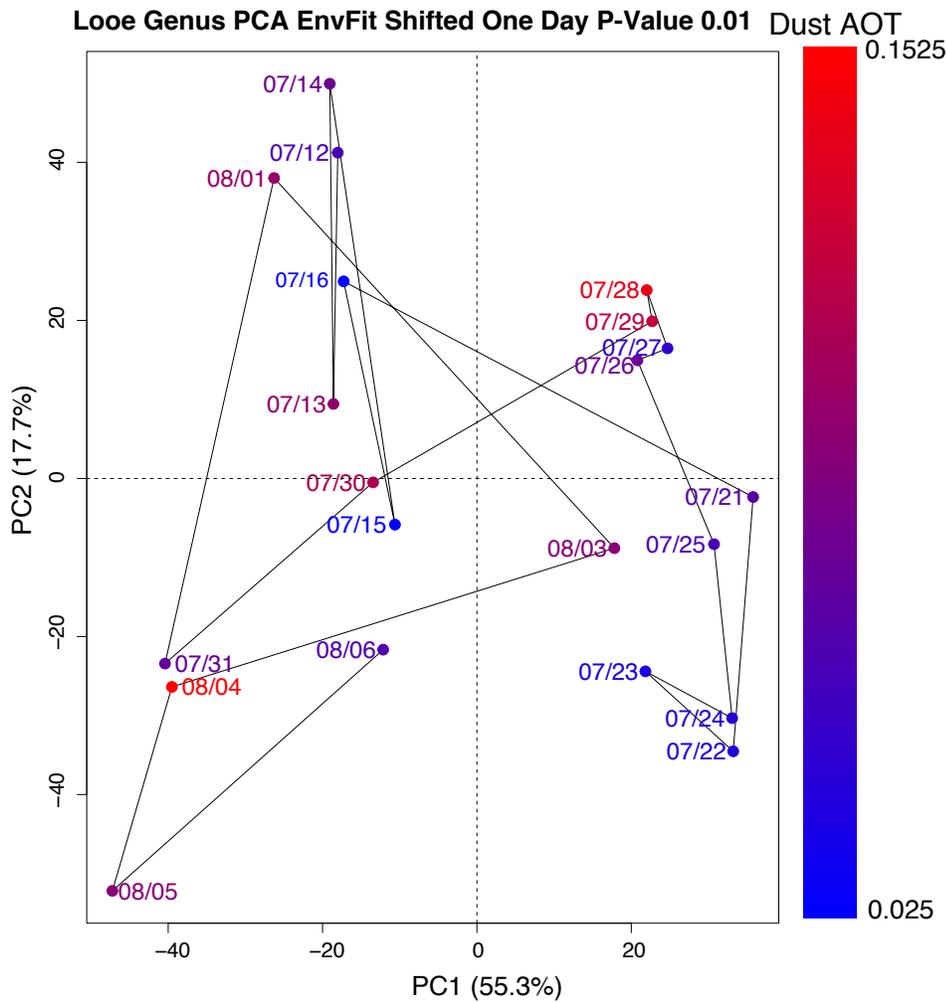


Figure S2.2: Principal components analysis showing bacterial community shifts over time over Looe Key Reef. Principal components analysis representing the OTU level classification of the bacterial community. Plot was generating using vegan package in R. Color of points/dates indicates the dust aerosol optical thickness measured on that day by NAAPS scaled from the lowest thickness to the highest thickness measured during sampling. The more dust measured in the atmosphere, the redder the color of the point. No environmental factors strongly correlated with the PCA plot (p value <0.01) using EnvFit function.

Supplemental Tables:

Table S2.1: Environmental metadata collected during fieldwork in the Florida Keys. Water collection time (UTC): Approximate time that samples were taken from Looe Key Reef for bacterial community and environmental and biological parameter investigation in Eastern Standard Time; Filter collection time (UTC): Time that large volume air sampler filters were collected and new filters were inserted in Eastern Standard Time. dFe: aerosol dissolved iron (nM); tFe: aerosol particulate total iron (nM); Dust AOT: dust aerosol optical thickness average from 00:00 to 00:00; Total AOT: Total aerosol optical thickness average from 00:00 to 00:00; Chl a: Chlorophyll-*a* (mg/L); DOC: dissolved organic carbon (μM); TDN: total dissolved nitrogen; DON: dissolved organic nitrogen; o-Phos: ortho-phosphate; *in situ* dFe: measurement of *in situ* dissolved iron; *in situ* pFe measurement of *in situ* particulate iron

| Date | Water Collection Time (UTC) | Filter Collection Time (UTC) | Temp. C | Current Speed (m/s) | Salinity | pH | dFe (nM) | tFe (nM) | Dust AOT | Total AOT |
|---------|-----------------------------|------------------------------|---------|---------------------|----------|------|----------|----------|----------|-----------|
| 7/12/16 | 17:30 | | 31.00 | | 35.99 | 8.02 | | | 0.0625 | 0.1125 |
| 7/13/16 | 18:00 | | 31.29 | 0.0359 | 35.98 | 8.00 | | | 0.0975 | 0.1525 |
| 7/14/16 | 16:30 | | 31.56 | 0.0296 | 36.07 | 8.02 | | | 0.08 | 0.1325 |
| 7/15/16 | 15:00 | | 31.52 | 0.0504 | 36.07 | 8.04 | 0.130 | 9.060 | 0.025 | 0.065 |
| 7/16/16 | 15:00 | 16:50 | 31.11 | 0.0460 | 36.01 | 8.05 | 0.557 | 25.52 | 0.025 | 0.075 |
| 7/17/16 | | 14:13 | 31.09 | 0.0685 | 36.00 | 8.05 | 0.866 | 104.7 | 0.0325 | 0.075 |
| 7/18/16 | | 15:12 | 31.07 | 0.0810 | 36.07 | 8.03 | 1.719 | 69.31 | 0.0375 | 0.0925 |
| 7/19/16 | | 13:58 | 30.83 | 0.1017 | 36.10 | 8.02 | 1.302 | 169.4 | 0.08 | 0.1575 |
| 7/20/16 | | 15:23 | 30.55 | 0.0782 | 36.17 | 8.02 | 1.629 | 94.70 | 0.0475 | 0.1175 |
| 7/21/16 | 17:00 | 18:50 | 29.93 | 0.0684 | 36.06 | 8.02 | 2.173 | 83.64 | 0.07 | 0.1825 |
| 7/22/16 | 14:45 | 15:39 | 29.40 | 0.0831 | 35.93 | 8.05 | 1.512 | 54.02 | 0.04 | 0.0875 |
| 7/23/16 | 15:00 | 14:08 | 29.61 | 0.0851 | 35.95 | 8.05 | 0.854 | 77.77 | 0.0375 | 0.0725 |
| 7/24/16 | 17:30 | 17:36 | 29.62 | 0.0688 | 35.86 | 8.04 | 1.805 | 123.4 | 0.045 | 0.0975 |
| 7/25/16 | 14:45 | 14:27 | 29.46 | 0.0814 | 35.92 | 8.04 | 4.083 | 331.3 | 0.0625 | 0.12 |
| 7/26/16 | 14:30 | 15:42 | 29.99 | 0.0844 | 36.13 | 8.30 | 1.094 | 103.0 | 0.08 | 0.1325 |
| 7/27/16 | 14:15 | 15:42 | 30.15 | 0.0808 | 36.12 | 8.49 | 2.422 | 181.8 | 0.05 | 0.1225 |
| 7/28/16 | 15:45 | 15:34 | 29.93 | 0.0813 | 36.04 | 8.54 | 10.57 | 693.8 | 0.1425 | 0.2225 |

| | | | | | | | | | | |
|---------|-------|-------|-------|--------|-------|------|-------|-------|--------|--------|
| 7/29/16 | 15:00 | 16:43 | 30.03 | 0.0481 | | | 4.725 | 754.9 | 0.1225 | 0.1875 |
| 7/30/16 | 14:30 | 17:18 | 30.19 | 0.0223 | | | 2.567 | | 0.1125 | 0.155 |
| 7/31/16 | 14:45 | 17:43 | 30.39 | 0.0226 | | | 7.495 | 648.8 | 0.075 | 0.1375 |
| 8/1/16 | 15:00 | 17:29 | 30.56 | 0.0577 | 36.22 | 8.62 | 3.169 | 372.2 | 0.1 | 0.1725 |
| 8/2/16 | | 17:19 | 30.78 | 0.0717 | 36.34 | 8.62 | 2.870 | 317.5 | 0.1025 | 0.2 |
| 8/3/16 | 15:30 | 17:05 | 30.43 | 0.0734 | 36.18 | 8.64 | 3.788 | 719.1 | 0.0925 | 0.1975 |
| 8/4/16 | 15:30 | 16:42 | 30.37 | 0.0728 | 36.14 | 8.65 | 3.986 | 310.3 | 0.1525 | 0.2475 |
| 8/5/16 | 17:00 | 17:06 | 30.61 | 0.0753 | 36.18 | 8.63 | 4.353 | 173.3 | 0.0925 | 0.1525 |
| 8/6/16 | 16:45 | 16:41 | 30.26 | 0.0616 | | | | | 0.065 | 0.13 |

| Date | Chl a (mg/L) | DOC (μM) | TDN (μM) | DON (μM) | Ammonia (μM) | Nitrate (μM) | Nitrite (μM) | o-Phos (μM) | Silicate (μM) | <i>in situ</i> dFe (nM) | <i>in situ</i> pFe (nM) |
|---------|--------------|----------|----------|----------|--------------|--------------|--------------|-------------|---------------|-------------------------|-------------------------|
| 7/12/16 | 0.50 | 124.2 | 10.5 | 8.1 | 1.68 | 0.02 | 0.11 | 0.06 | 0.19 | 3.74 | 5.47 |
| 7/13/16 | 0.23 | 89.3 | 15.7 | 13.2 | 2.01 | 0.81 | 0.13 | 0.05 | 0.42 | 2.56 | 7.68 |
| 7/14/16 | 0.66 | 126.7 | 11.6 | 9.2 | 1.79 | 0.28 | 0.11 | 0.01 | 1.37 | 3.67 | 10.1 |
| 7/15/16 | 0.75 | 93.5 | 8.6 | 6.7 | 1.99 | 0.20 | 0.12 | 0.06 | 0.58 | 2.51 | 14.2 |
| 7/16/16 | 0.67 | 92.0 | 8.7 | 6.5 | 1.58 | 0.02 | 0.11 | 0.16 | 0.01 | 10.0 | 25.9 |
| 7/17/16 | | | | | | | | | | | |
| 7/18/16 | | | | | | | | | | | |
| 7/19/16 | | | | | | | | | | | |
| 7/20/16 | | | | | | | | | | | |
| 7/21/16 | 0.28 | 76.7 | 8.6 | 6.1 | 2.39 | 0.17 | 0.11 | 0.04 | 0.48 | 2.32 | 25.1 |
| 7/22/16 | 0.22 | 85.4 | 7.8 | 5.7 | 1.77 | 0.09 | 0.10 | 0.04 | 0.54 | 1.47 | 10.3 |
| 7/23/16 | 0.18 | 74.1 | 8.3 | 4.7 | 1.73 | 0.40 | 0.12 | 0.03 | 0.05 | 1.48 | 3.15 |
| 7/24/16 | 0.28 | 77.4 | 7.5 | 3.9 | 4.67 | 0.29 | 0.12 | 0.06 | 2.10 | 1.65 | 3.79 |
| 7/25/16 | 0.26 | 69.0 | 8.4 | 6.7 | 1.75 | 0.03 | 0.10 | 0.05 | 0.13 | 0.81 | 5.96 |
| 7/26/16 | 0.19 | 74.6 | 9.4 | 7.8 | 1.61 | 0.02 | 0.11 | 0.04 | 0.39 | 1.55 | 3.61 |
| 7/27/16 | 0.26 | 84.5 | 7.9 | 6.2 | 1.30 | 0.03 | 0.10 | 0.01 | 0.03 | 1.85 | 13.7 |
| 7/28/16 | | 80.0 | 7.8 | 5.4 | 1.80 | 0.13 | 0.11 | 0.07 | 0.83 | 2.22 | 6.97 |
| 7/29/16 | 0.18 | 70.0 | 6.9 | 4.5 | 1.74 | 0.75 | 0.13 | 0.09 | 0.58 | 1.31 | 3.69 |
| 7/30/16 | 0.31 | 78.3 | 6.8 | 4.5 | 1.61 | 0.53 | 0.13 | 0.04 | 0.42 | 2.18 | 33 |
| 7/31/16 | 0.24 | 78.3 | 8.9 | 5.7 | 1.87 | 0.21 | 0.11 | 0.04 | 1.36 | 3.70 | 13.5 |
| 8/1/16 | 1.46 | 116.5 | 9.8 | 6.6 | 4.40 | 0.11 | 0.09 | 0.01 | 0.01 | 3.39 | 17.8 |
| 8/2/16 | | | | | | | | | | | |
| 8/3/16 | 0.23 | 77.4 | 9.3 | 6.7 | 1.68 | 0.11 | 0.09 | 0.01 | 0.08 | 1.62 | 9.07 |
| 8/4/16 | 0.34 | 89.1 | 6.5 | 3.6 | 2.55 | 0.47 | 0.08 | 0.02 | 0.91 | 3.14 | 11 |
| 8/5/16 | 0.35 | 89.3 | 11.4 | 8.9 | 2.55 | 0.02 | 0.09 | 0.29 | 0.25 | 1.77 | 10.1 |
| 8/6/16 | 0.35 | 85.3 | 9.9 | 6.9 | 2.59 | 0.06 | 0.08 | 0.07 | 0.20 | 2.12 | 10.1 |

Table S2.2: Number of sequences at each stage of analysis in mothur. The number of sequences from each sample as they were processed through the mothur standard operating procedure.

| Samples | make. contigs | screen. seqs | screen. seqs | chimera removal | remove lineage |
|--------------------|------------------|-----------------|-----------------|--------------------|-------------------|
| LOOE16S071216 | 101448 | 51637 | 51529 | 50967 | 50954 |
| LOOE16S071316 | 105075 | 80006 | 79931 | 73923 | 73858 |
| LOOE16S071416 | 130178 | 98249 | 98164 | 89993 | 89932 |
| LOOE16S071516 | 74540 | 38935 | 38866 | 38017 | 37945 |
| LOOE16S071616 | 198720 | 144603 | 144458 | 136719 | 136704 |
| LOOE16S072116 | 62416 | 32986 | 32913 | 32710 | 32506 |
| LOOE16S072216 | 217676 | 169482 | 169325 | 161361 | 160739 |
| LOOE16S072316 | 238821 | 181382 | 181161 | 172007 | 171520 |
| LOOE16S072416 | 221584 | 169078 | 168890 | 160168 | 159344 |
| LOOE16S072516 | 214511 | 160810 | 160647 | 153464 | 152427 |
| LOOE16S072616 | 149459 | 109532 | 109434 | 106246 | 105599 |
| LOOE16S072716 | 169973 | 126844 | 126719 | 120027 | 119344 |
| LOOE16S072816 | 188556 | 141161 | 141013 | 138601 | 137397 |
| LOOE16S072916 | 167541 | 123631 | 123405 | 119045 | 117507 |
| LOOE16S073016 | 180206 | 133436 | 133263 | 125225 | 123831 |
| LOOE16S073116 | 193634 | 140058 | 139910 | 130161 | 129660 |
| LOOE16S080116 | 157907 | 120222 | 120104 | 116512 | 116364 |
| LOOE16S080316 | 198376 | 156539 | 156375 | 145725 | 144630 |
| LOOE16S080416 | 188544 | 145881 | 145745 | 132088 | 131509 |
| LOOE16S080516 | 149831 | 115644 | 115578 | 102865 | 102685 |
| LOOE16S080616 | 198249 | 148870 | 148743 | 136282 | 135823 |
| MICROCOSM1CONTROL1 | 88590 | 45190 | 45142 | 40505 | 40496 |
| MICROCOSM1CONTROL2 | 69733 | 35089 | 35037 | 28086 | 28084 |
| MICROCOSM1CONTROL3 | 83961 | 40874 | 40823 | 33732 | 33718 |
| MICROCOSM1PREADD1 | 76535 | 38482 | 38441 | 34165 | 34147 |
| MICROCOSM1PREADD2 | 71699 | 36547 | 36511 | 31368 | 31351 |
| MICROCOSM2CONTROL1 | 82451 | 42063 | 42018 | 37002 | 36976 |
| MICROCOSM2CONTROL2 | 100180 | 51773 | 51719 | 46717 | 46703 |
| MICROCOSM2CONTROL3 | 77287 | 40062 | 40006 | 34665 | 34631 |
| MICROCOSM2PREADD1 | 80188 | 41707 | 41651 | 35246 | 35138 |
| MICROCOSM2PREADD2 | 85496 | 44205 | 44153 | 37484 | 37370 |
| MICROCOSM3CONTROL1 | 45143 | 22762 | 22718 | 19179 | 19154 |
| MICROCOSM3CONTROL2 | 67602 | 36272 | 36234 | 30692 | 30660 |
| MICROCOSM3CONTROL3 | 79066 | 42239 | 42186 | 36417 | 36357 |
| MICROCOSM3PREADD1 | 67871 | 36004 | 35963 | 29848 | 29723 |

| | | | | | |
|--------------------|---------|---------|---------|---------|---------|
| MICROCOSM3PREADD2 | 62249 | 32756 | 32713 | 26596 | 26516 |
| MICROCOSM4CONTROL1 | 75381 | 38682 | 38557 | 33991 | 33762 |
| MICROCOSM4CONTROL2 | 70228 | 36012 | 35866 | 31664 | 31513 |
| MICROCOSM4CONTROL3 | 69407 | 36087 | 35970 | 32372 | 32150 |
| MICROCOSM4PREADD1 | 54990 | 28932 | 28845 | 24147 | 23278 |
| MICROCOSM4PREADD2 | 66061 | 35004 | 34887 | 29355 | 28285 |
| MICROCOSM5CONTROL1 | 60517 | 32445 | 32378 | 27692 | 27641 |
| MICROCOSM5CONTROL2 | 66067 | 35255 | 35205 | 32214 | 32130 |
| MICROCOSM5CONTROL3 | 62415 | 32707 | 32644 | 29844 | 29789 |
| MICROCOSM5PREADD1 | 39602 | 20054 | 20012 | 17644 | 17446 |
| MICROCOSM5PREADD2 | 43085 | 23200 | 23157 | 20103 | 19763 |
| Totals | 5253049 | 3493389 | 3489009 | 3222834 | 3207059 |

Table S2.3: EnvFit regression values, data shifted one day. Values of the EnvFit regression function in the vegan package used to determine correlations between bacterial communities and environmental variables. P-values are based on 10,000 random permutations of sample labels. The environmental variables were shifted one day. P-values (<0.01 reported) are calculated as the proportion of times a randomized R^2 value is equal to or greater than the observed R^2 value.

| Environ. Variable | Genus Level Plot | |
|--------------------|------------------|----------|
| | R^2 | p-value |
| Dust AOT | 0.4029 | 0.008499 |
| Total AOT | 0.2851 | 0.047995 |
| DOC | 0.2027 | 0.18688 |
| TDN | 0.3861 | 0.0211 |
| DON | 0.3042 | 0.05959 |
| Ammonia | 0.0558 | 0.68993 |
| Nitrate | 0.1269 | 0.36916 |
| Nitrite | 0.1161 | 0.39616 |
| ortho-Phosphate | 0.0024 | 0.9895 |
| Silicate | 0.0047 | 0.9624 |
| Chlorophyll-a | 0.1802 | 0.2507 |
| <i>in situ</i> dFe | 0.372 | 0.0319 |
| <i>in situ</i> pFe | 0.0432 | 0.71773 |
| Current Speed | 0.6453 | 0.0002 |
| Water Temp | 0.4395 | 0.007199 |
| dFe filters | 0.5457 | 0.01560 |
| tFe filters | 0.5023 | 0.02990 |

Table S2.4: Spearman's rank correlations of Dust AOT, filter dFe and tFe to measured environmental variables. Comparisons of various nutrient measurements to Dust AOT and iron content in filters. Average dust over 24 hr from 12:00 to 12:00 were compared to the *in situ* measurements while average dust from 18:00 to 18:00 was compared to iron filter measurements. The only statistically significant correlations found were between the dust AOT measurements and the iron in filters.

| Dust AOT vs. | Spearman's rho | Spearman p-value |
|------------------------------|----------------|------------------------|
| <i>in situ</i> Chlorophyll-a | -0.08562807 | 0.7196 |
| <i>in situ</i> DOC | -0.04230394 | 0.8555 |
| <i>in situ</i> TDN | -0.06213404 | 0.789 |
| <i>in situ</i> DON | -0.104886 | 0.6509 |
| <i>in situ</i> Ammonia | 0.2017573 | 0.3805 |
| <i>in situ</i> Nitrate | 0.3727167 | 0.09611 |
| <i>in situ</i> Nitrite | -0.09060001 | 0.6961 |
| <i>in situ</i> O-Phosphate | -0.1141511 | 0.6222 |
| <i>in situ</i> Silicate | 0.248617 | 0.2772 |
| <i>in situ</i> dFe | 0.05526663 | 0.8119 |
| <i>in situ</i> pFe | 0.08718284 | 0.7071 |
| Filter dFe | 0.8948856 | 1.914x10 ⁻⁸ |
| Filter tFe | 0.9236556 | 6.328x10 ⁻⁹ |

| Filter dFe vs. | Spearman's rho | Spearman p-value |
|------------------------------|----------------|----------------------|
| <i>in situ</i> Chlorophyll-a | -0.07522132 | 0.7819 |
| <i>in situ</i> DOC | -0.08103132 | 0.7572 |
| <i>in situ</i> TDN | 0.009821979 | 0.9702 |
| <i>in situ</i> DON | -0.1058467 | 0.686 |
| <i>in situ</i> Ammonia | 0.2486188 | 0.3359 |
| <i>in situ</i> Nitrate | 0.1729239 | 0.5069 |
| <i>in situ</i> Nitrite | -0.2866657 | 0.2646 |
| <i>in situ</i> O-Phosphate | 0.01245469 | 0.9622 |
| <i>in situ</i> Silicate | 0.2240639 | 0.3873 |
| <i>in situ</i> dFe | 0.04291846 | 0.8701 |
| <i>in situ</i> pFe | -0.09809934 | 0.708 |
| Filter tFe | 0.8664912 | 7.8x10 ⁻⁷ |

| Filter tFe vs. | Spearman's rho | Spearman p-value |
|------------------------------|----------------|------------------|
| <i>in situ</i> Chlorophyll-a | -0.1830219 | 0.5311 |
| <i>in situ</i> DOC | -0.2680966 | 0.334 |
| <i>in situ</i> TDN | -0.08944558 | 0.7512 |
| <i>in situ</i> DON | -0.06093229 | 0.8292 |
| <i>in situ</i> Ammonia | 0.08936554 | 0.7515 |

| | | |
|----------------------------|------------|--------|
| <i>in situ</i> Nitrate | 0.1741497 | 0.5348 |
| <i>in situ</i> Nitrite | -0.3279347 | 0.2328 |
| <i>in situ</i> O-Phosphate | -0.1458194 | 0.6041 |
| <i>in situ</i> Silicate | 0.09660123 | 0.732 |
| <i>in situ</i> dFe | -0.2 | 0.4738 |
| <i>in situ</i> pFe | -0.325 | 0.237 |

Table S2.5: DESeq2 results of changing *in situ* microbial taxa. DESeq2 results for the days immediately following dust deposition.

Highlighted samples represent genera that are also represented in Figure 2.5. BaseMean represents the average counts over all samples taken.

| Changing Genera July 28th-29th | | | |
|------------------------------------------------------------------------------------------------------------------------|----------|------------|-------------|
| Taxa | baseMean | foldchange | padj |
| Archaea;Euryarchaeota;Thermoplasmata;E2;Marine_group_II;unclassified;unclassified; - Genus0040 | 1077.597 | -3.377 | 0.037888218 |
| Bacteria;Bacteroidetes;Flavobacteriia;Flavobacteriales;Cryomorphaceae;unclassified;unclassified; - Genus0015 | 2435.830 | -2.830 | 0.013322878 |
| Bacteria;Proteobacteria;Gammaproteobacteria;Oceanospirillales;Endozoicimonaceae;unclassified;unclassified; - Genus0053 | 87.271 | 4.709 | 0.00918074 |
| Bacteria;Proteobacteria;Gammaproteobacteria;Alteromonadales;Alteromonadaceae;unclassified;unclassified; - Genus0024 | 49.548 | 6.814 | 0.023549525 |
| Bacteria;Proteobacteria;Gammaproteobacteria;Vibrionales;unclassified;unclassified;unclassified; - Genus0052 | 29.844 | 9.405 | 0.013322878 |
| Bacteria;Proteobacteria;Deltaproteobacteria;Bdellovibrionales;Bacteriovoraceae;Bacteriovorax;unclassified; - Genus0038 | 37.721 | 9.505 | 0.00918074 |
| Bacteria;Planctomycetes;OM190;CL500-15;unclassified;unclassified;unclassified; - Genus0075 | 25.307 | 11.037 | 0.039637111 |
| Bacteria;Verrucomicrobia;Verrucomicrobiae;Verrucomicrobiales;Verrucomicrobiaceae;Rubritalea;unclassified; - Genus0083 | 44.151 | 15.359 | 5.20894E-05 |
| | | | |
| Changing Genera July 29th-30th | | | |
| Taxa | baseMean | foldchange | padj |
| Bacteria;Proteobacteria;Alphaproteobacteria;Caulobacterales;Caulobacteraceae;Caulobacter;vibrioides; - Genus0218 | 73.999 | -13.683 | 0.012013171 |
| Bacteria;Proteobacteria;Gammaproteobacteria;Alteromonadales;Alteromonadaceae;Alteromonas;unclassified; - Genus0048 | 171.662 | -5.720 | 0.028117548 |
| Bacteria;Verrucomicrobia;Verrucomicrobiae;Verrucomicrobiales;Verrucomicrobiaceae;Rubritalea;unclassified; - Genus0083 | 44.151 | -5.712 | 0.028739363 |
| Bacteria;Proteobacteria;Alphaproteobacteria;Rhodospirillales;unclassified;unclassified;unclassified; - Genus0011 | 1497.330 | 2.639 | 0.012013171 |
| Bacteria;Proteobacteria;Gammaproteobacteria;Alteromonadales;OM60;unclassified;unclassified; - Genus0010 | 1438.118 | 3.507 | 5.33617E-05 |
| Bacteria;Cyanobacteria;Synechococcophycideae;Synechococcales;Synechococcaceae;Synechococcus;unclassified; - Genus0041 | 9008.109 | 4.119 | 0.000124912 |
| Bacteria;Bacteroidetes;Flavobacteriia;Flavobacteriales;Cryomorphaceae;unclassified;unclassified; - Genus0015 | 2435.830 | 5.511 | 5.4027E-06 |
| Bacteria;Proteobacteria;Alphaproteobacteria;Kiloniellales;unclassified;unclassified;unclassified; - Genus0127 | 100.151 | 5.945 | 0.009630514 |
| | | | |
| Changing Genera July 30th-31st | | | |
| Taxa | baseMean | foldchange | padj |

| | | | | |
|----------------------------------------------------------------------------------------------------------------------------|----------|------------|-------------|-------------|
| Bacteria;Proteobacteria;Betaproteobacteria;Burkholderiales;Comamonadaceae;Paucibacter;unclassified; - Genus0640 | 31.469 | 101493.005 | - | 0.000521166 |
| Bacteria;Proteobacteria;Alphaproteobacteria;Rhodobacterales;Rhodobacteraceae;unclassified;unclassified; - Genus0006 | 2067.600 | 3.715 | 5.4032E-06 | |
| Bacteria;Proteobacteria;Alphaproteobacteria;Rickettsiales;unclassified;unclassified;unclassified; - Genus0219 | 139.548 | 226.701 | 9.29683E-09 | |
| Bacteria;Proteobacteria;Betaproteobacteria;Methylophilales;Methylophilaceae;unclassified;unclassified; - Genus0243 | 21.614 | 1841.237 | 0.005637183 | |
| Changing Genera July 31st- August 1st | | | | |
| Taxa | baseMean | foldchange | padj | |
| Bacteria;Proteobacteria;Alphaproteobacteria;Rickettsiales;Pelagibacteraceae;Pelagibacter;ubique; - Genus0026 | 28.501 | -178.989 | 0.014090869 | |
| Bacteria;SAR406;AB16;Arctic96B-7;A714017;SargSea-WGS;unclassified; - Genus0069 | 243.342 | -48.030 | 3.86231E-09 | |
| Bacteria;Proteobacteria;Alphaproteobacteria;Rhodospirillales;Rhodospirillaceae;Nisaea;unclassified; - Genus0204 | 41.275 | -34.860 | 0.020400818 | |
| Bacteria;Cyanobacteria;Synechococcophycideae;Synechococcales;Synechococcaceae;Prochlorococcus;unclassified; - Genus0014 | 3398.806 | -22.797 | 6.34967E-21 | |
| Bacteria;Proteobacteria;Deltaproteobacteria;PB19;unclassified;unclassified;unclassified; - Genus0065 | 48.429 | -12.236 | 0.000194294 | |
| Bacteria;Proteobacteria;Alphaproteobacteria;Rickettsiales;Pelagibacteraceae;unclassified;unclassified; - Genus0001 | 6383.632 | -9.185 | 0.002140482 | |
| Archaea;Euryarchaeota;Thermoplasmata;E2;Marine_group_III;unclassified;unclassified; - Genus0314 | 107.883 | -8.070 | 0.045041074 | |
| Bacteria;Proteobacteria;Gammaproteobacteria;HTCC2188;HTCC2089;unclassified;unclassified; - Genus0030 | 275.246 | -7.411 | 3.97355E-08 | |
| Bacteria;Bacteroidetes;Flavobacteriia;Flavobacteriales;NS9;unclassified;unclassified; - Genus0051 | 234.360 | -4.899 | 6.49001E-05 | |
| Bacteria;Proteobacteria;Deltaproteobacteria;Myxococcales;OM27;unclassified;unclassified; - Genus0045 | 67.783 | -4.468 | 0.02472909 | |
| Bacteria;Bacteroidetes;Cytophagia;Cytophagales;Flammeovirgaceae;unclassified;unclassified; - Genus0033 | 315.543 | -3.515 | 0.004668409 | |
| Bacteria;Bacteroidetes;Flavobacteriia;Flavobacteriales;unclassified;unclassified;unclassified; - Genus0022 | 189.413 | -3.082 | 0.018062438 | |
| Bacteria;Proteobacteria;Alphaproteobacteria;Rhodospirillales;unclassified;unclassified;unclassified; - Genus0011 | 1497.330 | -2.538 | 0.007855535 | |
| Bacteria;SAR406;AB16;Arctic96B-7;A714017;SGSH944;unclassified; - Genus0023 | 350.206 | -2.512 | 0.0413577 | |
| Bacteria;Proteobacteria;Alphaproteobacteria;unclassified;unclassified;unclassified;unclassified; - Genus0008 | 2716.220 | -2.094 | 0.017982188 | |
| Bacteria;Proteobacteria;Alphaproteobacteria;Rhodobacterales;Rhodobacteraceae;unclassified;unclassified; - Genus0006 | 2067.600 | -2.082 | 0.014090869 | |
| Bacteria;Bacteroidetes;Flavobacteriia;Flavobacteriales;Flavobacteriaceae;unclassified;unclassified; - Genus0004 | 6289.870 | 2.633 | 0.011820884 | |
| Bacteria;Bacteroidetes;unclassified;unclassified;unclassified;unclassified;unclassified; - Genus0009 | 649.383 | 2.829 | 0.027298211 | |
| Bacteria;Verrucomicrobia;Opitutae;Puniceococcales;Puniceococcaceae;Coraliomargarita;unclassified; - Genus0039 | 571.196 | 3.701 | 0.000240514 | |
| Bacteria;Verrucomicrobia;Verrucomicrobiae;Verrucomicrobiales;Verrucomicrobiaceae;Rubritalea;unclassified; - Genus0083 | 44.151 | 4.894 | 0.042736995 | |
| Bacteria;Proteobacteria;Gammaproteobacteria;Vibrionales;Vibrionaceae;Vibrio;shilonii; - Genus0093 | 82.291 | 5.852 | 0.006651578 | |
| Bacteria;Proteobacteria;Gammaproteobacteria;Vibrionales;Pseudoalteromonadaceae;Pseudoalteromonas;unclassified; - Genus0042 | 204.991 | 7.258 | 0.018062438 | |

| | | | |
|-------------------------------------------------------------------------------------------------------------------------|----------|------------|-------------|
| Bacteria;Bacteroidetes;[Saprosirae];[Saprosirales];Saprosiraceae;unclassified;unclassified; - Genus0018 | 223.109 | 7.955 | 7.98828E-05 |
| Bacteria;Proteobacteria;Betaproteobacteria;unclassified;unclassified;unclassified;unclassified; - Genus0078 | 44.199 | 8.074 | 0.027298211 |
| Bacteria;Bacteroidetes;[Rhodothermi];[Rhodothermales];[Balneolaceae];Balneola;unclassified; - Genus0059 | 405.652 | 9.359 | 3.86231E-09 |
| Bacteria;Actinobacteria;Actinobacteria;Actinomycetales;Microbacteriaceae;unclassified;unclassified; - Genus0122 | 60.429 | 13.187 | 0.007855535 |
| Bacteria;Proteobacteria;Gammaproteobacteria;Oceanospirillales;unclassified;unclassified;unclassified; - Genus0062 | 132.924 | 19.585 | 3.86231E-09 |
| Bacteria;Bacteroidetes;Flavobacteriia;Flavobacteriales;Flavobacteriaceae;Tenacibaculum;unclassified; - Genus0115 | 17.187 | 20.568 | 0.007251901 |
| Bacteria;Proteobacteria;Alphaproteobacteria;Rhodobacterales;Hyphomonadaceae;Hyphomonas;unclassified; - Genus0149 | 14.610 | 24.440 | 0.012351291 |
| Bacteria;Tenericutes;Mollicutes;Acholeplasmatales;Acholeplasmataceae;Acholeplasma;unclassified; - Genus0222 | 27.334 | 331.230 | 0.007265937 |
| Bacteria;Bacteroidetes;Sphingobacteriia;Sphingobacteriales;unclassified;unclassified;unclassified; - Genus0757 | 204.447 | 399.129 | 2.36793E-08 |
| Bacteria;Proteobacteria;Epsilonproteobacteria;Campylobacterales;unclassified;unclassified;unclassified; - Genus0250 | 7.107 | 1167.738 | 0.005437725 |
| Bacteria;Proteobacteria;Betaproteobacteria;Burkholderiales;Comamonadaceae;Paucibacter;unclassified; - Genus0640 | 31.469 | 357910.931 | 1.39681E-06 |
| | | | |
| Changing Genera August 3rd-4th | | | |
| Taxa | baseMean | foldchange | padj |
| Bacteria;SAR406;AB16;ZA3648c;AEGEAN_185;unclassified;unclassified; - Genus0168 | 26.868 | -21.784 | 0.019520116 |
| Archaea;Euryarchaeota;Thermoplasmata;E2;Marine_group_III;unclassified;unclassified; - Genus0314 | 107.883 | -15.812 | 3.625E-07 |
| Bacteria;Bacteroidetes;Cytophagia;Cytophagales;Flammeovirgaceae;unclassified;unclassified; - Genus0033 | 315.543 | -6.761 | 3.14457E-07 |
| Bacteria;SAR406;AB16;Arctic96B-7;A714017;SGSH944;unclassified; - Genus0023 | 350.206 | -6.140 | 1.09079E-07 |
| Bacteria;Proteobacteria;Deltaproteobacteria;Sva0853;unclassified;unclassified;unclassified; - Genus0566 | 145.320 | -5.816 | 0.00115428 |
| Bacteria;SBR1093;A712011;unclassified;unclassified;unclassified;unclassified; - Genus0268 | 36.626 | -5.749 | 0.04321187 |
| Bacteria;Proteobacteria;Gammaproteobacteria;Alteromonadales;Alteromonadaceae;HTCC2207;unclassified; - Genus0079 | 126.617 | -5.374 | 0.000827231 |
| Bacteria;Cyanobacteria;Synechococcophycideae;Synechococcales;Synechococcaceae;Prochlorococcus;unclassified; - Genus0014 | 3398.806 | -4.621 | 8.44565E-06 |
| Bacteria;SAR406;AB16;Arctic96B-7;A714017;SargSea-WGS;unclassified; - Genus0069 | 243.342 | -3.903 | 0.003450339 |
| Bacteria;Verrucomicrobia;Opitutae;Puniceococcales;Puniceococcaceae;MB11C04;unclassified; - Genus0044 | 129.267 | -3.355 | 0.019520116 |
| Archaea;Euryarchaeota;Thermoplasmata;E2;Marine_group_II;unclassified;unclassified; - Genus0040 | 1077.597 | -3.296 | 0.019520116 |
| Bacteria;Verrucomicrobia;Verruco-5;R76-B128;unclassified;unclassified;unclassified; - Genus0070 | 307.948 | -2.392 | 0.04321187 |
| Bacteria;unclassified;unclassified;unclassified;unclassified;unclassified;unclassified; - Genus0003 | 702.496 | -2.191 | 0.027561015 |
| Bacteria;Proteobacteria;Alphaproteobacteria;unclassified;unclassified;unclassified;unclassified; - Genus0008 | 2716.220 | -1.833 | 0.04321187 |
| Bacteria;Proteobacteria;Alphaproteobacteria;Rhodospirillales;unclassified;unclassified;unclassified; - Genus0011 | 1497.330 | 2.144 | 0.024504084 |
| Bacteria;Bacteroidetes;Flavobacteriia;Flavobacteriales;Cryomorphaceae;unclassified;unclassified; - Genus0015 | 2435.830 | 2.291 | 0.031870648 |

| | | | |
|-----------------------------------------------------------------------------------------------------------------------|----------|------------|-------------|
| Bacteria;Proteobacteria;Alphaproteobacteria;Rhodobacterales;Rhodobacteraceae;unclassified;unclassified; - Genus0006 | 2067.600 | 3.300 | 3.30344E-06 |
| Bacteria;Cyanobacteria;Synechococcophycideae;Synechococcales;Synechococcaceae;Synechococcus;unclassified; - Genus0041 | 9008.109 | 3.372 | 0.000377624 |
| Bacteria;Proteobacteria;Gammaproteobacteria;Alteromonadales;OM60;unclassified;unclassified; - Genus0010 | 1438.118 | 3.585 | 4.49185E-06 |
| Bacteria;Bacteroidetes;[Saprospirae];[Saprospirales];Saprospiraceae;unclassified;unclassified; - Genus0018 | 223.109 | 4.905 | 0.00438268 |
| Bacteria;Bacteroidetes;[Rhodothermi];[Rhodothermales];[Balneolaceae];Balneola;unclassified; - Genus0059 | 405.652 | 7.439 | 1.09079E-07 |
| Bacteria;Planctomycetes;OM190;CL500-15;unclassified;unclassified;unclassified; - Genus0075 | 25.307 | 8.997 | 0.020267966 |
| Bacteria;Proteobacteria;Alphaproteobacteria;Kiloniellales;unclassified;unclassified;unclassified; - Genus0127 | 100.151 | 10.979 | 1.90521E-05 |
| Bacteria;Proteobacteria;Gammaproteobacteria;Oceanospirillales;unclassified;unclassified;unclassified; - Genus0062 | 132.924 | 15.424 | 5.27934E-08 |
| Bacteria;Proteobacteria;Alphaproteobacteria;Rickettsiales;unclassified;unclassified;unclassified; - Genus0219 | 139.548 | 56.984 | 3.10738E-08 |
| Bacteria;Proteobacteria;Betaproteobacteria;Methylophilales;Methylophilaceae;unclassified;unclassified; - Genus0243 | 21.614 | 59.768 | 0.008840168 |
| Bacteria;Bacteroidetes;Sphingobacteriia;Sphingobacteriales;unclassified;unclassified;unclassified; - Genus0757 | 204.447 | 1753.880 | 1.9023E-05 |
| Bacteria;Proteobacteria;Betaproteobacteria;Burkholderiales;Comamonadaceae;Paucibacter;unclassified; - Genus0640 | 31.469 | 133030.285 | 2.20187E-05 |

Table S2.6: Changing microbial genera in incubation experiments. Changing microbial groups from water incubated for 24hr after collection on the 16th, 21st, 26th, 29th and 31st of July using DESeq2. The number of changing taxa was highly dependent upon date of collection. On the 16th, 26th, and 31st of July 1, 3, and 4 taxa significantly changed post-incubation, respectively. The samples collected from the 21st and 29th had 29 and 51 taxa change, respectively. Few environmental variables were measured before the sample was taken on the 21st due to inclement weather, but the sample on the 29th happened approximately 36 hr after high dust AOT measurements began in our study site and discoloration was noted on the high volume air sampler filters. BaseMean represents the average counts over all samples taken.

| Changing Genera July 16 th | | | |
|-------------------------------------------------------------------------------------------------------------------------|----------|------------|-------------|
| Taxa | baseMean | foldchange | padj |
| Bacteria;Cyanobacteria;Synechococcophycideae;Synechococcales;Synechococcaceae;Prochlorococcus;unclassified; - Genus0014 | 1296.518 | 2.735 | 0.020229616 |
| Changing Genera July 21 st | | | |
| Taxa | baseMean | foldchange | padj |
| Bacteria;Proteobacteria;Alphaproteobacteria;Rickettsiales;unclassified;unclassified;unclassified; - Genus0219 | 27.385 | -30.221 | 0.003848075 |
| Bacteria;Proteobacteria;Gammaproteobacteria;Vibrionales;Vibrionaceae;Vibrio;shilonii; - Genus0093 | 17.358 | -8.358 | 0.025096758 |
| Bacteria;SAR406;AB16;Arctic96B-7;A714017;SargSea-WGS;unclassified; - Genus0069 | 59.548 | -5.017 | 3.27423E-07 |
| Bacteria;SAR406;AB16;Arctic96B-7;A714017;SGSH944;unclassified; - Genus0023 | 65.450 | -4.041 | 0.000177193 |
| Bacteria;Proteobacteria;Deltaproteobacteria;Bdellovibrionales;Bacteriovoraceae;unclassified;unclassified; - Genus0021 | 27.636 | -3.626 | 0.004041815 |
| Archaea;Euryarchaeota;Thermoplasmata;E2;Marine_group_II;unclassified;unclassified; - Genus0040 | 299.137 | -3.437 | 0.002377589 |
| Bacteria;Proteobacteria;Gammaproteobacteria;Oceanospirillales;Endozoicimonaceae;unclassified;unclassified; - Genus0053 | 24.926 | -3.353 | 0.043260562 |
| Bacteria;Proteobacteria;Deltaproteobacteria;Sva0853;unclassified;unclassified;unclassified; - Genus0566 | 32.890 | -2.922 | 0.016712542 |
| Bacteria;SAR406;AB16;Arctic96B-7;A714017;ZA3312c;unclassified; - Genus0037 | 286.377 | -2.332 | 9.49294E-05 |
| Bacteria;unclassified;unclassified;unclassified;unclassified;unclassified;unclassified; - Genus0003 | 200.738 | -1.658 | 0.018864756 |
| Bacteria;Proteobacteria;Gammaproteobacteria;unclassified;unclassified;unclassified;unclassified; - Genus0002 | 505.670 | -1.608 | 0.006468564 |
| Bacteria;Bacteroidetes;Flavobacteriia;Flavobacteriales;Flavobacteriaceae;unclassified;unclassified; - Genus0004 | 2227.910 | 1.990 | 0.003848075 |
| Bacteria;Proteobacteria;Gammaproteobacteria;Alteromonadales;Alteromonadaceae;Alteromonas;unclassified; - Genus0048 | 639.453 | 2.584 | 0.040700258 |
| Bacteria;Proteobacteria;Gammaproteobacteria;Alteromonadales;OM60;unclassified;unclassified; - Genus0010 | 752.409 | 2.658 | 6.26827E-13 |
| Bacteria;Cyanobacteria;Synechococcophycideae;Synechococcales;Synechococcaceae;Synechococcus;unclassified; - Genus0041 | 5387.514 | 2.781 | 7.11276E-08 |
| Bacteria;Planctomycetes;Phycisphaerae;Phycisphaerales;unclassified;unclassified;unclassified; - Genus0036 | 307.327 | 2.962 | 0.000134883 |
| Bacteria;Bacteroidetes;[Saprosirae];[Saprosirales];Saprosiraceae;unclassified;unclassified; - Genus0018 | 90.102 | 3.484 | 0.001685304 |

| | | | |
|--------------------------------------------------------------------------------------------------------------------------|----------|------------|-------------|
| Bacteria;Actinobacteria;Acidimicrobia;Acidimicrobiales;wb1_P06;unclassified;unclassified; - Genus0102 | 42.228 | 3.784 | 4.80179E-05 |
| Bacteria;Proteobacteria;Gammaproteobacteria;Alteromonadales;Alteromonadaceae;unclassified;unclassified; - Genus0024 | 39.634 | 4.201 | 0.025956537 |
| Bacteria;Proteobacteria;Alphaproteobacteria;Rhodobacterales;Hyphomonadaceae;Hyphomonas;unclassified; - Genus0149 | 17.335 | 4.559 | 0.03962057 |
| Bacteria;Proteobacteria;Alphaproteobacteria;Rhodobacterales;Rhodobacteraceae;unclassified;unclassified; - Genus0006 | 1609.792 | 5.307 | 9.16618E-25 |
| Bacteria;Bacteroidetes;Flavobacteriia;Flavobacteriales;unclassified;unclassified;unclassified; - Genus0022 | 148.367 | 5.516 | 1.28301E-06 |
| Bacteria;Bacteroidetes;Flavobacteriia;Flavobacteriales;Cryomorphaceae;unclassified;unclassified; - Genus0015 | 2500.650 | 5.668 | 5.14066E-15 |
| Bacteria;Proteobacteria;Gammaproteobacteria;Oceanospirillales;Oleiphilaceae;unclassified;unclassified; - Genus0111 | 39.720 | 7.595 | 0.004455892 |
| Bacteria;Proteobacteria;Gammaproteobacteria;Pseudomonadales;Moraxellaceae;Acinetobacter;unclassified; - Genus0032 | 450.082 | 11.773 | 0.010654093 |
| Bacteria;Proteobacteria;Alphaproteobacteria;Kiloniellales;unclassified;unclassified;unclassified; - Genus0127 | 84.057 | 16.212 | 2.95097E-10 |
| Bacteria;Proteobacteria;Alphaproteobacteria;Rhodobacterales;Rhodobacteraceae;Pseudoruegeria;unclassified; - Genus0328 | 35.786 | 34.259 | 2.95097E-10 |
| Bacteria;Proteobacteria;Alphaproteobacteria;Rhodobacterales;Rhodobacteraceae;Thalassobius;mediterraneus; - Genus0176 | 22.168 | 72.479 | 2.70783E-05 |
| Bacteria;Proteobacteria;Alphaproteobacteria;Rhodobacterales;Rhodobacteraceae;Nautella;unclassified; - Genus0216 | 51.467 | 87.793 | 1.91189E-05 |
| July 26 th | | | |
| Taxa | baseMean | foldchange | padj |
| Bacteria;Proteobacteria;Deltaproteobacteria;Myxococcales;Cystobacterineae;unclassified;unclassified; - Genus0098 | 11.197 | -8.511 | 0.008333668 |
| Bacteria;Planctomycetes;Phycisphaerae;Phycisphaerales;unclassified;unclassified;unclassified; - Genus0036 | 307.327 | 3.042 | 0.004035711 |
| Changing Genera July 29 th | | | |
| Taxa | baseMean | foldchange | padj |
| Bacteria;Planctomycetes;vadinHA49;DH61;unclassified;unclassified;unclassified; - Genus0085 | 4.739 | -25.662 | 0.002936998 |
| Bacteria;Proteobacteria;Deltaproteobacteria;Myxococcales;OM27;unclassified;unclassified; - Genus0045 | 20.923 | -15.468 | 0.003543694 |
| Bacteria;Planctomycetes;OM190;agg27;unclassified;unclassified;unclassified; - Genus0066 | 4.901 | -11.400 | 0.037503692 |
| Bacteria;Bacteroidetes;Cytophagia;Cytophagales;Flammeovirgaceae;JTB248;unclassified; - Genus0145 | 4.723 | -10.704 | 0.015438397 |
| Archaea;Euryarchaeota;Thermoplasmata;E2;Marine_group_II;unclassified;unclassified; - Genus0040 | 299.137 | -8.782 | 1.09396E-08 |
| Bacteria;SAR406;AB16;Arctic96B-7;A714017;SargSea-WGS;unclassified; - Genus0069 | 59.548 | -8.361 | 6.09324E-09 |
| Bacteria;Planctomycetes;OM190;CL500-15;unclassified;unclassified;unclassified; - Genus0075 | 12.388 | -7.781 | 0.024299102 |
| Bacteria;Proteobacteria;Deltaproteobacteria;Spirobacillales;unclassified;unclassified;unclassified; - Genus0043 | 5.447 | -7.275 | 0.013661298 |
| Bacteria;Proteobacteria;Deltaproteobacteria;Bdellovibrionales;Bacteriovoracaceae;unclassified;unclassified; - Genus0021 | 27.636 | -6.532 | 3.66275E-07 |
| Bacteria;Proteobacteria;Gammaproteobacteria;Oceanospirillales;Endozoicimonaceae;unclassified;unclassified; - Genus0053 | 24.926 | -6.046 | 0.000796971 |
| Bacteria;Proteobacteria;Deltaproteobacteria;PB19;unclassified;unclassified;unclassified; - Genus0065 | 20.476 | -5.652 | 0.049946433 |
| Bacteria;ZB3;BS119;unclassified;unclassified;unclassified;unclassified; - Genus0047 | 11.514 | -5.613 | 0.003787517 |
| Bacteria;Bacteroidetes;Cytophagia;Cytophagales;[Amoebophilaceae];Ucs1325;unclassified; - Genus0056 | 6.625 | -5.400 | 0.01802801 |
| Bacteria;SAR406;AB16;Arctic96B-7;A714017;SGSH944;unclassified; - Genus0023 | 65.450 | -5.274 | 5.23082E-05 |
| Bacteria;Proteobacteria;Deltaproteobacteria;Sva0853;unclassified;unclassified;unclassified; - Genus0566 | 32.890 | -4.818 | 0.001599854 |
| Archaea;Euryarchaeota;Thermoplasmata;E2;Marine_group_III;unclassified;unclassified; - Genus0314 | 27.961 | -4.800 | 0.024299102 |
| Bacteria;Proteobacteria;Deltaproteobacteria;Bdellovibrionales;Bacteriovoracaceae;Bacteriovorax;unclassified; - Genus0038 | 10.865 | -3.888 | 0.024299102 |
| Bacteria;Proteobacteria;Gammaproteobacteria;Alteromonadales;HTCC2188;HTCC;unclassified; - Genus0088 | 35.780 | -3.887 | 0.0020654 |
| Bacteria;SAR406;AB16;Arctic96B-7;A714017;ZA3312c;unclassified; - Genus0037 | 286.377 | -3.786 | 8.35846E-10 |
| Bacteria;Verrucomicrobia;Opitutae;Puniceococcales;Puniceococcaceae;Coraliomargarita;unclassified; - Genus0039 | 184.096 | -3.337 | 4.95463E-05 |

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|------------------------------------------------------------------------------------------------------------------------------|----------|------------|-------------|
| Bacteria;Proteobacteria;Alphaproteobacteria;BD7-3;unclassified;unclassified;unclassified; - Genus0035 | 15.158 | -2.907 | 0.024017504 |
| Bacteria;Verrucomicrobia;Verruco-5;R76-B128;unclassified;unclassified;unclassified; - Genus0070 | 92.132 | -2.842 | 0.001070005 |
| Bacteria;unclassified;unclassified;unclassified;unclassified;unclassified;unclassified; - Genus0003 | 200.738 | -2.687 | 7.72529E-08 |
| Bacteria;Actinobacteria;Acidimicrobia;Acidimicrobiales;OCS155;unclassified;unclassified; - Genus0013 | 2865.534 | -2.282 | 7.16652E-10 |
| Bacteria;Proteobacteria;Alphaproteobacteria;Rickettsiales;AEGEAN 112;unclassified;unclassified; - Genus0020 | 195.751 | -2.229 | 0.001029286 |
| Bacteria;Proteobacteria;Gammaproteobacteria;Oceanospirillales;Halomonadaceae;Candidatus Portiera;unclassified; - Genus0007 | 3374.455 | -1.959 | 1.1531E-06 |
| Bacteria;Cyanobacteria;Synechococcophycideae;Synechococcales;Synechococcaceae;Prochlorococcus;unclassified; - Genus0014 | 1296.518 | -1.885 | 0.030737398 |
| Bacteria;Proteobacteria;Gammaproteobacteria;unclassified;unclassified;unclassified;unclassified; - Genus0002 | 505.670 | -1.604 | 0.005745214 |
| Bacteria;Bacteroidetes;Flavobacteriia;Flavobacteriales;NS9;unclassified;unclassified; - Genus0051 | 98.847 | 2.180 | 0.030737398 |
| Bacteria;Proteobacteria;Alphaproteobacteria;Rhodospirillales;unclassified;unclassified;unclassified; - Genus0011 | 703.674 | 2.253 | 0.000973031 |
| Bacteria;Actinobacteria;Acidimicrobia;Acidimicrobiales;wb1 P06;unclassified;unclassified; - Genus0102 | 42.228 | 3.044 | 0.001599854 |
| Bacteria;Cyanobacteria;Synechococcophycideae;Synechococcales;Synechococcaceae;Synechococcus;unclassified; - Genus0041 | 5387.514 | 3.402 | 3.99689E-11 |
| Bacteria;Bacteroidetes;Cytophagia;Cytophagales;Flammeovirgaceae;Roseivirga;unclassified; - Genus0166 | 15.597 | 3.418 | 0.023582564 |
| Bacteria;Proteobacteria;Alphaproteobacteria;Rhodobacterales;Hyphomonadaceae;Oceanicaulis;unclassified; - Genus0220 | 7.614 | 3.806 | 0.047628638 |
| Bacteria;Proteobacteria;Gammaproteobacteria;Alteromonadales;Alteromonadaceae;Marinobacter;hydrocarbonoclasticus; - Genus0107 | 31.588 | 4.099 | 0.037503692 |
| Bacteria;Proteobacteria;Gammaproteobacteria;Alteromonadales;OM60;Congregibacter;unclassified; - Genus0188 | 7.214 | 4.472 | 0.037503692 |
| Bacteria;Proteobacteria;Alphaproteobacteria;Rhodobacterales;Hyphomonadaceae;Hyphomonas;unclassified; - Genus0149 | 17.335 | 6.166 | 0.003543694 |
| Bacteria;Bacteroidetes;Flavobacteriia;Flavobacteriales;Flavobacteriaceae;Tenacibaculum;unclassified; - Genus0115 | 10.272 | 6.680 | 0.013991231 |
| Bacteria;Proteobacteria;Gammaproteobacteria;Alteromonadales;Alteromonadaceae;Alteromonas;unclassified; - Genus0048 | 639.453 | 11.025 | 2.67761E-10 |
| Bacteria;Proteobacteria;Betaproteobacteria;Burkholderiales;Comamonadaceae;unclassified;unclassified; - Genus0074 | 8.157 | 11.328 | 0.026413814 |
| Bacteria;Proteobacteria;Alphaproteobacteria;Kiloniellales;unclassified;unclassified;unclassified; - Genus0127 | 84.057 | 11.644 | 1.7211E-09 |
| Bacteria;Proteobacteria;Gammaproteobacteria;Alteromonadales;OM60;unclassified;unclassified; - Genus0010 | 752.409 | 11.740 | 7.67988E-80 |
| Bacteria;Proteobacteria;Alphaproteobacteria;Rhodobacterales;Rhodobacteraceae;unclassified;unclassified; - Genus0006 | 1609.792 | 11.862 | 1.56407E-54 |
| Bacteria;Proteobacteria;Alphaproteobacteria;Rhodobacterales;Rhodobacteraceae;Ruegeria;lacuscaerulensis; - Genus0165 | 15.664 | 13.096 | 5.23082E-05 |
| Bacteria;Bacteroidetes;Flavobacteriia;Flavobacteriales;Cryomorphaceae;unclassified;unclassified; - Genus0015 | 2500.650 | 13.179 | 1.31475E-33 |
| Bacteria;Proteobacteria;Gammaproteobacteria;Oceanospirillales;Oceanospirillaceae;Oleibacter;unclassified; - Genus0068 | 221.417 | 50.937 | 1.056E-20 |
| Bacteria;Proteobacteria;Alphaproteobacteria;Rhodobacterales;Rhodobacteraceae;Pseudoruegeria;unclassified; - Genus0328 | 35.786 | 63.808 | 1.27794E-09 |
| Bacteria;Proteobacteria;Alphaproteobacteria;Rhodobacterales;Rhodobacteraceae;Nautella;unclassified; - Genus0216 | 51.467 | 94.594 | 3.15592E-10 |
| Bacteria;Proteobacteria;Gammaproteobacteria;Oceanospirillales;Oleiphilaceae;unclassified;unclassified; - Genus0111 | 39.720 | 105.031 | 3.67693E-14 |
| Bacteria;Proteobacteria;Alphaproteobacteria;Rhodobacterales;Rhodobacteraceae;Thalassobius;mediterraneus; - Genus0176 | 22.168 | 866.331 | 3.59763E-08 |
| | | | |
| Changing Genera July 31 st | | | |
| Taxa | baseMean | foldchange | padj |
| Archaea;Euryarchaeota;Thermoplasmata;E2;Marine_group_II;unclassified;unclassified; - Genus0040 | 299.137 | -3.941 | 0.012350525 |
| Bacteria;Proteobacteria;Gammaproteobacteria;Alteromonadales;Alteromonadaceae;Alteromonas;unclassified; - Genus0048 | 639.453 | 5.463 | 0.002686234 |
| Bacteria;Proteobacteria;Gammaproteobacteria;Oceanospirillales;unclassified;unclassified;unclassified; - Genus0062 | 50.799 | 5.513 | 0.032351864 |
| Bacteria;Proteobacteria;Gammaproteobacteria;Oceanospirillales;Oceanospirillaceae;Oleibacter;unclassified; - Genus0068 | 221.417 | 14.721 | 1.20066E-06 |

CHAPTER 3

CONCLUSIONS

It is well established that Saharan dust deposition has the ability to greatly impact the marine environments in which it settles. Dust deposition supplies a substantial portion of marine nutrient input, especially in non-coastal areas, and can lead to changes in marine water chemistry, biogeochemical cycles, and microbial community composition. In order to study marine microbial responses to Sahara dust deposition, we have conducted a long term, *in situ* time series of measurements assessing both the biotic and abiotic factors affected by Saharan dust deposition. Through this work we have composed a unique dataset that provides new insight into the impacts of dust on marine biogeochemistry.

Across the study period, increases in atmospheric dust content did not result in immediate increases in the *in situ* concentrations of nutrients commonly found in Saharan dust, including carbon, nitrogen, phosphate, or iron. Instead, we observed a short-term decrease in dissolved iron followed by a subsequent increase in iron as dust deposition continued, which was likely caused by increased iron ligands that kept dissolved iron in solution. The iron content in dust was measured alongside satellite tracking of aerosol dust, and the two measurements were significantly correlated suggesting iron increase was due to dust deposition. This decrease and then increase in dissolved iron also corresponded to a short-term decrease in total bacterial abundance followed by a longer-term increase in total bacterial abundance. This delayed increase in bacterial abundance was accompanied by an increase in dissolved organic carbon and chlorophyll-*a*.

Throughout the time series, we conducted incubations in which dissolved nutrients often found in dust were added to seawater and changes in bacterial abundance over a 24 hr period was measured. In general, we did not observe growth responses to individual nutrients that were substantially greater than those observed in a no-addition control. This result suggests that either the nutrient(s) supplied by dust that led to an increase in bacterial abundance was not among those added experimentally, or that the particular chemical makeup of particulate dust is important in shaping *in situ* microbial responses.

These chemical and biological changes were accompanied by changes in microbial community composition. The immediate decrease in bacterial abundance was associated with a spike in bacterial abundance and an increase in the number and abundance of numerically rare taxa. These trends were also accompanied by increases in a number of bacterial taxa, including *Vibrionales*, *Flavobacteriaceae*, *Rhodobacteraceae*, *Cryomorphaceae*, *Bdellovibrionales* and *Synechococcus*, as well as a decrease in the relative abundance of *Prochlorococcus*.

To confirm some of the results we observed *in situ*, unamended seawater was incubated for 24 hr and the resultant changes in microbial community composition was observed. In general, these bottle incubations exhibited similar trends in microbial community composition to those observed *in situ*. This evidence supports our hypothesis that observed microbial community responses were driven by dust deposition and resultant changes in local abiotic and biotic conditions rather than passive shifts driven by hydrodynamic mixing between water masses carrying different microbial communities.

Although only one definitive dust event occurred during our study period, we believe this data adds valuable insight to fill a missing knowledge gap as to what effect Saharan dust has on

the *in situ* marine environment. By capturing more *in situ* dust events researchers have the potential to strengthen this evidence and gain a deeper understanding of this phenomenon.