

# Saharan dust nutrients promote *Vibrio* bloom formation in marine surface waters

Jason R. Westrich<sup>a,b</sup>, Alina M. Ebling<sup>c</sup>, William M. Landing<sup>c</sup>, Jessica L. Joyner<sup>a,b,1</sup>, Keri M. Kemp<sup>a,b</sup>, Dale W. Griffin<sup>d</sup>, and Erin K. Lipp<sup>a,2</sup>

<sup>a</sup>Department of Environmental Health Science, University of Georgia, Athens, GA 30602; <sup>b</sup>Odum School of Ecology, University of Georgia, Athens, GA 30602; <sup>c</sup>Department of Earth, Ocean, and Atmospheric Science, Florida State University, Tallahassee, FL 32306; and <sup>d</sup>Coastal and Marine Science Center, US Geological Survey, St. Petersburg, FL 33701

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Vibrio is a ubiquitous genus of marine bacteria, typically comprising a small fraction of the total microbial community in surface waters, but capable of becoming a dominant taxon in response to poorly characterized factors. Iron (Fe), often restricted by limited bioavailability and low external supply, is an essential micronutrient that can limit Vibrio growth. Vibrio species have robust metabolic capabilities and an array of Fe-acquisition mechanisms, and are able to respond rapidly to nutrient influx, yet Vibrio response to environmental pulses of Fe remains uncharacterized. Here we examined the population growth of Vibrio after natural and simulated pulses of atmospherically transported Saharan dust, an important and episodic source of Fe to tropical marine waters. As a model for opportunistic bacterial heterotrophs, we demonstrated that Vibrio proliferate in response to a broad range of dust-Fe additions at rapid timescales. Within 24 h of exposure, strains of Vibrio cholerae and Vibrio alginolyticus were able to directly use Saharan dust-Fe to support rapid growth. These findings were also confirmed with in situ field studies; arrival of Saharan dust in the Caribbean and subtropical Atlantic coincided with high levels of dissolved Fe, followed by up to a 30-fold increase of culturable Vibrio over background levels within 24 h. The relative abundance of Vibrio increased from ~1 to ~20% of the total microbial community. This study, to our knowledge, is the first to describe Vibrio response to Saharan dust nutrients, having implications at the intersection of marine ecology, Fe biogeochemistry, and both human and environmental health.

Saharan dust | Vibrio | iron | marine biogeochemistry | microbial ecology

Bacteria in the *Vibrio* genus are globally distributed in marine environments but typically make up a minor portion of the total microbial assemblage (1, 2); however, Vibrio have been shown to bloom in response to often poorly characterized environmental factors (3, 4). Like other opportunistic heterotrophic bacteria, Vibrio can have disproportionately large impacts on carbon and nutrient processing because of their ability to reproduce rapidly and respond to pulses of newly available resources (2, 5-7). Characterized as "opportunitrophs," Vibrio have a broad genomic and metabolic repertoire (8), allowing them to compete in highly variable nutrient environments ranging from the open ocean to pathogenic associations with animal hosts (3, 9). This genus includes many well-known pathogens of marine organisms and humans, and disease incidence has risen sharply in the last 20 y (10, 11). Common human pathogens include the causative agent of the severe diarrheal disease cholera (Vibrio cholerae), shellfish-associated gastroenteritis (Vibrio parahaemolyticus and Vibrio vulnificus), and seawater-associated wound infections (Vibrio vulnificus and Vibrio alginolyticus) (10). Studies examining the environmental drivers and distribution of Vibrio have largely focused on the role of Vibrio in disease, generally overlooking the importance of Vibrio in the biogeochemical cycling of key nutrients and trace metals (3, 4). Iron (Fe) is an essential micronutrient for Vibrio growth in the environment as well as during host invasion, where it is actively sequestered by the host to prevent bacterial colonization (9). Vibrio have evolved to be adept scavengers of Fe in a variety of conditions

(12). Despite the importance of Fe for growth, there has been little characterization of the effects of environmental Fe enrichment on *Vibrio* population dynamics and the role of these bacteria in Fe cycling in marine systems.

Fe can be a limiting micronutrient in marine primary and secondary production (13, 14). As an essential cofactor in many metabolic processes-including aerobic respiration, photosynthesis, and nitrogen fixation-its availability can be a determinant in the cycling of carbon (C) and biologically important macronutrients, like nitrogen (N) and phosphorus (P) (13, 15, 16). Dissolved Fe (dFe) is believed to be the most biologically available fraction of Fe, but is present in vanishingly low amounts in marine systems around the world, especially due to the low solubility of Fe(III) in seawater (17). Heterotrophic bacteria, including Vibrio, play a key role in Fe cycling (14, 15, 18, 19), in part by modulating Fe solubility through secretion of high-affinity Fe-chelating siderophores (20, 21). Fe-siderophore complexes allow active uptake into the bacterial cell (20) and provide a usable exogenous source of Fe for phytoplankton (22, 23). Although most studies of Fe enrichment in marine systems have focused on autotrophs (24, 25), heterotrophic bacteria have been shown to have a higher Fe per biomass quota than many phytoplankton (18), accounting for up to 80% of the total planktonic uptake in some systems (26).

# Significance

Atmospherically transported dust from the Saharan desert provides pulses of biologically important nutrients, including iron, to ocean surface waters. The biological response to these ephemeral events is not fully known, especially among the heterotrophic microbial community. Here we use the wellcharacterized *Vibrio* genus as a model for heterotrophic bacterial response. We demonstrate that Saharan dust nutrients, deposited in tropical marine waters, can promote *Vibrio* bloom formation and suggest that dust-associated iron is an important driver of *Vibrio* population dynamics. This work shows not only the role of fast-acting heterotrophs in the biogeochemical cycles of environmental pulses of iron, but it also highlights an important factor in the growth of bacteria that can cause disease in humans and marine organisms.

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<sup>&</sup>lt;sup>1</sup>Present address: Department of Biology, Brooklyn College, City University of New York, Brooklyn, NY 11210.

<sup>&</sup>lt;sup>2</sup>To whom correspondence should be addressed. Email: elipp@uga.edu.

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**Fig. 1.** Florida Keys surface water *Vibrio* response to a range of Saharan Dust<sub>SIM</sub> additions. *Vibrio* growth was normalized among experiments by comparing the ratio of cfu/mL 24 h after Dust<sub>SIM</sub> addition (T<sub>24</sub>) to time 0 (T<sub>0</sub>) for [n] replicates (mean  $\pm$  SEM). Asterisks indicate those amendments in which growth was significantly different from the no-dust (0 mg·L<sup>-1</sup>) control (mixed linear model; Tukey's post hoc test). \**P* < 0.05; \*\*\*\**P* < 0.0001. Additional data are shown in Table S4.

Atmospheric dust deposition is a major source of Fe in the global ocean (27) and is estimated to deliver more than triple the amount of dFe as riverine inflow (28). Globally, the Saharan desert is the largest source region of this atmospheric dust-Fe (27). Dust originating in northern Africa is swept across the Atlantic Ocean along easterly trade winds, producing spatiotemporal gradients of dust deposition in the Caribbean and southeastern United States, especially during the summer months (29, 30). Increased atmospheric processing time, associated with long-range transport as well as wet deposition (rain washout), are hypothesized to alter components of atmospheric dust and produce a soluble and highly biologically available form of Fe (17, 27). Although the response of marine autotrophs to dust deposition has been investigated (15, 25), the full biological response to the episodic deposition of dust-Fe to ocean surface water, especially among microbial communities, has yet to be clearly elucidated. Evidence is growing that heterotrophic bacteria, especially among the class  $\gamma$ -proteobacteria, may play a role in processing deposited minerals and nutrients (31, 32), but studies to date, which have largely focused on bulk bacterial response and longer timescales, have shown equivocal results (33, 34). We hypothesized that specific opportunistic bacteria, like Vibrio, can respond quickly to newly available dust-associated Fe and suggest a role of dust-Fe as a driver of Vibrio population dynamics.

### Results

Vibrio Response to Simulated Saharan Dust Deposition in Marine Surface Water. To determine the effect of Saharan dust nutrients on Vibrio growth, source material from the Saharan desert (Morocco) was added to microcosms containing natural unfiltered seawater collected in the Florida Keys (US). Source material (characterization shown in Tables S1 and S2) was manipulated to simulate effects from long-range atmospheric transport and wet deposition and is referred to as Dust<sub>SIM</sub> (SI Methods). Microcosms included surface water collected over multiple dates from three sites for each experiment, representing a cross-shelf gradient (onshore, near shore, and offshore (at Looe Key Reef in the lower Florida Keys)] (Fig. S1). A broad range of dust deposition scenarios  $(20 \ \mu g \cdot L^{-1} \text{ to } 30 \ \text{mg} \cdot L^{-1})$  were simulated. The lowest Dust<sub>SIM</sub> addition (20  $\mu$ g·L<sup>-1</sup>) increased dFe in seawater to 1.19 nM (±0.08 SEM) above the background levels of 0.90 nM (±0.04 SEM) found in nonamended surface water (Table S3). This addition provided a

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small but significant increase (P < 0.05), consistent with in situ observations of dFe during dust events (Table S3; also see Fig. 4).

After the Dust<sub>SIM</sub> amendments to seawater, the growth of total culturable *Vibrio* on a selective medium was normalized across experiments by calculating the ratio of colony-forming units (cfu) per milliliter at 24 h to those at 0 h. All Dust<sub>SIM</sub> additions, except the 40 µg·L<sup>-1</sup> addition (due to high variability among replicates), had significantly higher growth compared with nondust controls, and the response was largely dose-dependent (Fig. 1; Table S4). At the lowest Dust<sub>SIM</sub> addition (20 µg·L<sup>-1</sup>), mean growth was six times as great as that for nondust controls (49.0 ± 19.6 SEM and 8.5 ± 3.6 SEM, respectively, P < 0.001). Neither the location (inshore, near shore, or offshore) nor the date of sampling had a statistically significant effect (P > 0.05).

Vibrio Utilization of Dust-Associated Fe. To evaluate the specific effects of Fe in Saharan dust on Vibrio growth, cultures of individual strains were grown in a novel, Fe-limited seawater (Vib-FeL), which was replete in key macronutrients (N and P) and carbon substrate and supplemented with all essential trace elements needed for growth, except for Fe (SI Methods). The relative growth of individual strains of V. alginolyticus and V. cholerae (identified as dust-responsive in initial experiments) were tested in three separate culture conditions: (i) Vib-FeL alone, (ii) Vib-FeL with Dust<sub>SIM</sub> (providing 0.89 µM Fe), and (iii) Vib-FeL with FeCl<sub>3</sub> (providing 4.37 µM Fe), as a positive control. After overnight incubation (18-24 h), the proportional growth was compared for all treatments (Fig. 2; Table S5). Vib-FeL alone restricted growth of both test strains. The addition of Dust<sub>SIM</sub> led to significant growth of both V. cholerae and V. alginolyticus compared with nondust controls (13 and 18 times as great, respectively; P < 0.05). The



**Fig. 2.** Vibrio spp. response to Fe and dust. Growth of V. alginolyticus (n = 3; A) and V. cholerae (n = 2; B) in Fe-limited seawater (Vib-FeL) alone, amended with 4  $\mu$ M FeCl<sub>3</sub> (Fe), and Dust<sub>SIM</sub> (Dust) containing 0.89  $\mu$ M Fe. Vibrio growth was normalized among experiments by comparing the ratio of cfu·mL<sup>-1</sup> after Dust<sub>SIM</sub> addition ( $T_n$ ) to time 0 ( $T_0$ ) (mean  $\pm$  SEM). Asterisks indicate significantly greater growth with the addition of Fe and dust compared with growth in Vib-FeL alone (ANOVA). \*P < 0.05; \*\*P < 0.01; \*\*\*P < 0.001. There was no significant difference between treatment with Dust<sub>SIM</sub> and treatment with Fe. Additional data are shown in Table S5.

proportional growth for the Dust<sub>SIM</sub> amendments was not significantly different from that noted for the FeCl<sub>3</sub> controls, which had 20 and 23 times as much growth for *V. cholerae* and *V. alginolyticus*, respectively, as did nondust controls (Fig. 2; Table S5) and confirmed that Dust<sub>SIM</sub> could alleviate Fe limitation in this medium.

Fe concentrations across dust deposition events are highly variable (27, 35); therefore, we evaluated growth of *V. alginolyticus* in Vib-FeL across a range of scenarios, providing additional dFe at concentrations from 5 to 836 nM. All Dust<sub>SIM</sub> additions increased the proportional growth of *V. alginolyticus* (Fig. 3; Table S6). The lower additions of 5, 10, and 21 nM dFe resulted in approximately four times the growth of no-addition controls. The higher dFe amendments, 201 and 836 nM, resulted in growth that was 8 to 11 times that of controls (P < 0.001), respectively (Fig. 3; Table S6).

*Vibrio* Growth in Response to Natural Saharan Dust Events. Offshore sampling sites at Looe Key Reef, in the lower Florida Keys (US), and Ragged Point, Barbados, were chosen based on a 30-y dataset of atmospheric dust sampling, demonstrating strong seasonal pulses of African dust arriving at these locations almost entirely in the summer months (June through September) (29, 30). Satellite and aerosol-modeling products were used to monitor evolution of individual dust events from the coast of Africa (typically every 5–10 d, July through August) and their transit across the Atlantic (Fig. 4). Field collections were conducted in the Florida Keys (summer 2013 and 2014) and Barbados (summer 2014) during three separate Saharan dust events (SDEs).

In July 2014, 1 wk before the arrival of dust, dFe in surface waters in the lower Florida Keys was 0.90 nM (±0.08 SEM), increasing to 3.24 nM (±0.04 SEM) with the arrival of a SDE (P < 0.001) (Table S3). Similarly, the highest dFe during the August 2014 study period in Barbados (2.22 nM ± 0.20 SEM) was measured during the arrival of a SDE. dFe levels were not measured in 2013. Within 14-24 h of the arrival of SDE (and concomitant dFe increase), surface water concentrations of culturable Vibrio increased significantly over background levels in all three sampling campaigns at levels ranging from 5 to 30 times the nondust levels (Fig. 4). At the peak of the Vibrio blooms in 2014, a 1.6- and 3.6-fold decrease of dFe was measured in Barbados and Florida, respectively (Fig. 4). Vibrio bloom conditions were transient, and levels returned to baseline within 24-48 h of the measured peak. As the Vibrio bloom expired, an increase of dFe was measured, followed by a tapering decline in dFe over the following 1-4 d to ~1.6-fold decline in dFe compared to dust arrival values.



**Fig. 3.** Response of *Vibrio alginolyticus* to a range of Dust<sub>SIM</sub> dFe concentrations in Fe-limited artificial seawater (Vib-FeL). *Vibrio* growth was normalized among experiments by comparing the ratio of cfu-mL<sup>-1</sup> of *V. alginolyticus* 24 h after Dust<sub>SIM</sub> addition (T<sub>24</sub>) to time 0 (T<sub>0</sub>) (n = 3; mean  $\pm$  SEM). Asterisks indicate those amendments in which growth was significantly different from the no dust addition (0 Dust<sub>SIM</sub>) control (ANOVA) \**P* < 0.05; \*\*\**P* < 0.001. Additional data are shown in Table S6.

Bacterial Community Composition Changes in Response to SDE. As part of a co-occurring study at Looe Key Reef, microbial community data were obtained for an additional four surface water samples between August 2011 and July 2013 using Illuminabased sequencing of the community 16S rDNA. Three of the samples were collected outside of a dust event. The final sample coincided with the dust event captured in July 2013. The abundance of operational taxonomic units in the Vibrio genus was significantly greater during this event than during all other sampling dates (P < 0.001). The relative abundance of Vibrio increased from <1.4% during nondust conditions to 19.8% of the total bacterial community during the 2013 SDE (Figs. S2 and S3). This increase was also confirmed by Vibrio culture counts and cell equivalent counts [quantitative PCR (qPCR)] (Table S7). The relative abundance of other genera including Pseudoalteromonas and Acinetobacter, belonging to the same class of bacteria as Vibrio (y-proteobacteria), also increased significantly, whereas Pelagibacter declined (P < 0.05) (Fig. S3).

## Discussion

There has been considerable interest in the biological response of marine surface water communities to dust deposition, but results to date on the role of heterotrophic microorganisms have been equivocal. These recent investigations of heterotrophic response to dust-associated nutrients as well as the direct effect of Fe addition to marine waters generally measured bulk parameters (such as total bacterial abundance, bacterial respiration, or bacterial production), which could potentially fail to recognize community shifts and mask the emergence of functionally important taxa that can rapidly respond to nutrients (19, 31, 36). Additionally, studies that did assess community structure in response to dust typically focused on  $\geq 48$  h after dust addition, which could miss taxa that mount a more rapid response (31, 36). Finally, much of the recent work in this area has examined response in experimental microcosms and mesocosms (15, 31, 36), with few studies able to capture in situ response to natural dust events. In this study, evidence from both experimental manipulations and in situ time course observations demonstrated that opportunistic heterotrophic genera like Vibrio mount a robust and rapid growth response to dust addition and potentially play an important, but currently largely unexplored, role in the cycling of Fe.

Fe acquisition is essential for Vibrio fitness and survival, both in the environment and in a host during infection (9, 12). V. cholerae, which is arguably the most studied of the Vibrio species and has a very well characterized genome, has >50 Fe acquisition genes spread across its two chromosomes for ferrous, ferric, and biologically complexed Fe uptake (12). This genetic repertoire suggests that Vibrio are effective competitors for Fe in many different environmental niches. The availability of Fe can also control the metabolism of other nutrients such as N and P, and can limit C utilization, effectively setting limits on growth for both open ocean and coastal heterotrophic bacteria (16, 33, 34). Potential colimitation is especially important in light of the fundamental contribution of heterotrophic bacteria to the cycling of C in marine ecosystems (33, 37). Vibrio and other rapidly responding heterotrophs likely play a pivotal, but as yet largely unexplored, role, in coupling Fe flux with C cycling in marine food webs, ultimately influencing global climate processes (18, 19, 37). In this study, we demonstrated that Vibrio rapidly exploit Fe and potentially other nutrients provided by Saharan dust, driving a significant, but temporary, population bloom. These blooms, which were observed within 24 h of dust arrival, also likely preceded stimulation of autotrophic picoplankton and other phytoplankton, which have previously been shown to take  $\geq$ 48 h to respond to dust or Fe inputs (e.g., ref. 31). This finding suggests that Vibrio blooms were not due to increased organic matter production from autotrophs, but were responding directly to the dust inputs, which is also supported by the microcosm



**Fig. 4.** *Vibrio* response to natural SDEs. (*Left*) *Vibrio* concentrations (cfu·mL<sup>-1</sup>) (n = 3; mean  $\pm$  SEM) in surface waters during the arrival (shaded bar) of SDE and 3–5 d after dust arrival in Barbados (A) and the Florida Keys (B and C). Dashed lines represent baseline surface water *Vibrio* concentrations (348  $\pm$ 122 SEM, n = 3 for Barbados and 45.4  $\pm$  2.5 SEM, n = 42 for Florida), determined during the dust season (April– August) but not associated with a SDE. For each SDE, *Vibrio* concentration on the date of peak response was significantly different from all other dates. \*P < 0.05; \*\*\*P < 0.001. Double hash indicates non-consecutive sampling date (C). Mean ( $\pm$  SEM, n = 3) dFe concentrations were determined for A and B only; bold values indicate significantly lower dFe than that observed on the dust arrival date (ANOVA P < 0.05). (*Right*) Modeled dust aerosol depths (Naval Research Laboratory (www.nrlmry.navy.mil/aerosol/) (study site indicated by red circle).

studies using monocultures of Vibrio. Furthermore, the data suggest that dust-Fe can support blooms across a wide range of dust and Fe deposition scenarios. Vibrio growth in natural seawater continued even at the highest Dust<sub>SIM</sub>-Fe additions (836 nM), suggesting increasing Fe limitation, which was unexpected (34). Although the bioavailable fraction of Fe added to the microcosms was likely reduced because of rapid oxidation and precipitation due physiochemical factors in natural seawater (17), Vibrio physiology suggests a high Fe demand with up to 5 µM needed for replete growth (12). Growth rates in Vibrio are among the fastest known of any bacteria, with doublings every 8-9 min recorded in some species (5). Additionally, several Vibrio species are able to fix N, a process that has a very high Fe demand (38, 39). Dust additions also likely added other limiting nutrients in addition to Fe, especially phosphate, which may help to explain the continued response even at very high levels (16). Finally, although the focus of this work was on Vibrio as a model for dust response, the

relative abundance of other taxa (e.g., *Pseudoalteromonas* and *Acinetobacter*) also increased significantly with dust events and likely competed with *Vibrio* for uptake of additional Fe and nutrients.

During in situ time course observations, *Vibrio* showed a robust bloom within 24 h of the arrival of SDE and concomitant high dFe concentrations. At the peak of the bloom, *Vibrio* species increased their proportion in the community by more than an order of magnitude, relative to nondust conditions. These results indicate that this is not an exogenous import of bacteria, but rather an autochthonous response to the addition of biologically necessary nutrients like dFe. Although it has been reported that some bacteria can travel associated with dust aerosols, genus-level profiling of Saharan dust has not revealed the presence of *Vibrio* (40). During the 2014 field studies, the drawdown of dFe to the predust level of 0.9 nM (Fig. 4 and Table S3) at the peak of the bloom also ENVIRONMENTAL SCIENCES indicated utilization of the majority of introduced dFe by blooming *Vibrio* and other responsive  $\gamma$ -proteobacteria (31).

As a genus, Vibrio is one of the most highly investigated groups of environmental microbes. Aided in part by its ease of culturability (3), Vibrio is an excellent candidate model to examine opportunistic responses and roles in larger ecosystem functioning (8). Vibrio, which typically comprise <1% of the ocean surface bacterioplankton community (2), could be considered conditionally rare taxa (CRT) (41). CRT are subject to dramatic blooms, potentially playing an outsized role in the ecology of a system (1, 41, 42). Vibrio have shown explosive growth in response to nutrient enrichment (6, 7). This adaptive feast-or-famine life strategy allows exploitation of spatially and temporally variable resources, leading to bloom conditions. This strategy also subjects Vibrio to kill-the-winner top-down controls, such as grazing and viral lysis, both of which tightly control y-proteobacteria and Vibrio populations (7, 43, 44). The population declines observed in the field 24-48 h after SDE-induced Vibrio blooms could be attributed to these topdown control pressures. The bloom decline corresponded with a spike in dFe concentrations, supporting the notion of lysis and bacterivory in the release of dFe, warranting further investigation. The ecosystem consequences of such a large turnover of dFe on biogeochemical cycles also remains to be determined. Bacterial grazing experiments have demonstrated that 90% of Fe remains in the dissolved fraction after 24 h (14). Additionally, Fe released by viral lysis of heterotrophic bacteria (as demonstrated in V. alginolyticus) is highly bioavailable to the plankton community, including autotrophic diatoms, with the bioavailability of this released Fe exceeding that of siderophore-bound Fe (21). This dFe is capable of supporting up to 90% of primary production in some systems (45). Taken together, the bloom-bust cycle of Vibrio population growth in response to Saharan dust could have an important role in trophic transfer of labile Fe to primary producers.

*Vibrio* can overcome predation pressure by forming close associations with marine organisms and plankton (46). In this work, the population bloom of *Vibrio* appeared transient, but further investigation is needed to determine whether planktonic-associated hot spots exist after bloom termination. The potential for particle attachment is particularly salient in the case of disease-causing species like *V. cholerae* or *V. alginolyticus*, which have both been shown to be highly responsive to dust–Fe. These species are known to associate with zooplankton and marine organisms, directly influencing their survival in the environment and routes of transmission to potential hosts (3, 9, 46).

This study, to our knowledge, is the first to demonstrate that Vibrio species, as a model of a rapidly responding opportunistic heterotroph, are highly responsive to Saharan dust-Fe and associated nutrients and indicate a role for these bacteria in processing dust-Fe in marine ecosystems. In particular, these results suggest that otherwise rare heterotrophic bacterial taxa are among the first responders to introduced Fe and other nutrients from dust and likely precede responses by autotrophs. The Sahara and Sahel are particularly vulnerable to further drying due to changes in climate and land-use patterns (47), potentially increasing dust export from this region. Coupled with the fact that dust-Fe fertilization of marine systems has been suggested as a driver of past paleoclimatic change (48), a mechanistic understanding in the modern ocean is critical to making predictions about future oceanic production and climate scenarios. The discovery of dust-Fe as a factor in Vibrio population dynamics is an important first step that warrants further investigation to inform future predictions about Vibrio-related disease and Vibrio impacts on global biogeochemical cycles.

### Methods

**Dust<sub>SIM</sub> Experimental Additions.** The US Geological Survey (USGS) provided mineralogical and elementally characterized Saharan source material (*SI Methods*) collected from a highly weathered dune in Morocco (exact

location was not specified). Saharan source material was manipulated in the laboratory to simulate atmospheric processing and wet deposition and is referred to as Dust<sub>SIM</sub> (SI Methods). Natural surface water from the Florida Keys and artificial Vib-FeL microcosm experiments were seeded with a broad range of  $\mathsf{Dust}_{\mathsf{SIM}}$  additions because of the high spatial and temporal heterogeneity of dust deposition in any single event, as well as the high variability in dust concentrations resulting from rain washout, which is the dominant mode of deposition in Florida (~80%) (29). To quantify Dust<sub>SIM</sub> loadings for experimental additions, Dust<sub>SIM</sub> was added [1:150 (vol/vol)] to 5 mL of ultrapure Milli-Q water by using trace metal clean chemistry techniques (49), followed by further 1:2 serial dilutions in Milli-Q water. dFE (<0.2 µm) was measured by using inductively coupled plasma MS (ICP-MS) elemental analysis (SI Methods) for triplicate samples of each dilution. The Fe content of trans-Atlantic transported dust has been measured to be close to the upper crustal value of 3.5% (29, 30); we therefore quantified  $\mathsf{Dust}_{\mathsf{SIM}}$ amendments by Fe content to allow for an approximate calculation of dust loading (mg·L<sup>-1</sup>) for each addition, considering a fractional solubility of the Moroccan source material to be 4.39% (SI Methods). Dust<sub>SIM</sub> additions for seeding experiments were calculated to be: 0.02, 0.04, 0.18, 0.37, 0.78, 7.3, and 30 mg L<sup>-1</sup> of dust (Table S8). The higher values include representative amounts of deposition in regions closer to African source areas (e.g., Mediterranean), and the lowest values were environmentally relevant for the Caribbean and Florida Keys (e.g., during a wet deposition event) (29, 35).

In microcosm experiments using natural seawater communities, surface water from the upper 1 m of the water column was collected in sterile trace-metal clean polypropylene bottles at sites in the lower Florida Keys (Fig. S1). Dust<sub>SIM</sub> solutions for seeding experiments were prepared as described above and added to replicate natural seawater microcosms. Microcosms were mixed and held at 30 °C for 24 h. *Vibrio* counts at the time of seeding (0 h) and after 24 h were determined by culture (cfu) on selective thiosulfate-citrate-bile salt-sucrose agar (TCBS; Oxoid), in triplicate. Additional details are provided in *SI Methods*.

Fe-Limited Seawater (Vib-FeL) Experiments. To investigate the specific effect of Fe from Saharan dust on Vibrio growth dynamics, experimentation was done in a Fe-limited medium, referred to as Vib-FeL (SI Methods). Frozen cell stocks of V. alginolyticus [American Type Culture Collection (ATCC) strain 33839] and V. cholerae (ATCC 39315) were recovered in sterilized artificial seawater amended with 1% peptone and 0.5% yeast extract (ASW+PYE). Recovered cells, incubated for 12 h at 30 °C, were subcultured in 5 mL of fresh ASW+PYE (1:100 dilution) and allowed to grow to log phase as monitored by optical density at 600 nm (OD<sub>600</sub>) on a spectrophotometer. Cells were washed twice and resuspended in Vib-FeL to eliminate Fe carryover. The experiment was initiated at time 0 by inoculating washed cells (1:100) into 5 mL of the appropriate culture conditions: Vib-FeL alone; Vib-FeL with FeCl<sub>3</sub>; Dust<sub>SIM</sub> added to Vib-FeL (1:150 vol/vol); and incubated for 24 h at 30 °C on a shaking platform to maintain aeration. Vibrio abundance was determined by spread plating aliquots from each culture onto ASW+PYE agar plates at times 0, 18, and 24 h. Spread plates were incubated at 30 °C for 24 h, and cfu were enumerated and compared. Because dust deposition is highly variable (35), we also evaluated growth of V. alginolyticus (following the same cell preparation methodology) across a broad range of Fedeposition scenarios by diluting  $\mathsf{Dust}_{\mathsf{SIM}}$  as described above into Vib-FeL, providing dFe at concentrations from 5 to 836 nM dFe (Table S8).

In Situ Response to Natural SDEs. SDEs were monitored by using satellite and modeling products from NASA (https://worldview.earthdata.nasa.gov/) and the Naval Research Laboratory (www.nrlmry.navy.mil/aerosol/), allowing for virtual real-time monitoring of SDE arrival and passage at two study sites: Ragged Point, Barbados (easternmost point of the island) (13.1667° N, 59.4333° W) and Looe Key Reef, FL (24.5475° N, 81.4067° W). Samples were collected within 24 h of the arrival of dust (Fig. 4). All surface water samples were collected in triplicate and kept at ambient temperature until processing (within 1 h). Sampling collection continued at 24-h intervals for 3-5 d after the modeled arrival of dust. Vibrio abundance was determined by spread plating each replicate surface water sample on Vibrio-selective TCBS medium, in triplicate. Spread plates were incubated at ambient temperature (~30 °C) for 24 h, and cfu were enumerated and compared. Background nondust associated summer (May-August) Vibrio levels at Looe Key were determined by routine sampling between 2012 and 2014. Background levels at Barbados were determined in April 2013 (predust season). DNA was extracted from surface water samples collected from Looe Key Reef during nondust conditions and during the July 2013 SDE. Community DNA was sequenced by using Illumina MiSeq PE 250 sequencing of the V4 hypervariable region of the 16S rRNA gene (Tables S9-S11) (50) (SI Methods). Additionally, qPCR was conducted for total Vibrio counts from the extracted DNA (SI Methods). Field collections for SDE

occurred in the summer rainy season, and isolated local showers were common; however, no precipitation data were available for the specific collection sites. Rain (very light) was only noted during or immediately before sampling at Barbados (11 and 12 August 2014). No rain was observed during sampling at Looe Key Reef.

All statistical analyses are described in *SI Methods*.

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