Colonies of marine cyanobacteria *Trichodesmium* interact with associated bacteria to acquire iron from dust

Subhajit Basu\(^1,2\), Martha Gledhill\(^3\), Dirk de Beer\(^4\), S.G. Prabhu Matondkar\(^5\) & Yeala Shaked\(^1,2\)

Iron (Fe) bioavailability limits phytoplankton growth in vast ocean regions. Iron-rich dust uplifted from deserts is transported in the atmosphere and deposited on the ocean surface. However, this dust is a poor source of iron for most phytoplankton since dust-bound Fe is poorly soluble in seawater and dust rapidly sinks out of the photic zone. An exception is *Trichodesmium*, a globally important, N\(_2\) fixing, colony forming, cyanobacterium, which efficiently captures and shuffles dust to its colony core. *Trichodesmium* and bacteria that reside within its colonies carry out diverse metabolic interactions. Here we show evidence for mutualistic interactions between *Trichodesmium* and associated bacteria for utilization of iron from dust, where bacteria promote dust dissolution by producing Fe-complexing molecules (siderophores) and *Trichodesmium* provides dust and optimal physical settings for dissolution and uptake. Our results demonstrate how intricate relationships between producers and consumers can influence productivity in the nutrient starved open ocean.
In large parts of the ocean, supply of the nutrients iron (Fe), phosphorous (P), and nitrogen (N) limit phytoplankton growth. Some phytoplankton supply their N-demands by fixing the inert gaseous nitrogen (N₂) into biologically accessible nitrogen and further fuel the ocean primary productivity by releasing excess fixed-nitrogen. The cyanobacterium *Trichodesmium* spp., an important ecosystem player in oligotrophic ocean regions, contributes to ~50% of marine N₂-fixation and forms extensive surface blooms visible even from space (Fig. 1a). Large fluxes of nutrients, organic molecules, and toxins released from *Trichodesmium* blooms have strong impact on both chemical and biological components of marine ecosystems. Colonies of *Trichodesmium* host many associated bacteria which are distinct from free-living bacteria in seawater. *Trichodesmium* and its associated bacteria exchange nutrients and organic molecules between them and act together to optimize the growth of the whole consortium.

Atmospheric dust is considered an important source of iron to Fe-poor ocean regions, but the rapid sinking of dust from the ocean surface and the low solubility of iron from dust (dust-Fe) restricts its utilization by phytoplankton. Buoyant *Trichodesmium* colonies overcome these constraints by efficient trapping of dust particles deposited at the ocean surface and subsequent shuffling of dust to the colony center, where it is protected from loss (Fig. 1b). In addition to dust capturing, *Trichodesmium* colonies are shown to chemically modify dust and increase dust-Fe solubility and bioavailability. The two most common mechanisms microorganisms apply for dissolving mineral-Fe are reductive dissolution and siderophore promoted dissolution, both of which were suggested to play a role in *Trichodesmium*-dust interactions. In reductive dissolution, conversion of mineral Fe(III) to soluble Fe(II) facilitates dissolution. In siderophore promoted dissolution, Fe-specific ligands react with Fe(III) at the mineral surface and then the Fe-siderophore complexes return to solution.

A large group of siderophores, produced by bacteria, fungi, and cyanobacteria, are involved in active dissolution of Fe-minerals in many terrestrial and aquatic environments. In the ocean, siderophores from the ferrioxamine group are frequently detected in surface waters and hence are considered important for the marine Fe-cycle. Although *Trichodesmium* captures and shuffles dust to its colony core (Fig. 1b), it does not possess known pathways for siderophore synthesis and hence in isolation cannot utilize siderophore promoted dissolution for dissolving dust-bound Fe. However, some of the bacteria residing within natural *Trichodesmium* colonies have the ability to produce siderophores. We therefore hypothesize that bacteria associated with *Trichodesmium* colonies increase solubility of dust-bound Fe by releasing siderophores (Fig. 1c-I) that dissolve iron from dust trapped within the colony center (Fig. 1c-II). The siderophore-mediated dust dissolution would be beneficial for *Trichodesmium* if it can utilize the Fe that is complexed by siderophores (Fig. 1c-III). In this scenario, the bacterial strategy of Fe dissolution from dust by siderophores is favorable for *Trichodesmium* and thus of mutual advantage for the consortium.

In this contribution, we explored the role of biotic interactions in actively mining dust-bound iron within *Trichodesmium* colonies. Firstly, we examined the occurrence of siderophores in natural *Trichodesmium* blooms from the coastal Arabian Sea and the Gulf of Aqaba at the northern end of the Red Sea. We detected siderophores in all *Trichodesmium* blooms and observed active siderophore production in response to dust addition. Then, using radiolabeled ⁵⁵Fe-oxyhydroxide (⁵⁵ferrihydrite) and natural colonies from the Gulf of Aqaba, we examined the effect of siderophores on mineral-Fe dissolution and uptake by both members of the *Trichodesmium* consortium. We found that addition of siderophores increased ⁵⁵ferrihydrite dissolution and iron uptake in natural colonies. The siderophore promoted

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**Fig. 1** Cartoon representation of the proposed dust-bound Fe acquisition pathway employed mutually by *Trichodesmium* colonies and associated bacteria. 

- **a** The N₂-fixing marine cyanobacterium *Trichodesmium* spp., which commonly occurs in tropical and sub-tropical waters, is of large environmental significance in fertilizing the ocean with important nutrients.
- **b** *Trichodesmium* can establish massive blooms in nutrient poor ocean regions with high dust deposition, partly due to their unique ability to capture dust, center it, and subsequently dissolve it.
- **c** The current study explores biotic interactions within *Trichodesmium* colonies that lead to enhanced dissolution and acquisition of iron from dust. Bacteria residing within the colonies produce siderophores (c-I) that react with the dust particles in the colony core and generate dissolved Fe (c-II). This dissolved Fe, complexed by siderophores, is then acquired by both *Trichodesmium* and its resident bacteria (c-III), resulting in a mutual benefit to both partners of the consortium.
Results
Siderophore production by isolates of associated bacteria. First, we confirmed that associated bacteria from natural *Trichodesmium* colonies can produce siderophores in culture. We repeatedly plated individual *Trichodesmium* colonies from the Gulf of Aqaba on nutrient rich marine agar medium and isolated 23 bacterial strains. When grown in Fe-limited liquid media, the majority of these isolates (~75%) were screened as Chrome Azurol-S assay positive, which is indicative of siderophore production (Supplementary Fig. 1). These findings add up to previous genetic and physiological reports confirming the wide occurrence of this trait within *Trichodesmium*’s consortium.

In contrast, we analyzed a supernatant of cultured Fe-limited *Trichodesmium crythraeus* (strain IMS101) using high-performance liquid chromatography electrospray ionization mass spectrometry (HPLC-ESI-MS) and observed no known siderophores.

Occurrence of ferrioxamine siderophores in *Trichodesmium* blooms. Next, we studied the occurrence of the ubiquitous marine siderophores, ferrioxamines B, G, and E in *Trichodesmium* blooms from the Arabian Sea and Gulf of Aqaba (Supplementary Fig. 2), employing high-resolution HPLC-ESI-MS. These surface blooms contained buoyant healthy colonies at moderate to high densities of 2–27 × 10⁹ trichomes L⁻¹ (Fig. 2). Colony microbes were found at concentrations of 6–41 × 10⁸ bacteria per trichome (Supplementary Table 1), in accord with reported values from *Trichodesmium* blooms worldwide. This density amounted to 7–15 × 10⁸ bacteria per liter (Fig. 2), which is 10–20 times higher than their density in seawater. Ferrioxamine concentrations were lower in the Arabian Sea bloom than in the Gulf of Aqaba bloom (2 pM and 45 pM, respectively, Fig. 2), and are in the range observed in surface seawater. Normalizing in situ ferrioxamine concentrations to bacterial biomass, measured values were 0.2–3 × 10⁻²¹ mol per bacteria, comparable or slightly lower than ratios reported for open water in the Atlantic Ocean.

Siderophores enhance Fe-mineral dissolution and bioavailability. Next, we examined the influence of ferrioxamines on dust-Fe solubility and bioavailability, using radiolabeled amorphous Fe-oxyhydroxide – ⁵⁵Fe-ferrihydrite – as a proxy for dust. In a series of dissolution and uptake experiments, we followed the iron path from the solid to the dissolved phase and into *Trichodesmium* and its associated bacteria, implementing a method we recently optimized for this purpose. We added Ferrioxamine B and E (FOB & FOE), that were detected in natural blooms (Fig. 2) to the experiments and tested their effect on ⁵⁵Fe-ferrihydrite dissolution.
dissolution rates and uptake by the consortium. Furthermore, the added FOE was extracted from one of the bacteria we isolated from natural Trichodesmium colonies from the Gulf of Aqaba. Baseline values (controls) for non-siderophore assisted dissolution and uptake rates were obtained in the presence of heat-inactivated ferrioxamines. In the absence of Trichodesmium, the ferrioxamines enhanced ferrihydrite dissolution rates by 4–6-fold compared to controls with heat-inactivated siderophores (Fig. 4a–c, black diamonds), demonstrating that these compounds can dissolve Fe-minerals present in dust. Uptake experiments with natural colonies and cultures showed that the siderophore enhanced dissolution directly benefitted the Trichodesmium consortium, with up to 10-fold higher uptake rates compared to controls (Fig. 4). Remarkably, Fe uptake rates were of the same order of magnitude as the observed dissolution rates, which imply that all the iron that was dissolved from ferrihydrite was assimilated (Fig. 4a–c). In the cultures, both ferrioxamines had a strong and positive effect on Fe uptake (Fig. 4c), while in natural colonies FOE had a much stronger positive effect on Fe-uptake than FOB (Fig. 4a, b). These differences may reflect the larger exposure of natural colonies from the Gulf of Aqaba to FOE compared to FOB (Fig. 3b–d), and possibly hint at specificity in the uptake systems. This observation is supported by studies showing that Trichodesmium indeed has proteins capable of siderophore transport33. Interestingly, siderophore additions enhanced Fe-uptake in natural Trichodesmium to a greater extent than for associated bacteria (Fig. 4d–f). The lack of benefit for the bacteria from the added siderophores may indicate that these siderophore producers are sufficiently supplied with Fe even without the additions. Yet their siderophore production is also favorable for themselves, as enhanced Trichodesmium growth favors associated bacteria via production of exudates2,3. The confined colony core is favorable for mineral-Fe uptake. Particles concentrated in the colony core provide a localized.
source of mineral-Fe that can be dissolved by siderophores. Hence, *Trichodesmium* and bacteria cells in the colony core may benefit from proximity to dissolved Fe and can internalize more Fe than cells in the colony periphery. We tested the spatial distribution of Fe internalized by several natural *Trichodesmium* colonies that were incubated for 24 h with 100 nM 55ferrihydrite, using radio imaging. Indeed, internalized Fe was detected mostly in the colony core and less in the periphery (Fig. 5). This finding of mineral-Fe utilization in the colony core further demonstrated how this consortium overcomes various physical and chemical constrains related to mineral-Fe availability. *Trichodesmium* combines physiological and behavioral traits enabling it to encounter, capture, and center dust within a microenvironment, where, assisted by its colony microbes, it dissolves mineral-Fe and effectively acquires it before it is lost by diffusion.

**Discussion**

*Trichodesmium* colonies form a cohabitation that actively reacts to dust by capturing it and extracting its nutrients. The colony microenvironment is an ideal physical setting for siderophore-mediated dissolution, which is highly effective under low
turbulence, high bacterial density, and short-range organism-mineral interactions. *Trichodesmium*’s ability to trap dust and confine it in the colony center, provides an optimal environment for dust dissolution by siderophores, allowing buildup of high siderophore concentrations with minimal diffusive losses of siderophores, either free or as the Fe-containing complex14. The confined colony microenvironment is also favorable for buildup of quorum sensing molecules known to play a role in coordinating siderophore production by different bacteria15,16. In addition, low carbon and nitrogen resources likely limit siderophore production by free-living bacteria, while *Trichodesmium* colonies provide the substrate for bacterial colonization and large fluxes of carbon and nitrogen in the form of exudates17-19. Hence, bacteria residing within *Trichodesmium* colonies have a distinct advantage over free-living bacteria in dissolving and utilizing Fe-minerals. In return, *Trichodesmium* gains a source of bioavailable dissolved Fe that would have otherwise remained as insoluble dust-bound Fe. We conclude that the collaborative effort within *Trichodesmium* colonies to increase bioavailability of iron from dust is mutualistic.

Our study is unique among the many genomic-based attempts to untangle the complex *Trichodesmium*-bacteria interactions, because it provides direct experimental evidence for the actual components of dust-Fe acquisition by the consortium. We confirmed genomic predictions of siderophore production and uptake by the consortium members20,21 and support the hypothesis that *Trichodesmium* and its colony microbes act as a synchronized metabolic circuit sharing key resources13. Our study adds to a growing body of research indicating that interspecies interactions control cycling of nutrients, such as nitrogen, carbon, phosphorus, iron, and vitamin B12.22-28. The microbial interactions within the colonies expand *Trichodesmium*’s metabolic diversity and contribute to their success in oligotrophic systems14,22,28.

In the open ocean, *Trichodesmium* is often co-limited by Fe and P and relies on dust inputs to supplement the supply of these limiting nutrients29. Wind-driven dust deposition into the oceans is predicted to intensify due to global warming driven desertification15. These future climatic scenarios of increased particulate Fe (and possibly P) inputs from dust deposition are favorable for *Trichodesmium*, owing to the unique mining strategies of Fe from dust elucidated in this study. As a result, in the future ocean *Trichodesmium* may increase in abundance and by nourishing other phytoplankton with essential nutrients can accelerate ocean primary production and biogeochemical cycling of elements.

**Methods**

**Collection of individual *Trichodesmium* colonies and surface blooms.** Samples were obtained from two study sites: the coastal Arabian Sea (15.448°N, 73.767°E) and the Gulf of Aqaba, at the northern end of the Red Sea (29.501°N, 34.917°E). In the Arabian Sea natural *Trichodesmium* bloom was collected from surface waters with a small boat in April 2014. In the Gulf of Aqaba several transient *Trichodesmium* blooms were observed next to the pier of Interuniversity Institute for Marine Sciences during April and May 2016 (Supplementary Fig. 2). These surface blooms were collected using acid-washed wide-mouth 5L polypropylene containers, examined for integrity under stereomicroscope and handpicked from polypropylene containers, examined for integrity under stereomicroscope and then diluted with 1 mL of 0.1% formic acid. Weights were recorded to allow for calculation of the percent fraction of Fe after extraction. The percent reduction in absorbance of Chrome Azurol-S assay was used to test the effect of siderophores on *ferrithydrate* dissolution and uptake by natural and cultured *Trichodesmium* and bacteria, which is fully detailed in Basu and Shaked28.

**Characterization of ferrioxamines from natural *Trichodesmium* blooms.** Analysis of ferrioxamines: siderophores were identified and quantified by high-performance liquid chromatography – electrospray ionization mass spectrometry (HPLC-ESI-MS; Ultimate 3000 and Q Exactive, Thermo Scientific) following preconcentration via solid-phase extraction22,28. Between 300 and 500 mL of incubated sample was preconcentrated over 200 mg ENV+ solid-phase extraction (SPME) (Biotage) at ambient pH. Prior to analysis, columns were desorbed, washed with 10 mM ammonium carbonate (pH 8.3), and eluted with 5 mL of acetonitrile: propan-2-ol: water: formic acid (80:15:5:0.1 v/v/v/v/v). A 1-mL aliquot was evaporated in a centrifugal evaporator (Thermo) to a volume of ~100 µL and then diluted with 1 mL of 0.1% formic acid.Weights were recorded to allow for calculation of the percent fraction of Fe after extraction. The percent reduction in absorbance of Chrome Azurol-S assay was used to test the effect of siderophores on *ferrithydrate* dissolution and uptake by natural and cultured *Trichodesmium* and bacteria, which is fully detailed in Basu and Shaked28.

**Epibiont isolation, siderophore screening, and extraction.** Individual *Trichodesmium* colonies were repeatedly collected from the Gulf of Aqaba during winter of 2014 to isolate associated bacteria. Colonies were washed thrice with microwave sterilized filtered seawater, homogenized by vortex, plated on Zobell 2216E solid medium, and incubated for 72 h at 25 °C. These plates, 23 associated bacteria colonies were isolated, purified, and screened for siderophore production, using Chrome Azurol-S assay32 (Supplementary Fig. 1). Siderophore producers were identified by growing purified isolates in Fe-limited cFSW media amended with cleaned 0.05% tryptophane, phosphate (100 µM), ammonium chloride (5 µM), and MgSO4·7H2O (50 µM), at 25 °C, shaking 150 rpm for 72 h. The cells were spun down at 10,000 rpm and 100 µL of cell-free supernatant was allowed to equilibrate with 100 µL of Chroma Azurol S dye in a 96-well microtiter plate (Bio-Tek) for 30 min and absorbance measured at 630 nm. Synthetic siderophore Desferrioxamine B (100 µM) and blank media were used as positive and negative controls, respectively to confirm siderophore producers. The percent reduction in absorbance of Chroma Azurol S dye (630 nm) with respect to blank media was expressed as percent siderophore units.

A potent siderophore-producing epibiont strain E-23 was further grown in 1L cFSW low-Fe media and its secreted siderophores were extracted using Sep-Pak C18 columns.

In brief, stationary phase E-23 cells were spun down and the cell-free supernatant was slowly pumped through a series of three C18 Sep-Pak columns activated with methanol. The solution was circulated through the Sep-Pak three times to increase extraction yield. The columns were then eluted with three aliquots of 5 mL methanol, dried overnight in a laminar flowhood over ice, and reconstituted in 1 mL of 18.2 MΩ cm DDW. The presence of siderophores in the C18 extract was confirmed using the Chrome Azurol-S assay. HPLC-ESI-MS analysis of this extract of this detected a single Fe-binding ligand, identified as ferrioxamine E (Supplementary Fig. 3). Addition of 69Ga showed that ferrioxamine E was the dominant siderophore, although trace amounts of ferrioxamine G were also observed. This C18 extract was not purified thereafter by preparatory chromatography, its concentration was determined using the Chrome Azurol-S assay and the extract is referred to as FEO in this publication.

**Probing the effect of siderophores on mineral Fe-uptake and dissolution rates.** We used a recently optimized radiotracer assay with 57Fe to test the effect of siderophores on *ferrithydrate* dissolution and uptake by natural and cultured *Trichodesmium* and bacteria, which is fully detailed in Basu and Shaked28.
Mineral iron dissolution assay: radiolabeled iron oxohydroxide (amorphous ferrihydrite) was synthesized by titrating acidic $^{55}$Fe solution ($^{55}$FeCl$_3$, specific activity 10.18 mCi mg$^{-1}$, Perkin Elmer) with 0.1 N NaOH to pH 8.1. The amorphous mineral that formed was stabilized by heating (60°C, 2 h) and subsequent aging for 3 weeks. Dissolution rates were measured in FSW over 24 h at 25°C in the absence of cells using 100 nM $^{55}$Fe-ferrihydrite, by examining the fraction smaller than 0.22 μm. Sub-samples were filtered through 0.22 μm polycarbonate filter at the beginning and end of the incubation (or in additional intermediate time points). Aliquots were placed in Quick-Scint scintillation cocktail for β-counting in Tri-carb 1600 CA (Packard) liquid scintillation counter.

Mineral iron uptake assay: iron internalization rates were measured by incubating either natural Trichodesmium (30–40 colonies per treatment) or Fe-limited cultured Trichodesmium erythraeum IMS101 (1.7 ± 0.2 x 10$^3$ trichomes mL$^{-1}$) with radiolabeled 100 nM $^{55}$Fe-ferrihydrite for 24 h (25°C, 12:12 h photoperiod with ~80 μmol m$^{-2}$ s$^{-1}$). At the end of the incubation, Trichodesmium was washed in Ti-EDTA-citrate reagent (100 nM $^{55}$FeCl$_3$, specific activity 10.18 mCi mg$^{-1}$, Perkin Elmer) with 0.1 N NaOH to pH 8.1. The amorphous mineral that formed was stabilized by heating (60°C, 2 h) and subsequent aging for 3 weeks. Dissolution rates were measured in FSW over 24 h at 25°C in the absence of cells using 100 nM $^{55}$Fe-ferrihydrite, by examining the fraction smaller than 0.22 μm. Sub-samples were filtered through 0.22 μm polycarbonate filter at the beginning and end of the incubation (or in additional intermediate time points). Aliquots were placed in Quick-Scint scintillation cocktail for β-counting in Tri-carb 1600 CA (Packard) liquid scintillation counter.

Radio-imaging of 2D mineral Fe uptake. Individual Trichodesmium colonies were incubated with 100 nM $^{55}$Fe-ferrihydrite in a 96-well microtiter plate for 24 h. The colonies for radio imaging were carefully picked and soaked in Ti-EDTA-Citrate solution for 10 min to remove extracellular ferrihydrite. The colonies were fixed with 2% buffered glutaraldehyde (v/v), washed by five repeated transfers in fresh FSW using dropping pipette and placed on glass-slides. Here, by minimizing physical manipulation we managed to retain some intact colonies for the imaging. Killed individual colonies were treated as such to confirm absence of intracellular $^{55}$Fe. The slides were covered by a scintillation foil and the internalized $^{55}$Fe was radio-imaged and revealed no measurable counts above background.

Statistics and reproducibility. Given the low biomass of naturally occurring Trichodesmium population, we were unable to replicate all our measurements, let alone exceed two replicates (duplicates). However, the reproducibility of our results was attained by repeating the sidereophore measurements and the uptake experiment over multiple days during two seasons, and in two remote sites. When experimenting with Fe-limited cultured Trichodesmium erythraeum strain IMS101, five biological replicates were conducted to ensure statistical significance.

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability All data supporting the findings of this study are available in the Supplementary Information file.

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Author contributions
S.B. and Y.S. with inputs from M.G. designed the study. S.B. and S.G.P.M. collected the Arabian Sea sample. S.B., Y.S., and M.G. collected the Gulf of Aqaba samples. S.B., Y.S., M.G., and D.B. analyzed the data and wrote the paper.

Additional information
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Competing interests:
The authors declare no competing interests.

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