

Costs of dust collection by *Trichodesmium*: effect on buoyancy and toxic metal release

Siyuan Wang¹, Futing Zhang¹, Coco Koedooder², Odeta Qafoku³, Subhajit Basu⁴, Stephan Krisch⁵, Anna-Neva Visser¹, Meri Eichner⁶, Nivi Kessler⁷, Rene Boiteau⁸, Martha Gledhill⁹, and Yeala Shaked¹⁰

¹The Hebrew University of Jerusalem & The Interuniversity Institute for Marine Sciences in Eilat

²The Hebrew University of Jerusalem, The Interuniversity Institute for Marine Sciences in Eilat & Israel Limnology and Oceanography Research

³Pacific Northwest National Laboratory

⁴The Hebrew University of Jerusalem, The Interuniversity Institute for Marine Sciences in Eilat & UPES, Dehradun

⁵Bundesanstalt für Gewässerkunde

⁶Institute of Microbiology of the Czech Academy of Sciences

⁷The Hebrew University of Jerusalem, The Interuniversity Institute for Marine Sciences in Eilat & The water authority, Israel

⁸Massachusetts Institute of Technology

⁹GEOMAR Helmholtz Center for Ocean Research

¹⁰Hebrew University & Interuniversity Inst for Marine Sciences

December 10, 2023

Abstract

The marine cyanobacterium *Trichodesmium* has a remarkable ability to interact with and utilize air-borne dust as a nutrient source. However, dust may adversely affect *Trichodesmium* through buoyancy loss and exposure to toxic metals. Our study explored the effect of desert dust on buoyancy and mortality of natural Red Sea puff-shaped *Trichodesmium thiebautii*. Sinking velocities and ability of individual colonies to stay afloat with increasing dust loads were studied in sedimentation chambers. Low dust loads of up to ~400 ng per colony did not impact initial sinking velocity and colonies remained afloat in the chamber. Above this threshold, sinking velocity increased linearly with the colony dust load at a slope matching prediction based on Stoke's law. The potential toxicity of dust was assessed with regards to metal dissolution kinetics, differentiating between rapidly released metals that may impact surface blooms and gradually released metals that may impact dust-centering colonies. Incubations with increasing dust concentrations revealed colony demise, but the observed lethal dose far exceeded dust concentrations measured in coastal and open ocean systems. Removal of toxic particles as a mechanism to reduce toxicity was explored using SEM-EDX imaging of colonies incubated with Cu-minerals, yet observations did not support this pathway. Combining our current and former experiments, we suggest that in natural settings the nutritional benefits gained by *Trichodesmium* via dust collection outweigh the risks of buoyancy loss and toxicity. Our data and concepts feed into the growing recognition of the significance of dust for *Trichodesmium*'s ecology and subsequently to ocean productivity.

1 **Costs of dust collection by *Trichodesmium*: effect on buoyancy and toxic**
2 **metal release**

3

4 Siyuan Wang^{1,2}, Futing Zhang^{1,2}, Coco Koedooder^{1,2,3}, Odeta Qafoku⁴, Subhajit Basu^{1,2,5}, Stephan
5 Krisch⁸, Anna-Neva Visser^{1,2}, Meri Eichner⁶, Nivi Kessler^{1,2,9}, Rene M. Boiteau⁷, Martha Gledhill⁸
6 and Yeala Shaked^{1,2}

7

8 ¹ The Freddy and Nadine Herrmann Institute of Earth Sciences, Edmond J. Safra Campus, Givat Ram,
9 Hebrew University of Jerusalem, Jerusalem, Israel

10 ² The Interuniversity Institute for Marine Sciences in Eilat, Eilat, Israel

11 ³ Israel Limnology and Oceanography Research, Haifa, Israel

12 ⁴ Environmental Molecular Sciences Laboratory (EMSL), Pacific Northwest National Laboratory
13 (PNNL), Richland, WA, 99454, USA

14 ⁵ University of Petroleum and Energy Studies (UPES-SoHST), Energy Acres, Dehradun 248007, India

15 ⁶ Center Algatech, Institute of Microbiology of the Czech Academy of Sciences, Novohradská 237,
16 37981 Třeboň, Czech Republic

17 ⁷ Department of Chemistry, University of Minnesota, Minneapolis, MN 55455

18 ⁸ GEOMAR, Helmholtz Center for Ocean Research, Kiel, Germany

19 ⁹ Present address: The water authority, 7 Bank of Israel st, Jerusalem 9195021, Israel

20

21

22

23

24

25 **Corresponding author:** Yeala Shaked

26 Email: yeala.shaked@mail.huji.ac.il

27

28 Abstract

29 The marine cyanobacterium *Trichodesmium* has a remarkable ability to interact with and utilize air-
30 borne dust as a nutrient source. However, dust may adversely affect *Trichodesmium* through
31 buoyancy loss and exposure to toxic metals. Our study explored the effect of desert dust on
32 buoyancy and mortality of natural Red Sea puff-shaped *Trichodesmium thiebautii*. Sinking velocities
33 and ability of individual colonies to stay afloat with increasing dust loads were studied in
34 sedimentation chambers. Low dust loads of up to ~400 ng per colony did not impact initial sinking
35 velocity and colonies remained afloat in the chamber. Above this threshold, sinking velocity
36 increased linearly with the colony dust load at a slope matching prediction based on Stoke's law.
37 The potential toxicity of dust was assessed with regards to metal dissolution kinetics, differentiating
38 between rapidly released metals that may impact surface blooms and gradually released metals
39 that may impact dust-centering colonies. Incubations with increasing dust concentrations revealed
40 colony demise, but the observed lethal dose far exceeded dust concentrations measured in coastal
41 and open ocean systems. Removal of toxic particles as a mechanism to reduce toxicity was explored
42 using SEM-EDX imaging of colonies incubated with Cu-minerals, yet observations did not support
43 this pathway. Combining our current and former experiments, we suggest that in natural settings
44 the nutritional benefits gained by *Trichodesmium* via dust collection outweigh the risks of buoyancy
45 loss and toxicity. Our data and concepts feed into the growing recognition of the significance of
46 dust for *Trichodesmium's* ecology and subsequently to ocean productivity.

47

48 Plain Language Summary

49 The abundant marine phytoplankton *Trichodesmium* spp. are nitrogen-fixing cyanobacteria that
50 form extensive blooms in low latitude warm oceans and contribute significantly to carbon (C) and
51 nitrogen (N) fixation, recycling and export. Desert dust deposited on the ocean surface is an
52 important nutrient source for *Trichodesmium*. Spherical, millimeter-sized colonies of
53 *Trichodesmium* from different ocean basins were reported to strongly interact with dust and shuffle
54 dust particles to the colony core. While dust collection can optimize nutrient supply, it may come at
55 a cost to *Trichodesmium*. Heavy dust loads may send the colonies to the deep ocean and metal
56 release from dust may induce toxicity. Here, experimenting with Red Sea colonies and desert dust
57 we studied some of the trade-offs of dust collection. Interacting colonies with dust, we examined
58 the link between dust load and colony buoyancy. Combining dust dissolution measurements and
59 mortality assays we examined toxicity thresholds for *Trichodesmium* surface blooms and dust-
60 collecting colonies. We also studied the ability of colonies to remove particles and the effect of
61 particle loss on their sinking velocity. Our experimental findings and concepts are valuable for
62 assessing *Trichodesmium*'s distribution and ecophysiology and contribute to modeling of C or N
63 transport to the deep ocean.

64

65 Key Points

- 66 ● Dust collected by *Trichodesmium* colonies from seawater as a nutrient source may result in
67 metal toxification and buoyancy loss.
- 68 ● At moderate dust loads colonies maintained their buoyancy, but above a threshold sinking
69 velocities increased linearly with dust loads.
- 70 ● Desert dust induced *Trichodesmium* mortality through toxic metal release, but the lethal dose
71 far exceeded oceanic dust concentrations.

72

73 1. Introduction

74 *Trichodesmium* spp. is a filamentous, N₂-fixing, and bloom-forming cyanobacterium inhabiting
75 subtropical and tropical oligotrophic ocean regions and contributing ~40% of the annual global
76 marine nitrogen fixation (Capone et al., 1997; Tang et al., 2020; Zehr & Capone, 2020).
77 *Trichodesmium* spp. appear both as individual filaments (trichomes) and as colonies containing
78 hundreds to thousands of trichomes organized in millimeter-sized tuft- or puff-shaped aggregates
79 (Eichner et al., 2023). In the Red Sea, puff-shaped colonies are primarily composed of
80 *Trichodesmium thiebautii* while tuft-shaped colonies are typically comprised of *Trichodesmium*
81 *erythraeum* (Koedooder et al., 2022). The different colony morphologies also serve as micro-
82 habitats for diverse microbes including bacteria, phytoplankton and even zooplankton, all
83 exchanging nutrients and carbon throughout the colony life cycle from growth to demise (Anderson,
84 1977; Frischkorn et al., 2018; Lee et al., 2017; Rouco et al., 2016).

85 Natural *Trichodesmium* is often limited or co-limited by iron (Fe) and phosphorus (P) (Cerdan-Garcia
86 et al., 2022; Held et al., 2020). Aerosol dust deposited on the ocean surface is considered an
87 important nutrient source, but the low solubility of Fe and P minerals restricts its bioavailability for
88 phytoplankton (Mills et al., 2004; Shaked et al., 2023; Shaked & Lis, 2012; Stockdale et al., 2016).
89 Incubation studies revealed that *Trichodesmium* successfully grow on aerosol or dust (Chen et al.,
90 2011; Polyviou et al., 2018) and even increase the bioavailability of dust Fe and P (Basu et al., 2019;
91 Basu & Shaked, 2018; Shaked et al., 2023). An intriguing finding, which was reaffirmed in several
92 studies is the ability of *Trichodesmium* colonies to actively collect and transport dust particles into
93 the colony core (Kessler, Armoza-Zvuloni, et al., 2020; Rubin et al., 2011; Wang et al., 2022), which
94 may serve to enhance dust dissolution, minimize nutrient loss by diffusion and optimize uptake
95 (Eichner et al., 2023; Shaked et al., 2023). While these nutritional benefits are well established, yet
96 studies exploring negative sides of particle collection to *Trichodesmium* remain scarce. Collection of
97 heavy dust minerals may result in buoyancy loss and accelerate sinking to the deep ocean (Held et
98 al., 2022; Pabortsava et al., 2017). Dust also contains an array of toxic elements (Bozlaker et al.,
99 2013; Mackey et al., 2015), which upon gradual release within the colony core may induce toxicity
100 and cause mortality. Our study focuses on this “dark side” of particle collection by, firstly,
101 investigating the effect of dust on buoyancy and trace metal exposure of *Trichodesmium* and,
102 secondly, examining active particle removal.

103 Depending on composition, dust particle density was reported to range from 2.1 to 2.6 g·cm⁻³
104 (McConnell et al., 2008; Schladitz et al., 2009), much denser than *Trichodesmium* with density of ~1
105 g·cm⁻³ (J. Kromkamp & Walsby, 1992; White et al., 2006). Consequently, collection of dust particles
106 by *Trichodesmium* colonies increases their density and may affect *Trichodesmium's* buoyancy.
107 *Trichodesmium* spp. regulates its buoyancy through gas vesicles which can withstand high pressures
108 (up to 12-37 bars, Walsby, 1992). This allows *Trichodesmium* to float on the water surface while
109 also being able to resist hydraulic forces and conduct vertical migration to several hundred or
110 thousand meters (Benavides et al., 2022; Pabortsava et al., 2017; Walsby, 1992). While a recent
111 study modeled the effect of dust on sinking velocities of *Trichodesmium* (Held et al., 2022),
112 experimental evidence linking dust loads and sinking velocities are missing.

113 Dust and other aerosols contain an array of elements, some of which are required as nutrients,
114 while others such as cadmium (Cd), copper (Cu), lead (Pb) and arsenic (As) can be toxic (Guo et al.,
115 2022; Mackey et al., 2012; Paytan et al., 2009; Yang et al., 2019). The potential toxicity of dust (or
116 other aerosols) to *Trichodesmium* depends on the kinetics of toxic metal release to seawater, which
117 in turn vary with aerosol types and sources, reactions occurring during atmospheric transport and
118 particle to solvent ratios (Mackey et al., 2015; Mahowald et al., 2018; Stockdale et al., 2016).
119 Natural populations of *Trichodesmium* colonies are reported to be very sensitive to toxic metals
120 such as Cu and As (Hewson et al., 2009; Rueter et al., 1979). In addition to metals released from
121 dust to the seawater surrounding natural *Trichodesmium*, the collection of dust within colonies
122 further exposes them to toxic metals which gradually dissolve from the particles. However, dust
123 toxicity to *Trichodesmium*, especially at the level of individual colonies, is poorly understood.

124 Our study focuses on this “dark side” of particle collection by investigating the effect of dust on
125 buoyancy and trace metal exposure of *Trichodesmium* and examining active particle removal. These
126 effects were investigated through two sets of experiments with natural *Trichodesmium* colonies: 1)
127 sedimentation experiments with single colonies artificially loaded with dust, and 2) incubations with
128 increasing dust concentrations probing mortality and metal release rates. The ability of
129 *Trichodesmium* to mitigate these effects through particle removal was also examined. This research
130 highlights potential trade-offs associated with particle collection and may contribute to predicting
131 *Trichodesmium's* vertical distribution and role in C and N export to the deep ocean.

132

133 2. Material and methods

134 2.1 Colony & dust collection

135 *Trichodesmium* colonies were collected from the Gulf of Aqaba (29.56°N, 34.95°E) at the Northern
136 Red Sea via net tows during 2018-2022. Each tow was conducted for ~7 min at the boat's minimal
137 speed (1-2 knots) by deploying a 100 µm phytoplankton net (Aquatic Research Instrument, USA) to
138 10-20 m depth. The net concentrate was diluted into ~5 L seawater to minimize stress and well-
139 shaped puff colonies were quickly hand-picked by droppers, placed in clean Petri dishes and
140 washed three times with 0.22 µm filtered seawater (FSW). Dust samples were collected from the
141 Gulf of Aqaba shores at the Inter-University Institute for Marine Sciences in Eilat (IUI). Samples of
142 settled dust were collected from plastic surfaces located ~2 m from the sea, sieved through a 63 µm
143 mesh, air-dried and stored in a desiccator.

144 2.2 Effect of dust load on colony buoyancy

145 Sedimentation experiments – During autumn 2020, sedimentation experiments were conducted on
146 five consecutive days, on each testing five different colonies. Sinking velocities were measured in 18
147 cm tall sedimentation chambers (100 mL glass cylinders with 2.5 cm diameter). Colonies were
148 gently introduced to chambers filled with fresh seawater and their vertical positions were recorded
149 over time (see Fig. S1 for a schematic diagram and further details). Two types of data were
150 collected: Initial colony sinking velocities in the chamber and colony positions in the chamber after
151 15 min. Each colony was tested three times: as is, and following interactions with medium and then
152 high dust concentrations. All colonies were initially sinking and hence the sinking velocities were
153 always positive. However, after 15 min colonies appeared to adjust their buoyancy and resumed
154 different positions in the chamber. The ones at the bottom of the sedimentation chamber were
155 defined as “sinkers” and the ones further up in the water as “floaters”. Colony-dust interactions
156 were induced by gently and repetitively mixing colonies within an eppendorf vial which contained
157 seawater with the respective amount of dust. The dust load (weight) on each colony was calculated
158 from stereoscopic images taken prior to introducing the colonies to the sedimentation chamber.
159 Since many colonies lost dust particles during the experiments, another image was taken at the end
160 of each experiment and dust weight was re-calculated.

161 [Estimation of colony dust loads](#) – Dust load (weight) was estimated from colony images taken with a
162 stereoscope (Nikon, SMZ745). Using DinoCapture 2.0 and ImageJ software, the area of dust
163 centered by the colony (μm^2) was estimated. This area was converted to volume (μm^3) assuming a
164 constant thickness of 10 μm for the dust layer and then to mass using an average density of 2.5
165 $\text{g}\cdot\text{cm}^{-3}$ (see Fig. S2 for details; Kessler, Kraemer, et al., 2020). Similar analysis was done on published
166 images of dust-containing colonies (Held et al., 2021).

167 [Calculating the effect of dust on colony sinking velocities](#) – Stoke's law and its modified equations
168 has been widely applied in calculating and modeling sinking velocities of marine aggregates
169 including natural *Trichodesmium* colonies (Jacco Kromkamp & Walsby, 1990; Laurenceau-Cornec et
170 al., 2020; White et al., 2006). Recently, several attempts were made to assess the density change
171 induced by internal ballasts (Benavides et al., 2022; Held et al., 2022). When colonies collect dust
172 not only its mass needs to be considered but also its volume. To account for both, dust mass and
173 volume, the Stoke's law-based equation, adapted for *Trichodesmium* by White et al. (2006), was
174 modified (supplementary text S1). Based on this modified equation, the colony sinking velocity is
175 predicted to increase linearly with dust load:

176 Equation. 1 Sinking velocity (dust-loaded colony) ($\text{m}\cdot\text{d}^{-1}$) =
177 Sinking velocity (dust-free colony) ($\text{m}\cdot\text{d}^{-1}$) + $K (\text{m}\cdot\text{d}^{-1}\cdot\text{ng}^{-1}) \times \text{dust weight (ng)}$

178 The dust factor (K) is the velocity increase per dust mass with a unit of $\text{m}\cdot\text{d}^{-1}\cdot\text{ng}^{-1}$. Applying the
179 measured colony size and the density of dust, Red Sea seawater and *Trichodesmium* cells (Basu &
180 Shaked, 2018; Benaltabet et al., 2022; McConnell et al., 2008; Schladitz et al., 2009; White et al.,
181 2006), we calculated that $K=0.02-0.06 (\text{m}\cdot\text{d}^{-1}\cdot\text{ng}^{-1})$ (supplementary text S2).

182 **2.3 Metals in dust and toxicity to *Trichodesmium***

183 [Dust dissolution experiments](#) – Dust dissolution experiments were conducted in four separate
184 experiments during 2015, using trace metal clean procedures, as described in Basu et al. (2019) and
185 Gledhill et al. (2019). Local Red Sea dust was added to acid-cleaned Nalgene bottles containing
186 gravimetrically quantified filtered seawater at final concentrations of 2 and 10 $\text{mg}\cdot\text{L}^{-1}$ and incubated
187 at 25°C for 62 hours. 60 mL sub-samples were filtered through 0.22 μm syringe-filters (PVDF, Millex)
188 using a Dynamax (Rainin) 8-head peristaltic pump under a clean bench. Sub-samples were stored
189 for 6 months in trace metal cleaned high density polyethylene (HDPE) bottles and acidified to pH

190 ~1.7 with ultra-clean HNO₃ prior to analysis of metals. Metals were analyzed by inductively coupled
191 plasma mass spectrometry after preconcentration (SeaFAST pico) following the method of Rapp et
192 al. (2017) and were quantified by standard addition (Krisch et al., 2022) at GEOMAR, Helmholtz
193 Centre for Ocean Research, Kiel, Germany. Extending our experiments we also included dissolution
194 measurements of local Red Sea dust samples from Mackey et al. (2015). We then split the
195 dissolution data to two groups: 1) rapid dissolution (10 min and 6 h), and 2) gradual dissolution (1, 3
196 and 7 days).

197 Toxicity assays – Dust toxicity was investigated by incubating ~180 individual natural
198 *Trichodesmium* colonies for 24 h in 48 well-plates with either dust suspension or dust leachate.
199 Primary dust suspension was prepared daily in FSW and diluted to final concentrations of 2, 10, 100,
200 500, and 1000 mg·L⁻¹. Dust leachates were obtained after 10 min by filtering the dust suspensions
201 through 0.22 µm syringe-filters (PC membrane). Colonies were incubated in wells of a 48-well plate
202 containing 0.5 mL dust suspension or leachate and were kept in a culture room (25 °C, ~80 µE m⁻² s⁻¹,
203 10:14 h light-dark cycle). Visual changes of the colony and filament shape, structure, and color
204 were monitored under a stereoscope at 2, 5, and 24 h (supplementary text S4). Incubations were
205 repeated twice during spring 2022 and included controls without dust additions. Probing specifically
206 for Cu toxicity, colonies were also incubated with dissolved Cu (5-3000 nM CuSO₄, supplementary
207 text S4).

208 **2.4 Removal of Cu-containing minerals**

209 Hypothesizing that colonies may remove toxic minerals as a detoxification mechanism, 16 Red Sea
210 colonies were incubated with the Cu mineral malachite (Cu₂CO₃(OH)₂). To ensure optimal colony-
211 mineral interactions, malachite was mixed with hematite (α-Fe₂O₃), which is typically preferred by
212 *Trichodesmium*. Individual colonies were sampled at different time points, placed on filters and
213 probed for the presence of malachite via light microscopy and scanning electron microscopy with
214 energy dispersive X-Ray analysis (SEM-EDX). Experiments were repeated for three days in autumn
215 2021. Malachite was obtained from Timna National Park (Eilat, Israel), crushed and sieved (<38µm),
216 while hematite (<38µm) was obtained from the Mineral Collection at the National Natural History
217 Collections at the Hebrew University of Jerusalem. Colonies were incubated in eppendorf vials
218 under the IUI pier up to 24 hrs. At three time points, randomly selected colonies were imaged and

219 placed on a PES membrane filter (Supor®), air-dried and frozen prior to SEM-EDX analysis (see
220 supplementary text S5 for full details).

221 [*Microscopic SEM-EDX imaging*](#) – Colonies were placed on Supor® filters and coated with a ~10 nm
222 carbon layer by thermal evaporation using a 108C Auto Carbon Coater (Ted Pella, Inc.) to avoid
223 charging during the analysis. SEM images were collected with a FEI Helios NanoLab 600i field
224 emission electron microscope. Specimen morphology was examined using a secondary electron
225 Everhart-Thornley detector (ETD) in a field free mode at an acceleration voltage of 3 kV and a probe
226 of 86 to 170 pA at 4 mm working distance. EDX analysis was performed at 10 to 20 kV and 1 to 2 nA
227 with an X-Max 80mm² Silicon Drift Detector (SDD) from Oxford Instruments. Oxford AZtec software
228 was used to collect compositional maps and point spectrum analyses.

229

230 3. Results and discussion

231 3.1 Dust loads and buoyancy control

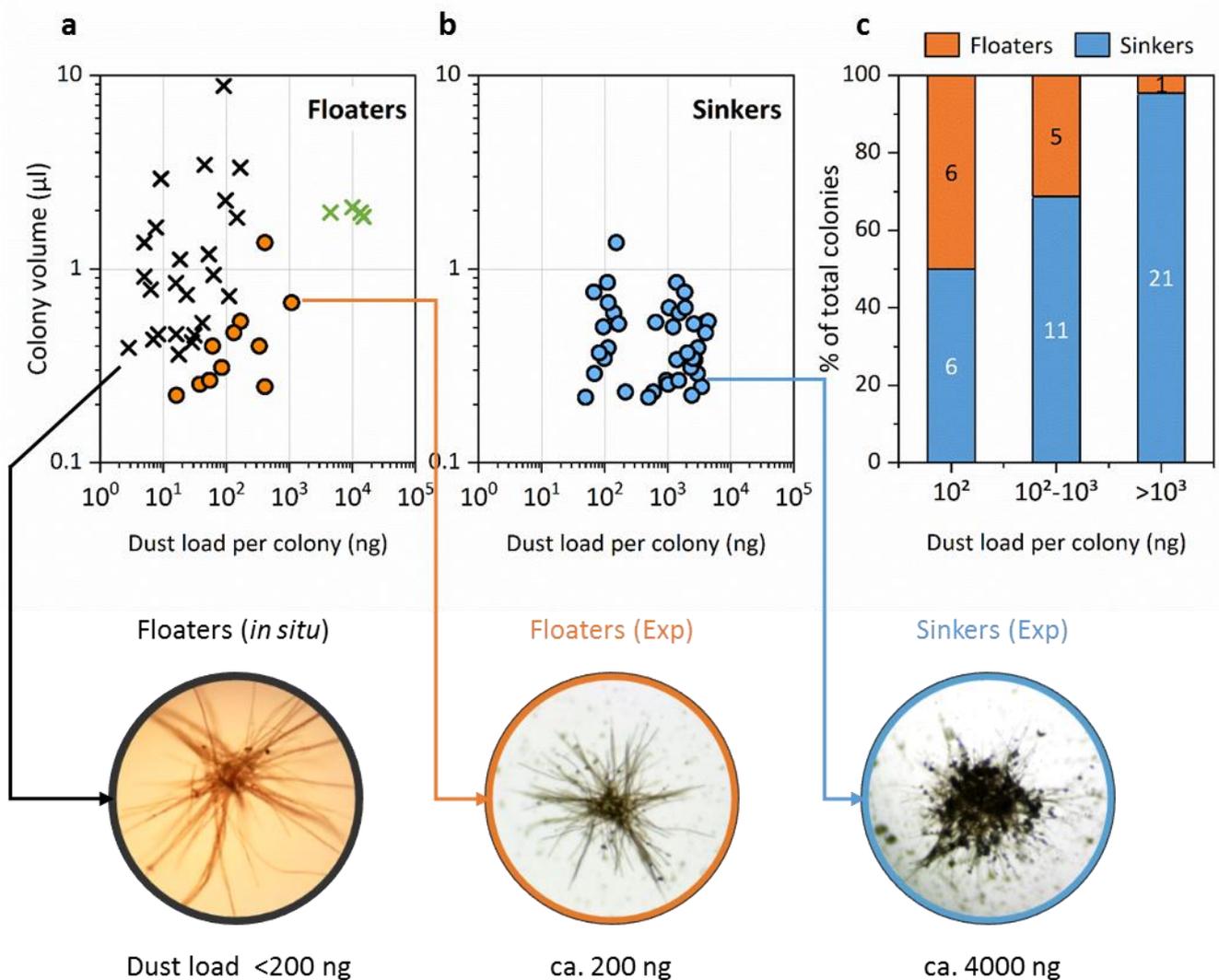
232 Collection and centering of dust particles by *Trichodesmium* colonies may result in buoyancy loss
233 and enhance their sinking velocities to the ocean depth. In the following section we present
234 experimental results of natural colonies that were interacted with dust and tested in sedimentation
235 chambers. The impact of dust on the colony buoyancy was examined by two different measures: 1)
236 initial, short-term (~5 min) sinking velocity, and 2) colony position in the chamber after a 15 min
237 acclimation period. All colonies had positive initial sinking velocities, but within 15 minutes some
238 colonies left the chamber bottom and were re-suspended in the water. Colonies that remained on
239 the bottom were considered as non-buoyant (“sinkers”), while those in the water were considered
240 as buoyant (“floaters”).

241 3.1.1 How much dust can a colony bear to stay afloat?

242 At low dust loads (<100 ng) half of the colonies were classified as “floaters” (Fig. 1, orange symbols).
243 At intermediate dust loads of 100-1000 ng, the fraction of “floaters” dropped but still accounted for
244 ~30% of the colonies (Fig. 1, orange symbols). These findings demonstrate a remarkable ability of
245 *Trichodesmium* to adjust their buoyancy to accommodate a significant dust load, assisted by their
246 gas vesicles (Walsby, 1992). At increasing dust loads, and especially above 1 µg dust per colony,
247 most colonies were defined as “sinkers” (Fig. 1, blue symbols), indicating a limit to *Trichodesmium*'s
248 capacity to adapt its buoyancy.

249 Expanding the experimental data to natural conditions, dust loads associated with Red Sea
250 *Trichodesmium* colonies collected from the upper 10-20 meters during 2018/19 were analyzed.
251 These colonies were considered buoyant since they populated the upper water column and were
252 plotted together with the experimentally determined “floaters” (Fig. 1a). Each colony typically
253 contained 1-7 particles in sizes ranging between 10-70 µm in diameter (Table S1). The calculated
254 weight of these particles amounted to 3-170 ng per colony and did not correlate with the colony
255 volume (Fig. 1a, black crosses). These estimated dust-loads of floating, naturally occurring colonies,
256 matched our experimental findings (Fig. 1a, orange circles). Similar weights of 200-300 ng dust per
257 colony were also reported by Kessler et al. (2020), who analyzed SEM images of colonies collected
258 from the upper 20 meters of the Gulf of Aqaba (Kessler, Kraemer, et al., 2020). Interestingly, the

259 Red Sea colonies fall short compared to Atlantic colonies collected from 20 m that remain afloat
 260 with much higher particle loads (Bif & Yunes, 2017; Held et al., 2021). Analyzing single colony
 261 images from the study of Held et al. (2021), we calculated dust loads of up to 10 μg per colony (Fig.
 262 1a, green crosses). The ability to keep afloat with a higher dust load may stem from larger number
 263 of filaments in the colonies from the Atlantic compared with those from the Red Sea colonies.
 264 Based on these experiments and observations, we draw the threshold of dust that Red Sea puff-
 265 shaped colonies can bear and stay afloat at few hundred nanograms.



266

267

268 **Figure 1. Effect of dust load on the buoyancy of natural *Trichodesmium* colonies.**

269 Data compilation from natural colonies either containing particles when collected (crosses) or interacted
 270 with dust and tested in sedimentation experiments (circles). Colonies were categorized as “floaters” or
 271 “sinkers” according to their position in sedimentation chambers after 15 min. *In situ* colonies were defined
 272 as “floaters” since they were collected from the upper water column for 10-20 m depth.

- 273 (a) Range of dust loads associated with “floaters” colonies tested in sedimentation experiments (n=12,
274 orange circles) and freshly collected from the Red Sea (n=24, black crosses) and the Atlantic Ocean (n=4,
275 green crosses, images from Held et al., 2021).
- 276 (b) Range of dust loads associated with “sinker” colonies tested in sedimentation experiments (n=38, blue
277 circles).
- 278 (c) Fraction of experimentally determined “floaters” and “sinkers” as a function of dust load per colony.
279 Pictures show typical dust loads as quantified through image analysis.

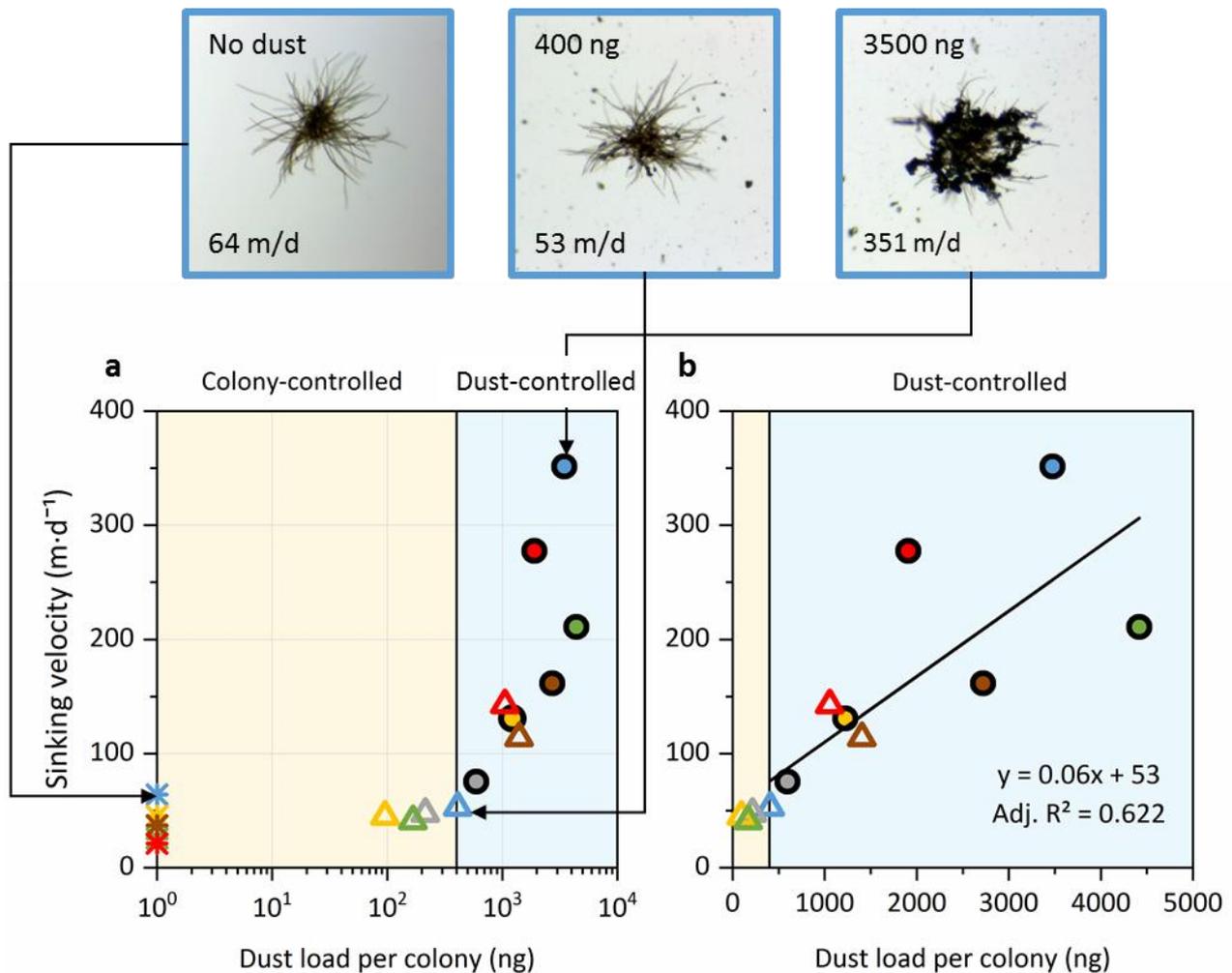
280 *3.1.2 Effect of dust on colony sinking velocity*

281 Initial sinking velocities for individual colonies were examined three times: without any dust, with
282 medium dust load (20 to 1400 ng colony⁻¹), and with high dust load (330 to 4400 ng colony⁻¹).
283 Experiments were repeated on five different days obtaining 75 data pairs of dust loads and sinking
284 velocities (Table S2). As before, colonies were imaged prior to and after each step to track their
285 actual dust loads. Data from two representative days (October 18th & 20th 2020) with six individual
286 colonies show that moderate dust load of 100-400 ng did not affect the colony’s sinking velocity,
287 which remained at 40-50 m·d⁻¹ (Fig. 2a). The initial colony sinking velocities at these low dust loads
288 were presumably controlled by colony size, colony composition (i.e. carbohydrate content) and gas
289 vesicles but not by dust (Held et al., 2022; Walsby, 1992), a region which we term “colony-
290 controlled” (Fig. 2, yellow area). This region is typified by the lack of effect of dust on the initial
291 colony sinking velocity and is in-line with our other observations from the sedimentation chambers
292 after 15 min (Fig. 1). Combined with field observations (Fig. 1a), our results suggest that Red Sea
293 colonies can maintain their buoyancy when interacting with several hundred nanograms of dust.

294 Further dust addition (1-4 µg per colony) shifted the measured sinking velocities into a dust-
295 controlled region (Fig 2, blue area). In this region, sinking velocities increased linearly with the
296 colony’s dust load (Fig. 2b). A linear relationship is expected based on theoretical considerations
297 (Stoke’s law) and direct sinking velocity measurements of size-specific ballasted aggregates (Engel
298 et al., 2009; Iversen & Ploug, 2010). However, according to Stoke’s law, sinking velocity is impacted
299 by both aggregate size and density (e.g. Laurenceau-Cornec et al., 2020). In our case, the colony size
300 remained unchanged for all dust loads since it was centered within the colony core (as confirmed
301 by microscopic observations). Taking into consideration the colony volume and density and the
302 centered dust we derived a linear relationship between dust load and colony sinking velocity (Eq. 1),
303 that should apply for the blue region (see methods and supplementary text S1 and S2). This
304 theoretical calculation predicted a slope (K) of 0.02-0.06 m·d⁻¹·ng⁻¹, implying that 100 ng dust will

305 increase the colony sinking velocity by 2-6 meters per day. Our experimental data yielded a slope (K)
306 of $0.06 \text{ m}\cdot\text{d}^{-1}\cdot\text{ng}^{-1}$ (Fig. 2b) very similar to these theoretical predictions and thus supports our
307 experimental approach. The match between experiments and predictions holds for dust-loaded
308 colonies but not for dust-free colonies. Our measured sinking velocities of particle-free colonies
309 ($40\text{-}55 \text{ m}\cdot\text{d}^{-1}$, Fig. 2) exceed their predicted sinking velocities ($0\text{-}9 \text{ m}\cdot\text{d}^{-1}$, Table S5). Yet, this
310 mismatch may be explained by *Trichodesmium's* ability to modify their density (Romans et al., 1994;
311 Tracy A. Villareal & Carpenter, 1990).

312 The sinking velocities measured ($20\text{-}60 \text{ m}\cdot\text{d}^{-1}$) for particle-free colonies (Fig. 2) compare well with
313 those of Walsby (1978), who experimentally observed maximal sinking velocities of $60 \text{ m}\cdot\text{d}^{-1}$ for
314 natural *Trichodesmium thiebautii* from the Sargasso and Caribbean Sea. The vertical motion of
315 *Trichodesmium* has been reported early-on (J. Kromkamp & Walsby, 1992; T. A. Villareal &
316 Carpenter, 2003), and draws large interest in terms of carbon export to depth (Bonnet et al., 2023),
317 and fueling of the deep ocean with fixed nitrogen (Benavides et al., 2022). Such vertical migration
318 was hypothesized to provide an ecological advantage to *Trichodesmium* and enable it to mine
319 phosphorus from the thermocline (Karl et al., 1992; White et al., 2006). Sinking of *Trichodesmium*
320 colonies can occur through gravitational sinking or downwelling events (Guidi et al., 2012), both of
321 which can further be accelerated by mineral ballasting (Pabortsava et al., 2017) or sudden
322 autocatalytic cell death in response to nutrient limitation (Berman-Frank et al., 2004). Our study is
323 the first to experimentally quantify the effect of dust on the colony's sinking velocity, and our
324 findings conform to theoretical predictions, modelling data and *in situ* observations (Laurenceau-
325 Cornec et al., 2020; Walsby, 1978; White et al., 2006). To conclude, our experiments show that
326 *Trichodesmium* colonies can control their buoyancy even when loaded with up to 300-400 ng dust
327 and that collection of $1 \mu\text{g}$ dust will slightly increase their sinking velocity by $\sim 60 \text{ m}\cdot\text{d}^{-1}$.



328

329 **Figure 2. Effect of dust load on sinking velocities of Rea Sea *T. thiebautii* colonies.**

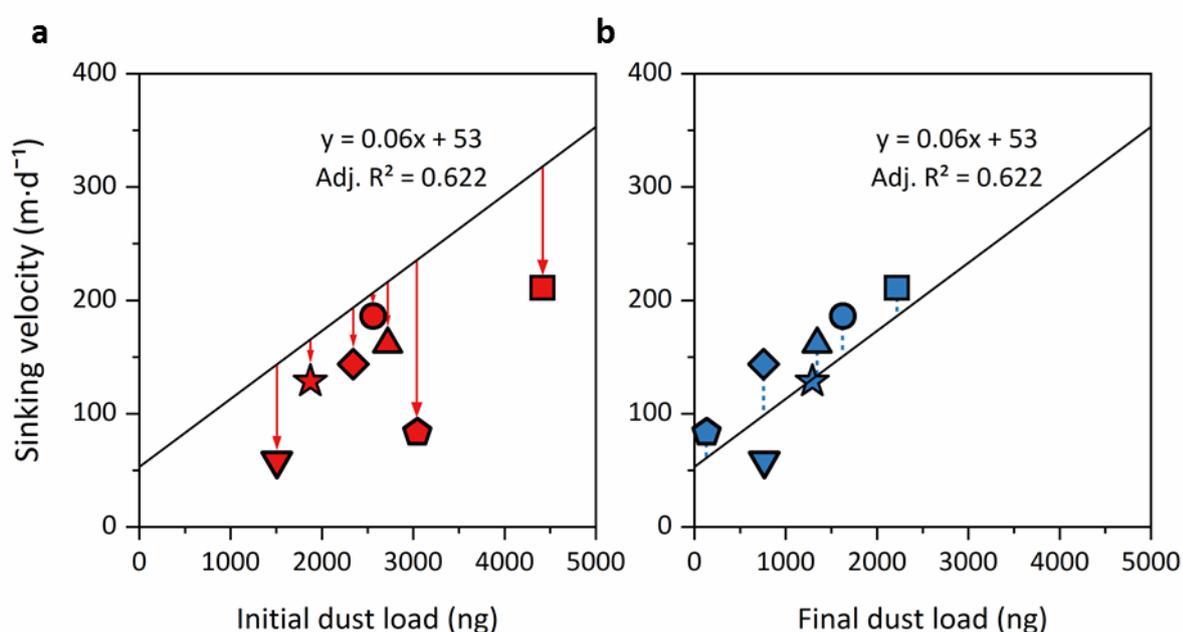
330 (a) Sinking velocities of six individual colonies each measured repeatedly with increasing dust loads and
 331 labeled with a distinct color. Sinking velocities of particle-free colonies are noted by stars, colonies with
 332 medium dust load by triangles and colonies with high dust load by circles. Two regions were identified:
 333 colony-controlled area (yellow shaded) and dust-controlled area (blue shaded). Images above show the
 334 increasing dust loads of a single colony (blue-labeled).

335 (b) Zoom in on the dust-controlled zone, where sinking velocity increased linearly with dust load, at a slope
 336 (K) that matched theoretical calculations (see text).

337 **3.1.3 Effect of dust loss on colony sinking velocity**

338 During sedimentation experiments a significant loss of particles from most colonies (42 out of 50
 339 total data pairs) was observed, especially from the heavily-loaded ones. Comparing colony images
 340 taken prior to and after the experiments, a loss of 10 ng - 3 μg dust per colony was calculated (Table
 341 S6). This massive loss of dust is expected to decrease the sinking velocity of colonies if the loss
 342 occurred in early stages of the experiment. Seeking to illustrate this effect, several representative

343 colonies were plotted in Fig. 3 (see supplementary text S3 for the selection criterion) were
 344 compared to the linear relationship established in Fig. 2b ($y = 0.06 \text{ m}\cdot\text{d}^{-1}\cdot\text{ng}^{-1} \times \text{dust weight (ng)} + 53$
 345 $\text{m}\cdot\text{d}^{-1}$). All these colonies plot below their expected sinking velocities noted by the black line,
 346 indicating that dust was lost during the experiment and decreased their sinking velocities (Fig. 3a).
 347 Replotting the measured sinking velocities of these colonies against their final dust loads (Fig. 3b),
 348 yield values that are nearer to the line. Thus, it seems that these colonies were sinking at velocities
 349 that match the final dust loads, probably since this loss occurred at the beginning of the experiment.
 350 Such analysis, made possible by the relationship established in this study, revealed that dust loss
 351 can decrease the colony sinking velocity in a predictable manner.



352

353 **Figure 3. Effect of dust loss on colony sinking velocity.**

354 Measured sinking velocities of seven representative colonies (shown as different symbols) plotted against
 355 their initial (a) and final (b) dust loads. The equation (black line) is the linear relationship established in Fig.
 356 2b. Arrows and dash lines indicate the mismatch of measured sinking velocities and expected velocities
 357 calculated from initial and final dust loads, respectively. See Fig. S3 for additional colonies.

358 **3.2 Toxic effects of dust on *Trichodesmium***

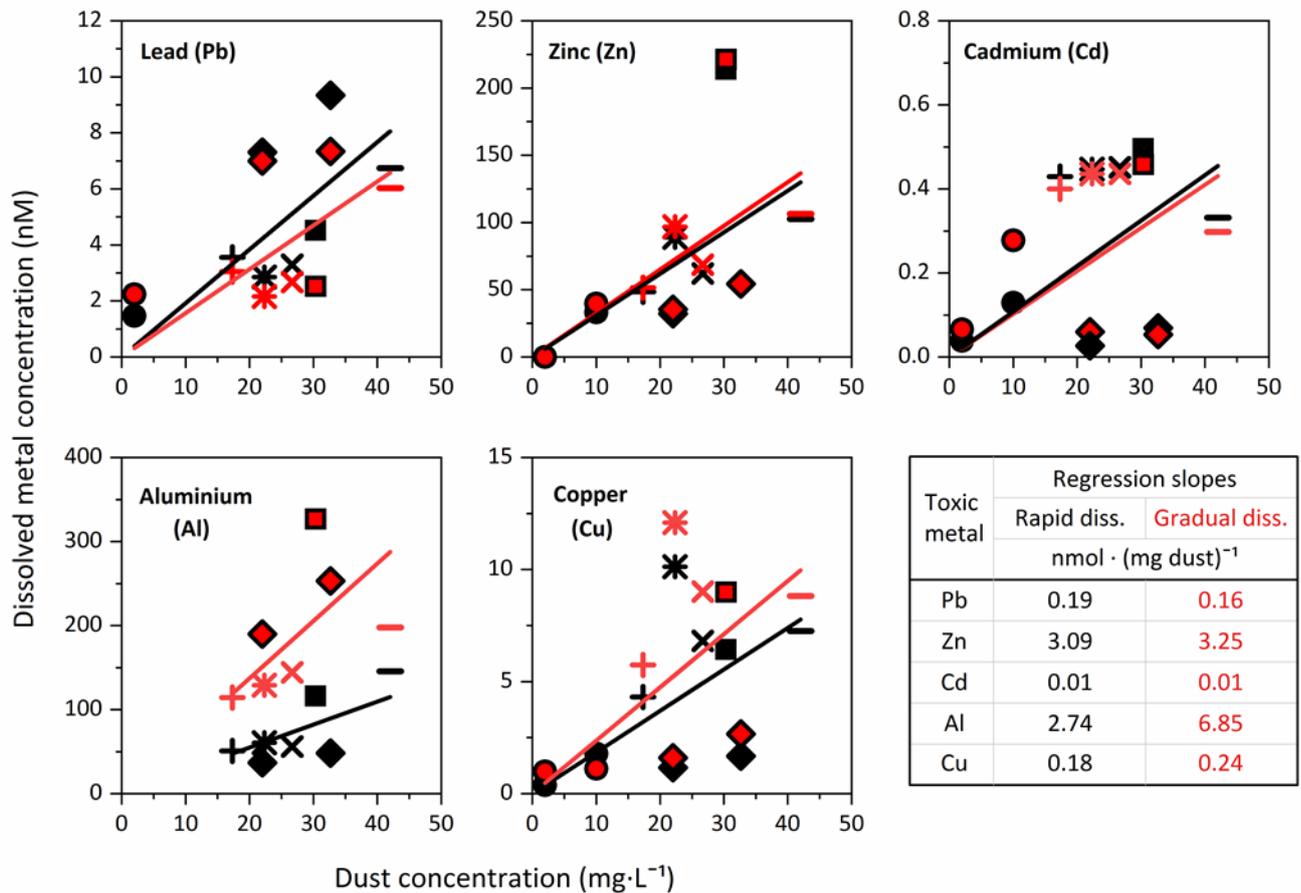
359 Dust and other aerosols contain an array of toxic elements (Bozlaker et al., 2013). Upon dust
 360 deposition on the surface ocean, some elements are rapidly released and may induce toxicity to
 361 positively buoyant *Trichodesmium* blooms that accumulate at the surface. Seeking to evaluate the
 362 toxicity of dust to *Trichodesmium* blooms, the fraction of rapidly released toxic metals was

363 measured and the impact of dust leachate on *Trichodesmium* mortality was observed. In addition,
364 colonies that concentrate dust may also experience a continuous flux of toxic metals that are
365 gradually released from the centered particles. The gradual release of metals was hereby measured
366 and the mortality of dust-loaded colonies was examined.

367 3.2.1 Kinetics of toxic metal release from dust

368 Toxic metal release to seawater was measured at two dust concentrations and data was gathered
369 according to time, differentiating between rapidly (10 min - 6 h) and gradually (12 h - 7 d) released
370 elements. To contextualize our data, we included additional dissolution measurements conducted
371 by Mackay et al. (2015) resulting in a dissolution dataset composed of seven different dust samples
372 collected from the Gulf of Aqaba over several years (Fig. 4, see Table S7 for additional elements). To
373 enable easy extrapolation to natural conditions, concentrations of dissolved metal released from
374 the different dust samples were plotted against the concentrations of dust used in the experiments.
375 In general, higher dissolved metals were recorded at higher dust concentrations and a linear
376 correlation can be fitted to the data (Fig. 4).

377 Since *Trichodesmium's* exposure to dust depends on the interaction time, special attention was
378 paid to the timing and release mode of each metal, following the Mackay et al. (2015) scheme.
379 Concentrations of zinc (Zn) and cadmium (Cd) remained constant with time (gradual=rapid, Fig. 4)
380 and hence were considered rapidly released elements. On the other hand, aluminum (Al) and
381 copper (Cu) accumulated with dissolution time (gradual>rapid, Fig. 4), and were considered
382 gradually released elements. Lead (Pb) concentration dropped slightly with time (gradual<rapid, Fig.
383 4), reflecting its tendency to adsorb onto particles and surfaces (Bruland et al., 2013). Based on
384 these linear slopes and release mode (rapid versus gradual), the “cocktail” of toxic elements
385 released during dust deposition events or within the colony center can be evaluated and linked to
386 the incubation studies with *Trichodesmium*.



387

388 **Figure 4. Compilation of dust dissolution experiments conducted in seawater using different dust**
 389 **samples and concentrations.**

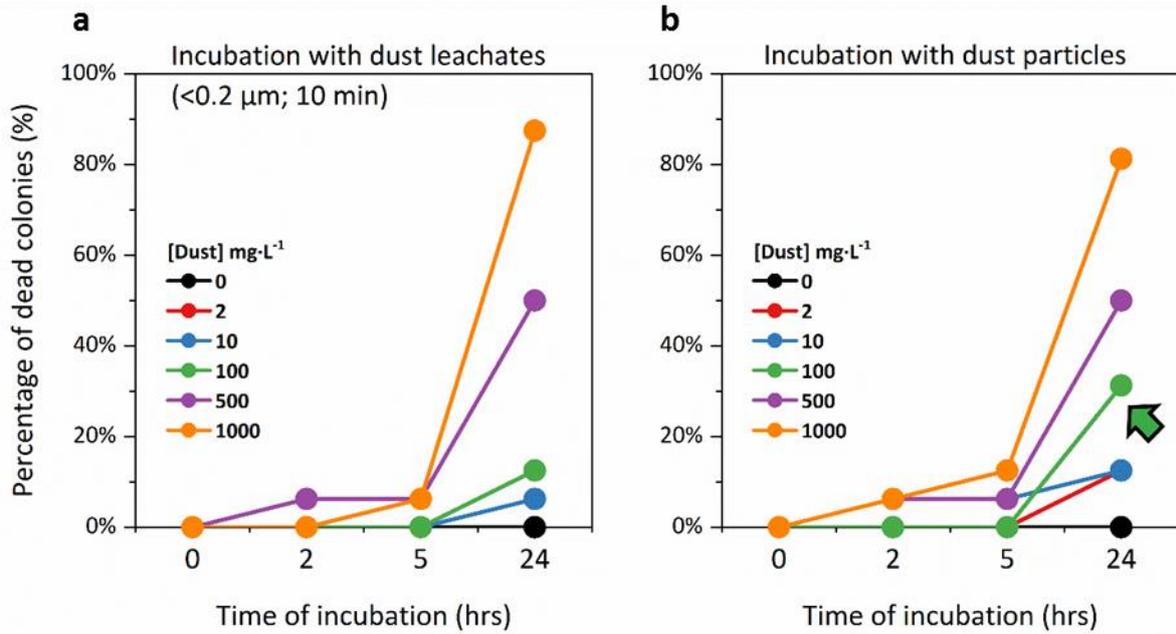
390 The dataset combines new measurements (circles) and published data from (Mackey et al., 2015) and
 391 includes seven dust samples plotted as different symbols. Metal release kinetics is presented by two
 392 categories - rapidly released metals (black, up to 6hrs) and gradually released metals (red, up to 7 days).
 393 Regression slopes linking dust and dissolved metal concentrations are plotted and summarized in the table
 394 next to the graph (see Fig. S6 for additional elements).

395 **3.2.2 Dust toxicity to *Trichodesmium* – fractions and doses**

396 To assess dust toxicity to *Trichodesmium*, ~180 freshly collected natural colonies were incubated
 397 with increasing dust concentrations for 24 hrs and mortality was assessed visually based on colony
 398 integrity and filament degradation (Fig. S4). To distinguish between the toxic effects of rapidly and
 399 gradually released metals, colonies were exposed to dust leachate and raw dust, respectively
 400 (where the leachate was obtained after 10 min from dust addition to seawater).

401 Incubating *Trichodesmium* with 2 and 10 mg·L⁻¹ dust resulted in negligible mortality of only one or
402 two of the 16 colonies incubated (red and blue lines in Fig. 5a and 5b). These dust loads are within
403 the range reported for natural dust storms (<10 mg·L⁻¹, Ren et al., 2011; Zhang et al., 2019), and
404 hence dust load from such storms are not predicted to induce *Trichodesmium* mortality. Low
405 mortality (13%) was observed in colonies incubated with 100 mg·L⁻¹ dust leachate, far below the
406 LC50 toxicity threshold, which is the lethal concentration that results in death of 50% of the
407 colonies (Echeveste et al., 2012). At higher dust concentrations of 500 and 1000 mg·L⁻¹, significant
408 mortality was observed, ranging from 50-90% of the colonies (purple and orange lines in Fig. 5a and
409 Fig. 5b), indicative of acute toxicity. Based on these incubations, we conservatively set the LC50
410 toxicity threshold at 500 mg·L⁻¹ (although it may occur anywhere above 100 mg·L⁻¹).

411 Overall, the mortality of *Trichodesmium* was comparable between the leachate (Fig. 5a) and dust
412 particles (Fig. 5b). This implies that metals released from dust during 10 min are the key
413 contributors to its toxicity to *Trichodesmium*. Utilizing the linear fit from Fig. 4, toxic metals
414 concentrations in each incubation can be estimated (Fig. 5c). For example, in the incubation with
415 500 mg·L⁻¹ dust that yielded 50% mortality, *Trichodesmium* is expected to experience 5 nM Cd, 95
416 nM Pb, 90 nM Cu, and >1 μM of Zn and Al (Fig. 5c). Interestingly, negligible mortality occurred in
417 the 100 mg·L⁻¹ dust leachate incubation, conditions where 1 nM Cd, ~20 nM Pb and Cu, and ~300
418 nM of Zn and Al were predicted (Fig. 5b and 5c). Given the absence of literature data on
419 *Trichodesmium's* response to a cocktail of toxic metals, it remains inconclusive whether these levels
420 were sub-lethal or *Trichodesmium* was capable of detoxifying these metals. Typically, toxicity
421 thresholds (e.g. effective concentration 50% (EC50s) or lethal concentration 50% (LC50s) are
422 obtained for a single metal, varying amongst phytoplankton types and sizes (Echeveste et al., 2012;
423 Paytan et al., 2009; Yang et al., 2019). To provide context, Cd and Pb toxicity thresholds (LC50s) for
424 natural phytoplankton from different ocean basins were reported to range from 2-4000 nM for Cd,
425 and 100-2000 nM for Pb (Echeveste et al., 2012).



c Calculated toxic metal release from dust

Dust concn. ($\text{mg}\cdot\text{L}^{-1}$)	Rapid release in dust-leachates (nM)					Gradual release (nM)	
	Pb	Zn	Cd	Al	Cu	Al*	Cu*
1000	190	3090	10	2740	180	4110	60
500	95	1545	5	1370	90	2055	30
100	19	309	1	274	18	411	6
10	1.9	31	0.1	27	1.8	41	0.6
2	0.4	6	0.0	5	0.4	8	0.1

* represents additional release during incubation

426

427 **Figure 5. Impact of dust on mortality of Red Sea *Trichodesmium* colonies and estimated toxic**
 428 **metals released during incubations.**

429 Mortality of natural colonies incubated for 24 hrs with increasing concentrations of (a) dust leachate and (b)
 430 whole dust. (c). Calculated metal release from dust during the mortality assays based on the regression
 431 slopes obtained in Fig. 4. Data was compiled from 2 different experiments. The dust leachate was filtered
 432 within 10 min of dust suspension in seawater to represent rapidly released metals, while whole dust
 433 provided also gradually released metals. The toxicity of dust leachate and whole dust was comparable at
 434 high concentrations, but as indicated by the green arrow, at $100 \text{ mg}\cdot\text{L}^{-1}$ dust, the mortality was higher with
 435 whole dust.

436

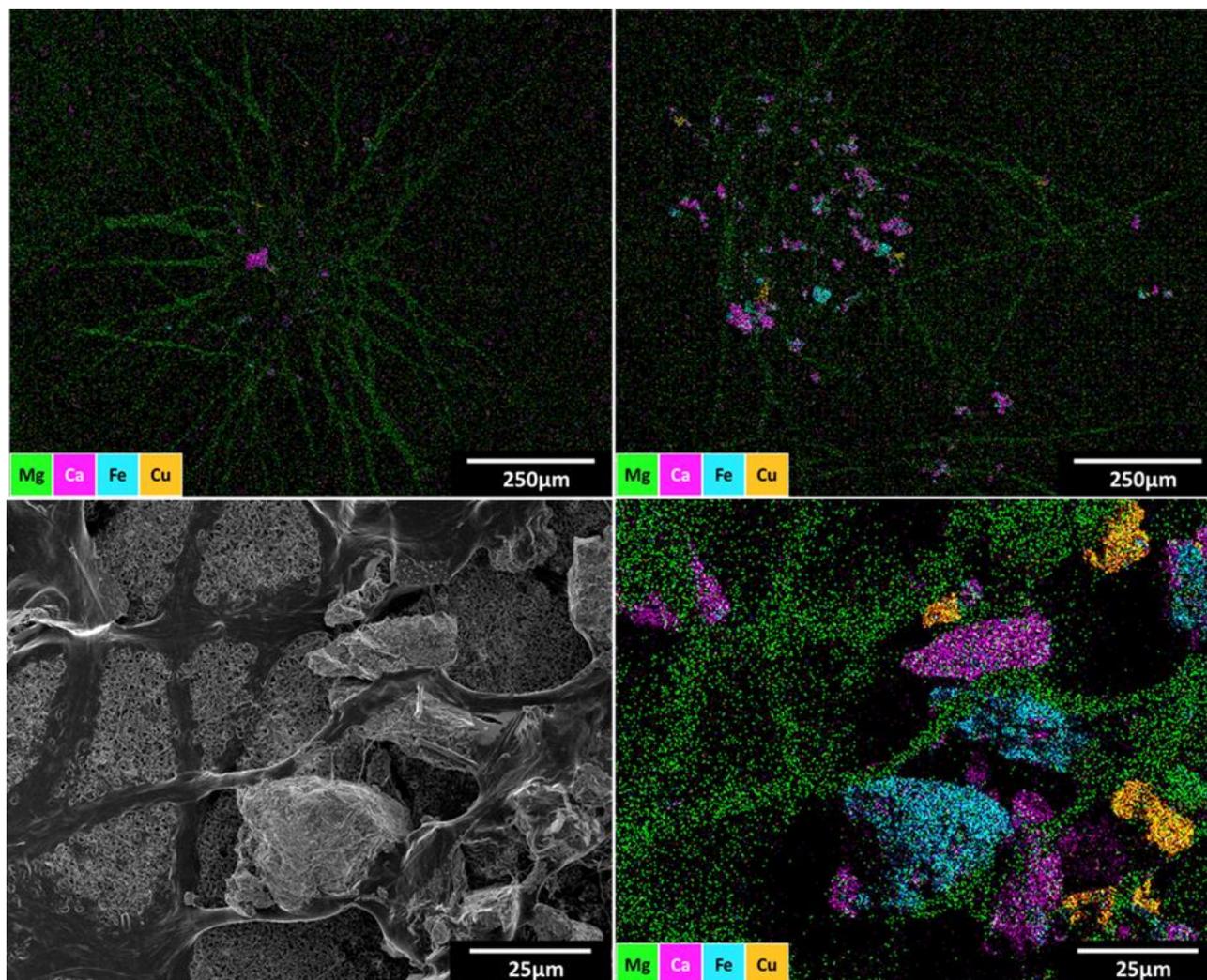
437 A more detailed look at the data shows subtle changes in the mortality of colonies incubated with
438 $100 \text{ mg}\cdot\text{L}^{-1}$ dust leachate compared to the whole dust (green arrow in Fig. 5). At these low dust
439 concentrations (e.g. $100 \text{ mg}\cdot\text{L}^{-1}$), only two colonies died in the leachate (13%), while five colonies
440 died in the whole dust (31%). This added mortality may have originated from the gradually released
441 metals Al and Cu (Fig. 5c). In a parallel set of experiments, we tested the mortality of colonies
442 incubated with increasing Cu concentrations, obtaining 30 and 50% mortality at 5 and 10 nM Cu,
443 respectively (Fig. S5). The estimated gradually release of 0.1-6 nM Cu (Fig. 5c) may hereby explain
444 the elevated mortality in the whole dust incubation, especially when also considering the high
445 levels of Al.

446 Regarding the toxicity of metals in dust-centering colonies, it appears that Pb, Zn and Cd are not a
447 major concern, as these elements are released from dust before they interact with the colonies. But
448 the gradually released elements Al and Cu may cause toxicity to colonies that center dust. As dust is
449 confined within the colony core and the diffusion to the surrounding water is limited, the colony or
450 its core volume should be considered as the relevant volume for metal release. Given $\sim 1 \mu\text{L}$ colony
451 volume, dust loads of 0.2-1 μg yield effective dust concentration of $200\text{-}1000 \text{ mg}\cdot\text{L}^{-1}$ (Fig. S7). At
452 these high dust concentrations, high exposure to gradually released Al and Cu is expected (Fig. 5c).
453 The exposure to these metals may be even larger when considering the volume of the colony core
454 where the dissolution occurs and not the entire colony volume. Nonetheless, colonies that
455 accumulated even higher dust loads (1-10 μg) showed no signs of mortality during incubations that
456 lasted 24 hrs (Fig. S8). The survival of colonies with an effective dust load of over $1000 \text{ mg}\cdot\text{L}^{-1}$ and
457 projected high Cu and Al fluxes (Fig. 5c) is intriguing. These observations call for further research
458 measuring metal fluxes within colonies and exploring possible detoxification and physiological
459 defense mechanisms. Such mechanisms may include metal binding by extracellular polymeric
460 substances (EPS) and specific ligands (Gledhill et al., 2019) and metal excretion through efflux
461 proteins (Hewson et al., 2009).

462 [3.2.3 Selective removal of Cu minerals](#)

463 Hypothesizing that colonies may try to reduce toxicity through the removal of particles, natural
464 colonies were incubated with Cu-containing minerals (malachite) for 24 hrs. To ensure optimal
465 colony-mineral interactions, the Cu minerals were mixed with Fe minerals (hematite), which are
466 typically preferred by *Trichodesmium*. All colonies interacted strongly with particles throughout the

467 incubation and showed strong preference for the Fe-minerals. Only few colonies contained Cu-
468 minerals, but these were present even at 24 hrs (Fig. 6). The finding of Cu minerals on colonies at
469 the end of the incubation does not support our hypothesis and there is currently no evidence to
470 support the selective removal of toxic minerals.



471

472 **Figure 6. SEM-EDX images of natural *Trichodesmium* colonies incubated with Cu-minerals**
473 **(malachite) and Fe-minerals (hematite).**

474 Probing the ability of *Trichodesmium* to distinguish and selectively remove toxic particles, colonies were
475 incubated with malachite and hematite up to 24 hrs. Several colonies were imaged at different magnification
476 (scale bars within images), showing the presence of both minerals throughout the incubation (Cu – yellow,
477 Fe – blue). *Trichodesmium* was imaged through its magnesium content (green) and the malachite sample
478 also contained calcium (Ca) minerals (pink). See Fig. S10-S13 for additional elemental maps.

479

480 4. Summary

481 Having studied the potential negative effects of dust on natural *Trichodesmium* colonies, we predict
482 that in a typical open-ocean setting, the potential benefit of dust as a nutrient source outweighs the
483 risks of buoyancy loss and toxification. In the Gulf of Aqaba, puff-shaped *T. thiebautii* colonies
484 collected *in situ* were usually observed to contain less than 200 ng of dust per colony, which is
485 below the threshold where sinking velocity becomes dust-controlled (Fig. 1) and is insufficient to
486 induce toxicity through metal release (Fig. 5). In other environments (e.g. coastal seas, Mackey et
487 al., 2012), however, *Trichodesmium* may encounter more toxic aerosols and the concepts laid here
488 may facilitate the evaluation of those risks. With regards to buoyancy, accelerated sinking velocities
489 due to interactions with dust may be significant to C export, and may help explain recent
490 measurements of active N₂ fixation by *Trichodesmium* at 1000 meters (Benavides et al., 2022). If
491 indeed colonies can modulate their particle load, the dust-induced sinking may
492 benefit *Trichodesmium* and expand its ecological niche.

493

494 **Author contributions**

495 **Conceptualization:** Siyuan Wang, Yeala Shaked

496 **Data curation:** Siyuan Wang

497 **Formal analysis:** Siyuan Wang, Futing Zhang, Coco Koedooder, Odeta Qafoku, Subhajit Basu,
498 Stephan Krisch, Anna-Neva Visser, Meri Eichner, Nivi Kessler

499 **Methodology:** Siyuan Wang, Futing Zhang, Odeta Qafoku, Subhajit Basu, Stephan Krisch, Anna-
500 Neva Visser

501 **Funding acquisition:** Rene M. Boiteau, Martha Gledhill, Yeala Shaked

502 **Supervision:** Yeala Shaked

503 **Writing – original draft:** Siyuan Wang, Yeala Shaked

504 **Writing – review & editing:** Futing Zhang, Coco Koedooder, Odeta Qafoku, Subhajit Basu, Stephan
505 Krisch, Anna-Neva Visser, Meri Eichner, Nivi Kessler, Rene M. Boiteau, Martha Gledhill

506

507 **Acknowledgements**

508 We extend our sincere gratitude to Murielle Dray (IUI) and Emanuel Sestieri (IUI) for their
509 invaluable assistance during this study. We appreciate the Mineral collection at the National
510 Natural History Collections at the Hebrew University for donating the mineral specimens (hematite)
511 used in this work. Siyuan Wang thanks Prof. Angelicque E. White for her insightful suggestions
512 regarding the model of sinking velocity and to Mr. Antonio Colussi and Dr. Lina Sakhneny for their
513 contributions to colony collection and toxicity assays. This study was funded by ISF-NSFC joint
514 research program (Grant No. 2398/18) and ISF (260/21). Siyuan Wang acknowledges CSC-HUJI
515 doctoral fellowship and Futing Zhang acknowledges PBC Postdoctoral fellowship.

516

517 **Conflict of interest**

518 The authors declare that they have no conflict of interest.

519

520 **Data availability statement**

521 Data generated for this study were uploaded as supplementary materials. All python codes for
522 sinking velocity can be found in Github (<https://github.com/Zhanzhu1110/Trichobuoyancy.git>) and
523 in Zenodo (<https://zenodo.org/records/10290901>; DOI:10.5281/zenodo.10290901)(Wang et al.,
524 2023). Data of metal release (dust concentrations = 17-42 mg·L⁻¹) are available from Mackay et al.
525 (2015), and a complete supplementary data file is also provided herein for ease of access.

526

527 **Reference**

- 528 Anderson, O. R. (1977). Fine Structure of a Marine Ameba Associated with a Blue-Green Alga in the
529 Sargasso Sea. *The Journal of Protozoology*, 24(3), 370–376.
530 <https://doi.org/10.1017/cbo9780511600586.003>
- 531 Basu, S., & Shaked, Y. (2018). Mineral iron utilization by natural and cultured *Trichodesmium* and
532 associated bacteria. *Limnology and Oceanography*, 63(6), 2307–2320.
533 <https://doi.org/10.1002/lno.10939>
- 534 Basu, S., Gledhill, M., de Beer, D., Prabhu Matondkar, S. G., & Shaked, Y. (2019). Colonies of marine
535 cyanobacteria *Trichodesmium* interact with associated bacteria to acquire iron from dust.
536 *Communications Biology*, 2(1), 1–8. <https://doi.org/10.1038/s42003-019-0534-z>
- 537 Benaltabet, T., Lapid, G., & Torfstein, A. (2022). Dissolved aluminium dynamics in response to dust
538 storms, wet deposition, and sediment resuspension in the Gulf of Aqaba, northern Red Sea.
539 *Geochimica et Cosmochimica Acta*, 335, 137–154. <https://doi.org/10.1016/j.gca.2022.08.029>
- 540 Benavides, M., Bonnet, S., Le Moigne, F. A. C., Armin, G., Inomura, K., Hallstrøm, S., et al. (2022).
541 Sinking *Trichodesmium* fixes nitrogen in the dark ocean. *ISME Journal*, 16(10), 2398–2405.
542 <https://doi.org/10.1038/s41396-022-01289-6>
- 543 Berman-Frank, I., Bidle, K. D., Haramaty, L., & Falkowski, P. G. (2004). The demise of the marine
544 cyanobacterium, *Trichodesmium* spp., via an autocatalyzed cell death pathway. *Limnology and*
545 *Oceanography*, 49(4 I), 997–1005. <https://doi.org/10.4319/lo.2004.49.4.0997>
- 546 Bif, M. B., & Yunes, J. S. (2017). Distribution of the marine cyanobacteria *Trichodesmium* and their
547 association with iron-rich particles in the South Atlantic Ocean. *Aquatic Microbial Ecology*,
548 78(2), 107–119. <https://doi.org/10.3354/ame01810>
- 549 Bonnet, S., Benavides, M., Le Moigne, F. A. C., Camps, M., Torremocha, A., Grosso, O., et al. (2023).
550 Diazotrophs are overlooked contributors to carbon and nitrogen export to the deep ocean.
551 *ISME Journal*, 17(1), 47–58. <https://doi.org/10.1038/s41396-022-01319-3>
- 552 Bozlaker, A., Prospero, J. M., Fraser, M. P., & Chellam, S. (2013). Quantifying the contribution of
553 long-range saharan dust transport on particulate matter concentrations in Houston, Texas,

554 using detailed elemental analysis. *Environmental Science and Technology*, 47(18), 10179–
555 10187. <https://doi.org/10.1021/es4015663>

556 Bruland, K. W., Middag, R., & Lohan, M. C. (2013). *Controls of Trace Metals in Seawater. Treatise on*
557 *Geochemistry: Second Edition* (2nd ed., Vol. 8). Elsevier Ltd. <https://doi.org/10.1016/B978-0->
558 08-095975-7.00602-1

559 Capone, D. G., Zehr, J. P., Paerl, H. W., Bergman, B., & Carpenter, E. J. (1997). *Trichodesmium*, a
560 globally significant marine cyanobacterium. *Science*, 276(5316), 1221–1229.
561 <https://doi.org/10.1126/science.276.5316.1221>

562 Cerdan-Garcia, E., Baylay, A., Polyviou, D., Woodward, E. M. S., Wrightson, L., Mahaffey, C., et al.
563 (2022). Transcriptional responses of *Trichodesmium* to natural inverse gradients of Fe and P
564 availability. *ISME Journal*, 16(4), 1055–1064. <https://doi.org/10.1038/s41396-021-01151-1>

565 Chen, Y., Tovar-Sanchez, A., Siefert, R. L., Sañudo-Wilhelmy, S. A., & Zhuang, G. (2011). Luxury
566 uptake of aerosol iron by *Trichodesmium* in the western tropical North Atlantic. *Geophysical*
567 *Research Letters*, 38(18). <https://doi.org/10.1029/2011GL048972>

568 Echeveste, P., Agustí, S., & Tovar-Sánchez, A. (2012). Toxic thresholds of cadmium and lead to
569 oceanic phytoplankton: Cell size and ocean basin-dependent effects. *Environmental Toxicology*
570 *and Chemistry*, 31(8), 1887–1894. <https://doi.org/10.1002/etc.1893>

571 Eichner, M., Inomura, K., Pierella Karlusich, J. J., & Shaked, Y. (2023). Better together? Lessons on
572 sociality from *Trichodesmium*. *Trends in Microbiology*, xx(xx), 1–13.
573 <https://doi.org/10.1016/j.tim.2023.05.001>

574 Engel, A., Szlosek, J., Abramson, L., Liu, Z., & Lee, C. (2009). Investigating the effect of ballasting by
575 CaCO₃ in *Emiliania huxleyi*: I. Formation, settling velocities and physical properties of
576 aggregates. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 56(18), 1396–1407.
577 <https://doi.org/10.1016/j.dsr2.2008.11.027>

578 Frischkorn, K. R., Haley, S. T., & Dyhrman, S. T. (2018). Coordinated gene expression between
579 *Trichodesmium* and its microbiome over day-night cycles in the North Pacific Subtropical Gyre.
580 *ISME Journal*, 12(4), 997–1007. <https://doi.org/10.1038/s41396-017-0041-5>

- 581 Gledhill, M., Basu, S., & Shaked, Y. (2019). Metallophores associated with: *Trichodesmium*
582 erythraeum colonies from the Gulf of Aqaba. *Metallomics*, *11*(9), 1547–1557.
583 <https://doi.org/10.1039/c9mt00121b>
- 584 Guidi, L., Calil, P. H. R., Duhamel, S., Björkman, K. M., Doney, S. C., Jackson, G. A., et al. (2012). Does
585 eddy-eddy interaction control surface phytoplankton distribution and carbon export in the
586 North Pacific Subtropical Gyre? *Journal of Geophysical Research: Biogeosciences*, *117*(2), 1–12.
587 <https://doi.org/10.1029/2012JG001984>
- 588 Guo, C., Zhou, Y., Zhou, H., Su, C., & Kong, L. (2022). Aerosol Nutrients and Their Biological Influence
589 on the Northwest Pacific Ocean (NWPO) and Its Marginal Seas. *Biology*, *11*(6), 1–18.
590 <https://doi.org/10.3390/biology11060842>
- 591 Held, N. A., Webb, E. A., McIlvin, M. M., Hutchins, D. A., Cohen, N. R., Moran, D. M., et al. (2020).
592 Co-occurrence of Fe and P stress in natural populations of the marine diazotroph
593 *Trichodesmium*. *Biogeosciences*, *17*(9), 2537–2551. <https://doi.org/10.5194/bg-17-2537-2020>
- 594 Held, N. A., Sutherland, K. M., Webb, E. A., McIlvin, M. R., Cohen, N. R., Devaux, A. J., et al. (2021).
595 Mechanisms and heterogeneity of *in situ* mineral processing by the marine nitrogen fixer
596 *Trichodesmium* revealed by single-colony metaproteomics. *ISME Communications*, *1*(1), 1–9.
597 <https://doi.org/10.1038/s43705-021-00034-y>
- 598 Held, N. A., Waterbury, J. B., Webb, E. A., Kellogg, R. M., McIlvin, M. R., Jakuba, M., et al. (2022).
599 Dynamic diel proteome and daytime nitrogenase activity supports buoyancy in the
600 cyanobacterium *Trichodesmium*. *Nature Microbiology*, *7*(2), 300–311.
601 <https://doi.org/10.1038/s41564-021-01028-1>
- 602 Hewson, I., Poretsky, R. S., Dyhrman, S. T., Zielinski, B., White, A. E., Tripp, H. J., et al. (2009).
603 Microbial community gene expression within colonies of the diazotroph, *Trichodesmium*, from
604 the Southwest Pacific Ocean. *ISME Journal*, *3*(11), 1286–1300.
605 <https://doi.org/10.1038/ismej.2009.75>
- 606 Iversen, M. H., & Ploug, H. (2010). Ballast minerals and the sinking carbon flux in the ocean: Carbon-
607 specific respiration rates and sinking velocity of marine snow aggregates. *Biogeosciences*, *7*(9),
608 2613–2624. <https://doi.org/10.5194/bg-7-2613-2010>

- 609 Karl, D. M., Letelier, R., Hebel, D. V., Bird, D. F., & Winn, C. D. (1992). *Trichodesmium* blooms and
610 new nitrogen in the North Pacific gyre. In J. G. Carpenter, E.J., Capone, D.G., Rueter (Ed.),
611 *Marine pelagic cyanobacteria* (pp. 219–237). Springer, Dordrecht.
612 https://doi.org/10.1007/978-94-015-7977-3_14
- 613 Kessler, N., Kraemer, S. M., Shaked, Y., & Schenkeveld, W. D. C. (2020). Investigation of
614 Siderophore-Promoted and Reductive Dissolution of Dust in Marine Microenvironments Such
615 as *Trichodesmium* Colonies. *Frontiers in Marine Science*, 7(March), 1–15.
616 <https://doi.org/10.3389/fmars.2020.00045>
- 617 Kessler, N., Armoza-Zvuloni, R., Wang, S., Basu, S., Weber, P. K., Stuart, R. K., & Shaked, Y. (2020).
618 Selective collection of iron-rich dust particles by natural *Trichodesmium* colonies. *ISME Journal*,
619 14(1), 91–103. <https://doi.org/10.1038/s41396-019-0505-x>
- 620 Koedooder, C., Landou, E., Zhang, F., Wang, S., Basu, S., Berman-Frank, I., et al. (2022).
621 Metagenomes of Red Sea Subpopulations Challenge the Use of Marker Genes and Morphology
622 to Assess *Trichodesmium* Diversity. *Frontiers in Microbiology*, 13(May).
623 <https://doi.org/10.3389/fmicb.2022.879970>
- 624 Krisch, S., Hopwood, M. J., Roig, S., Gerringa, L. J. A., Middag, R., Rutgers van der Loeff, M. M., et al.
625 (2022). Arctic – Atlantic Exchange of the Dissolved Micronutrients Iron, Manganese, Cobalt,
626 Nickel, Copper and Zinc With a Focus on Fram Strait. *Global Biogeochemical Cycles*, 36(5).
627 <https://doi.org/10.1029/2021GB007191>
- 628 Kromkamp, J., & Walsby, A. E. (1992). Buoyancy regulation and vertical migration of *Trichodesmium*:
629 a computer-model prediction. In J. G. Carpenter, E.J., Capone, D.G., Rueter (Ed.), *Marine*
630 *Pelagic Cyanobacteria: Trichodesmium and other Diazotrophs* (pp. 239–248). Springer,
631 Dordrecht. https://doi.org/10.1007/978-94-015-7977-3_15
- 632 Kromkamp, Jacco, & Walsby, A. E. (1990). A computer model of buoyancy and vertical migration in
633 cyanobacteria. *Journal of Plankton Research*, 12(1), 161–183.
634 <https://doi.org/10.1093/plankt/12.1.161>
- 635 Laurenceau-Cornec, E. C., Le Moigne, F. A. C., Gallinari, M., Moriceau, B., Toullec, J., Iversen, M. H.,
636 et al. (2020). New guidelines for the application of Stokes' models to the sinking velocity of

637 marine aggregates. *Limnology and Oceanography*, 65(6), 1264–1285.
638 <https://doi.org/10.1002/lno.11388>

639 Lee, M. D., Walworth, N. G., McParland, E. L., Fu, F. X., Mincer, T. J., Levine, N. M., et al. (2017). The
640 *Trichodesmium* consortium: Conserved heterotrophic co-occurrence and genomic signatures
641 of potential interactions. *ISME Journal*, 11(8), 1813–1824.
642 <https://doi.org/10.1038/ismej.2017.49>

643 Mackey, K. R. M., Buck, K. N., Casey, J. R., Cid, A., Lomas, M. W., Sohrin, Y., & Paytan, A. (2012).
644 Phytoplankton responses to atmospheric metal deposition in the coastal and open-ocean
645 Sargasso Sea. *Frontiers in Microbiology*, 3(OCT), 1–15.
646 <https://doi.org/10.3389/fmicb.2012.00359>

647 Mackey, K. R. M., Chien, C. Te, Post, A. F., Saito, M. A., & Paytan, A. (2015). Rapid and gradual
648 modes of aerosol trace metal dissolution in seawater. *Frontiers in Microbiology*, 6(JAN), 1–11.
649 <https://doi.org/10.3389/fmicb.2014.00794>

650 Mahowald, N. M., Hamilton, D. S., Mackey, K. R. M., Moore, J. K., Baker, A. R., Scanza, R. A., & Zhang,
651 Y. (2018). Aerosol trace metal leaching and impacts on marine microorganisms. *Nature*
652 *Communications*, 9(1). <https://doi.org/10.1038/s41467-018-04970-7>

653 McConnell, C. L., Highwood, E. J., Coe, H., Formenti, P., Anderson, B., Osborne, S., et al. (2008).
654 Seasonal variations of the physical and optical characteristics of saharan dust: Results from the
655 dust outflow and deposition to the ocean (DODO) experiment. *Journal of Geophysical Research*,
656 113, 1–19. <https://doi.org/10.1029/2007JD009606>

657 Mills, M. M., Ridame, C., Davey, M., La Roche, J., & Geider, R. J. (2004). Iron and phosphorus co-
658 limit nitrogen fixation in the eastern tropical North Atlantic. *Nature*, 429(6989), 292–294.
659 <https://doi.org/10.1038/nature03632>

660 Pabortsava, K., Lampitt, R. S., Benson, J., Crowe, C., McLachlan, R., Le Moigne, F. A. C., et al. (2017).
661 Carbon sequestration in the deep Atlantic enhanced by Saharan dust. *Nature Geoscience*, 10(3),
662 189–194. <https://doi.org/10.1038/ngeo2899>

663 Paytan, A., Mackey, K. R. M., Chen, Y., Lima, I. D., Doney, S. C., Mahowald, N., et al. (2009). Toxicity
664 of atmospheric aerosols on marine phytoplankton. *Proceedings of the National Academy of*

665 *Sciences of the United States of America*, 106(12), 4601–4605.
666 <https://doi.org/10.1073/pnas.0811486106>

667 Polyviou, D., Baylay, A. J., Hitchcock, A., Robidart, J., Moore, C. M., & Bibby, T. S. (2018). Desert dust
668 as a source of iron to the globally important diazotroph *Trichodesmium*. *Frontiers in*
669 *Microbiology*, 8(JAN), 1–12. <https://doi.org/10.3389/fmicb.2017.02683>

670 Rapp, I., Schlosser, C., Rusiecka, D., Gledhill, M., & Achterberg, E. P. (2017). Automated
671 preconcentration of Fe, Zn, Cu, Ni, Cd, Pb, Co, and Mn in seawater with analysis using high-
672 resolution sector field inductively-coupled plasma mass spectrometry. *Analytica Chimica Acta*,
673 976, 1–13. <https://doi.org/10.1016/j.aca.2017.05.008>

674 Ren, J. L., Zhang, G. L., Zhang, J., Shi, J. H., Liu, S. M., Li, F. M., et al. (2011). Distribution of dissolved
675 aluminum in the Southern Yellow Sea: Influences of a dust storm and the spring bloom. *Marine*
676 *Chemistry*, 125(1–4), 69–81. <https://doi.org/10.1016/j.marchem.2011.02.004>

677 Romans, K. M., Carpenter, E. J., & Bergman, B. (1994). Buoyancy regulation in the colonial
678 diazotrophic cyanobacterium *Trichodesmium tenue*: ultrastructure and storage of
679 carbohydrate, polyphosphate, and nitrogen. *Journal of Phycology*, 30(6), 935–942.

680 Rouco, M., Haley, S. T., & Dyhrman, S. T. (2016). Microbial diversity within the *Trichodesmium*
681 holobiont. *Environmental Microbiology*, 18(12), 5151–5160. [https://doi.org/10.1111/1462-](https://doi.org/10.1111/1462-2920.13513)
682 [2920.13513](https://doi.org/10.1111/1462-2920.13513)

683 Rubin, M., Berman-Frank, I., & Shaked, Y. (2011). Dust- and mineral-iron utilization by the marine
684 dinitrogen-fixer *Trichodesmium*. *Nature Geoscience*, 4(8), 529–534.
685 <https://doi.org/10.1038/ngeo1181>

686 Rueter, J. G., McCarthy, J. J., & Carpenter, E. J. (1979). The toxic effect of copper on *Oscillatoria*
687 (*Trichodesmium*) *thiebautii*. *Limnology and Oceanography*, 24(3), 558–562.
688 <https://doi.org/10.4319/lo.1979.24.3.0558>

689 Schladitz, A., Müller, T., Kaaden, N., Massling, A., Kandler, K., Ebert, M., et al. (2009). *In situ*
690 measurements of optical properties at Tinfou (Morocco) during the Saharan Mineral Dust
691 Experiment SAMUM 2006. *Tellus, Series B: Chemical and Physical Meteorology*, 61(1), 64–78.
692 <https://doi.org/10.1111/j.1600-0889.2008.00397.x>

- 693 Shaked, Y., & Lis, H. (2012). Disassembling iron availability to phytoplankton. *Frontiers in*
694 *Microbiology*, 3(APR), 1–26. <https://doi.org/10.3389/fmicb.2012.00123>
- 695 Shaked, Y., de Beer, D., Wang, S., Zhang, F., Visser, A. N., Eichner, M., & Basu, S. (2023). Co-
696 acquisition of mineral-bound iron and phosphorus by natural *Trichodesmium* colonies.
697 *Limnology and Oceanography*, 1–14. <https://doi.org/10.1002/lno.12329>
- 698 Stockdale, A., Krom, M. D., Mortimer, R. J. G., Benning, L. G., Carslaw, K. S., Herbert, R. J., et al.
699 (2016). Understanding the nature of atmospheric acid processing of mineral dusts in supplying
700 bioavailable phosphorus to the oceans. *Proceedings of the National Academy of Sciences of the*
701 *United States of America*, 113(51), 14639–14644. <https://doi.org/10.1073/pnas.1608136113>
- 702 Tang, W., Cerdán-García, E., Berthelot, H., Polyviou, D., Wang, S., Baylay, A., et al. (2020). New
703 insights into the distributions of nitrogen fixation and diazotrophs revealed by high-resolution
704 sensing and sampling methods. *ISME Journal*, 14(10), 2514–2526.
705 <https://doi.org/10.1038/s41396-020-0703-6>
- 706 Villareal, T. A., & Carpenter, E. J. (2003). Buoyancy regulation and the potential for vertical
707 migration in the oceanic cyanobacterium *Trichodesmium*. *Microbial Ecology*, 45(1), 1–10.
708 <https://doi.org/10.1007/s00248-002-1012-5>
- 709 Villareal, Tracy A., & Carpenter, E. J. (1990). Diel buoyancy regulation in the marine diazotrophic
710 cyanobacterium *Trichodesmium thiebautii*. *Limnology and Oceanography*, 35(8), 1832–1837.
711 <https://doi.org/10.4319/lo.1990.35.8.1832>
- 712 Walsby, A. E. (1978). The properties and buoyancy-providing role of gas vacuoles in *Trichodesmium*
713 Ehrenberg. *British Phycological Journal*, 13(2), 103–116.
714 <https://doi.org/10.1080/00071617800650121>
- 715 Walsby, A. E. (1992). The gas vesicles and buoyancy of *Trichodesmium*. In J. G. Carpenter, E.J.,
716 Capone, D.G., Rueter (Ed.), *Marine Pelagic Cyanobacteria: Trichodesmium and other*
717 *Diazotrophs* (pp. 141–161). Springer, Dordrecht. [https://doi.org/10.1007/978-94-015-7977-](https://doi.org/10.1007/978-94-015-7977-3_9)
718 [3_9](https://doi.org/10.1007/978-94-015-7977-3_9)
- 719 Wang, S., Koedooder, C., Zhang, F., Kessler, N., Eichner, M., Shi, D., & Shaked, Y. (2022). Colonies of
720 the marine cyanobacterium *Trichodesmium* optimize dust utilization by selective collection

721 and retention of nutrient-rich particles. *IScience*, 25(1), 103587.
722 <https://doi.org/10.1016/j.isci.2021.103587>

723 Wang, S., Zhang, F., Koedooder, C., Qafoku, O., Basu, S., Krisch, S., et al. (2023). Calculations and
724 simulations of dust factor (K) and sinking velocity of particle-free *Trichodesmium* colonies (v0).
725 *Zenodo*. <https://doi.org/10.5281/zenodo.10290901>

726 White, A. E., Spitz, Y. H., & Letelier, R. M. (2006). Modeling carbohydrate ballasting by
727 *Trichodesmium* spp. *Marine Ecology Progress Series*, 323(Oliver 1994), 35–45.
728 <https://doi.org/10.3354/meps323035>

729 Yang, T., Chen, Y., Zhou, S., & Li, H. (2019). Impact of copper on marine phytoplankton: A Review.
730 *Atmosphere*, 10(414), 599–602. Retrieved from
731 http://inis.iaea.org/search/search.aspx?orig_q=RN:41131251

732 Zehr, J. P., & Capone, D. G. (2020). Changing perspectives in marine nitrogen fixation. *Science*,
733 368(6492). <https://doi.org/10.1126/science.aay9514>

734 Zhang, C., Ito, A., Shi, Z., Aita, M. N., Yao, X., Chu, Q., et al. (2019). Fertilization of the Northwest
735 Pacific Ocean by East Asia Air Pollutants. *Global Biogeochemical Cycles*, 33(6), 690–702.
736 <https://doi.org/10.1029/2018GB006146>

737

Journal of Geophysical Research: Biogeosciences

Supplementary information for

Costs of dust collection by *Trichodesmium*:

Effect on buoyancy and toxic metal release

Siyuan Wang^{1,2}, Futing Zhang^{1,2}, Coco Koedooder^{1,2,3}, Odeta Qafoku⁴, Subhajit Basu^{1,2,5}, Stephan Krisch⁸, Anna-Neve Visser^{1,2}, Meri Eichner⁶, Nivi Kessler^{1,2,9}, Rene M. Boiteau⁷, Martha Gledhill⁸ and Yeala Shaked^{1,2}

¹The Freddy and Nadine Herrmann Institute of Earth Sciences, Edmond J. Safra Campus, Givat Ram, Hebrew University of Jerusalem, Jerusalem, Israel

²The Interuniversity Institute for Marine Sciences in Eilat, Eilat, Israel

³Israel Limnology and Oceanography Research, Haifa, Israel

⁴Environmental Molecular Sciences Laboratory (EMSL), Pacific Northwest National Laboratory (PNNL), Richland, WA, 99454, USA

⁵University of Petroleum and Energy Studies (UPES-SoHST), Energy Acres, Dehradun 248007, India

⁶Center Algatech, Institute of Microbiology of the Czech Academy of Sciences, Novohradská 237, 37981 Třeboň, Czech Republic

⁷Department of Chemistry, University of Minnesota, Minneapolis, MN 55455

⁸GEOMAR, Helmholtz Center for Ocean Research, Kiel, Germany

⁹Present address: The water authority, 7 Bank of Israel st, Jerusalem 9195021, Israel

Contents of this file:

Text S1 to S5

Figures S1 to S13

Tables S1 to S7

Introduction:

This supplementary material provides readers with details regarding sedimentation experiments, toxicity assays and SEM-EDX analysis for examining the removal of toxic particles. **Sedimentation experiments** - experimental procedures (Fig. S1 and S2), raw data files (Table S1 and S2), modeling of colony sinking velocity (Text S1 and S2, Table S3, S4 and S5) and dust loss analysis (Text S3 and Fig. S3). **Toxicity assays** - experimental procedures (Text S4 and Fig. S4), colony mortality (incubated with CuSO₄; Fig. S5) and calculation of metal release (Table S6 and Fig. S6). Effective dust concentrations calculated for *in situ* colonies (Fig. S7) and colonies from incubations (Fig. S8). **SEM-EDX analysis** - experimental procedures (Fig. S9) and elemental maps (Fig. S10, S11, S12 and S13).

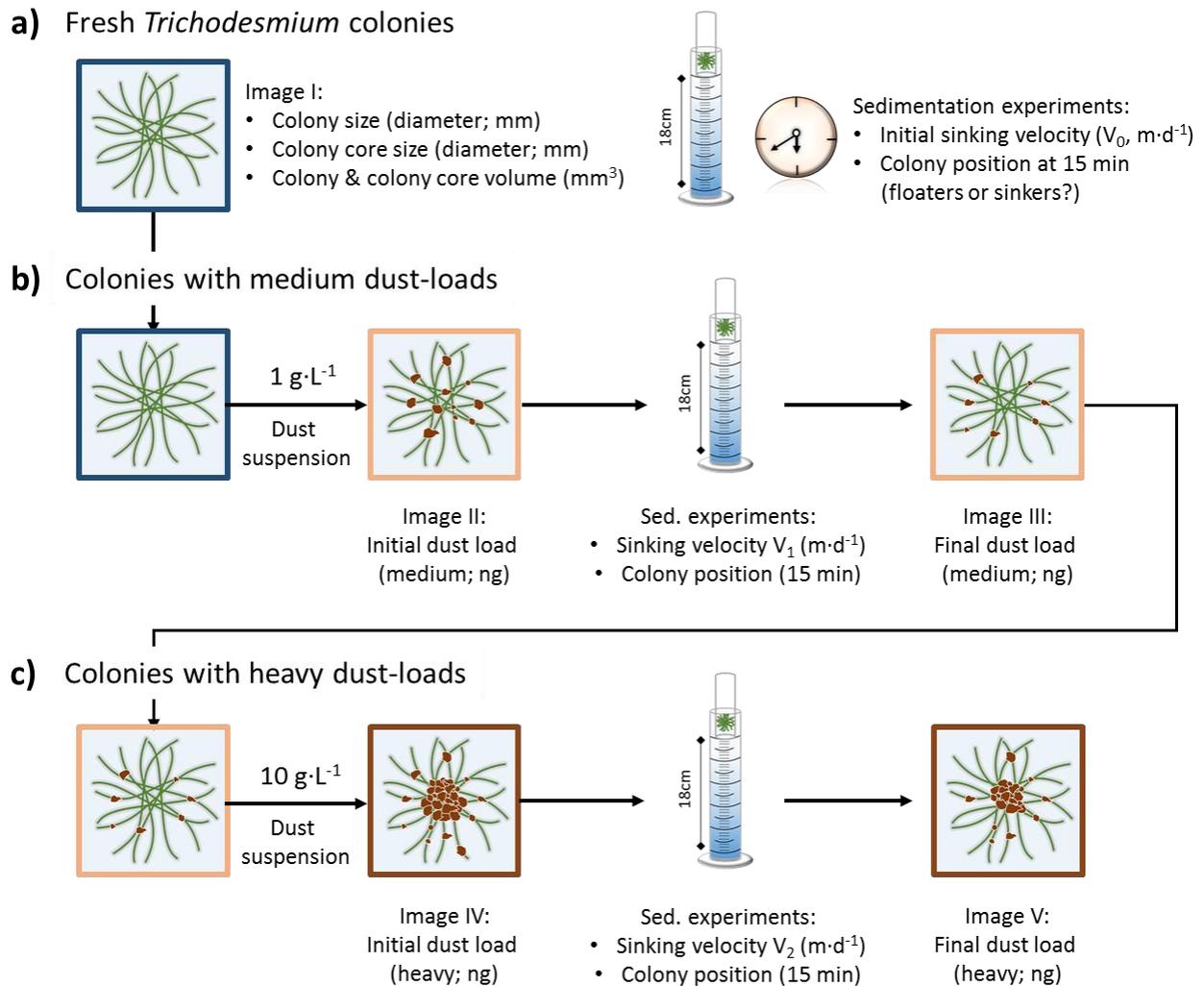
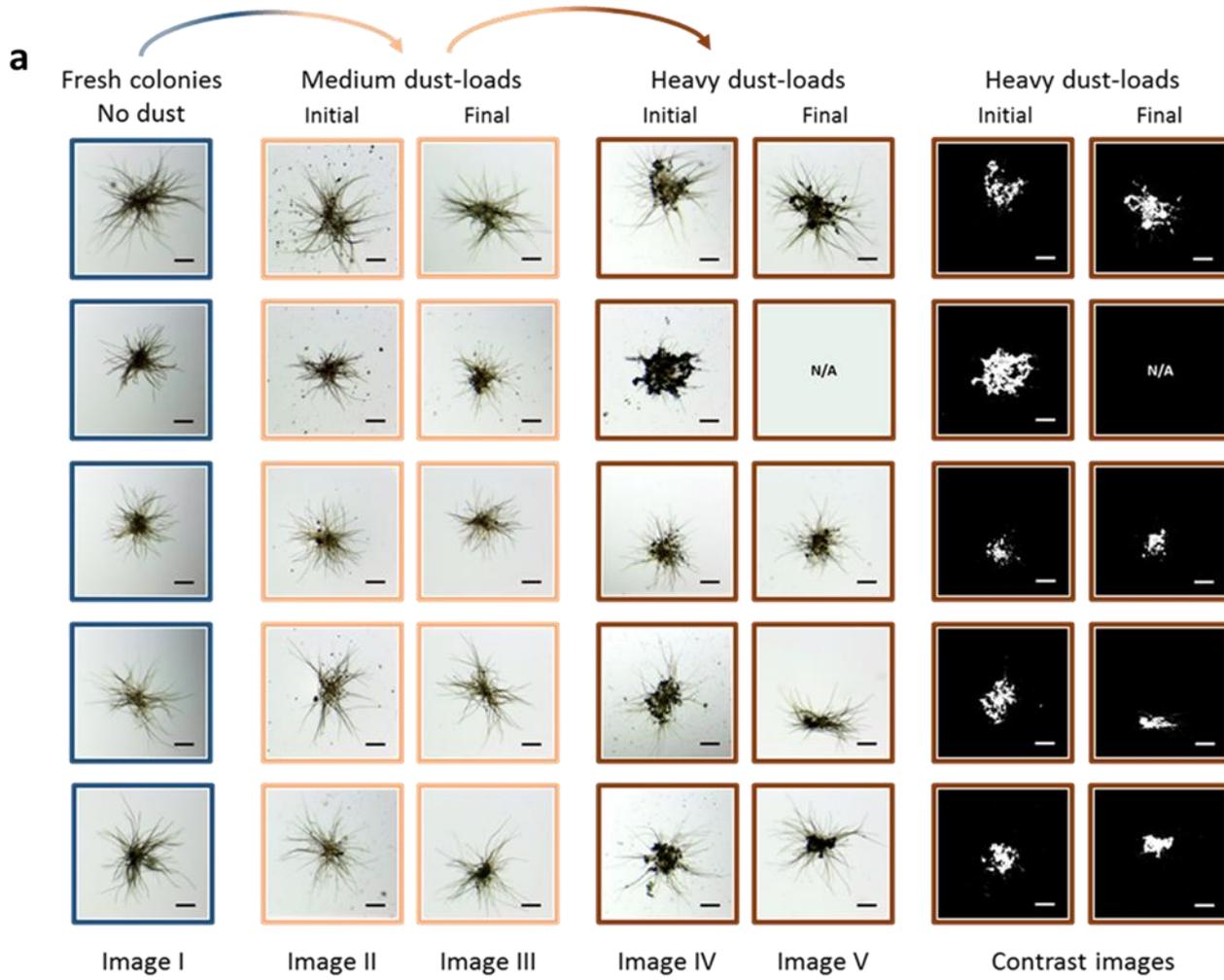


Figure S1. A schematic diagram of the experimental design for measuring the sinking velocity of a *Trichodesmium* colony at different dust loads.

The sinking velocity of *Trichodesmium* was measured on 5 individual days in the 2020 autumn season using 25 single colonies: without any dust particles (a) and with two manipulated dust-loads (medium and heavy, b and c).

- (a) Freshly-collected colonies were first imaged under a stereoscope to determine their basic parameters (Image I). Each colony was then placed into a sedimentation chamber containing 100 mL fresh seawater using a 20 μL pipette equipped with cut tips to minimize the initial force added to the colony sinking velocity. Upon careful injection, a timer was started to measure the sinking time while the colony position (before reaching the bottom) was tracked and recorded by a researcher. The sinking velocity of a colony was calculated as the distance it travelled divided by time. Measurements of sinking velocity usually lasted less than 5 min, after which colonies were left in the same chamber and their positions at 15 min were observed. Some colonies remained at the bottom while others left the bottom and were relocated at different depth. We refer to these observations as indicators of the colony buoyancy and define those at the bottom as “sinkers” and the others as “floaters”.
- (b) After measuring the initial sinking velocity (V_0), the colony was transferred with a long serological pipette into an eppendorf containing 1 $\text{g}\cdot\text{L}^{-1}$ dust suspension and mixed gently for loading dust particles (medium dust loads). Sinking velocity (V_1) measurements (and floatation status at 15 min) were performed using the same manner as described in (a). Stereoscopic images were taken prior to (Image II) and after experiments (Image III), for calculating initial and final dust loads via image analysis.
- (c) Subsequently, the same colony was transferred into 10 $\text{g}\cdot\text{L}^{-1}$ dust suspension and mixed gently for measuring the sinking velocity (V_2) at heavy dust loads. Measurements of sinking velocity (V_2), determination of floatation status, as well as stereoscopic images (Image III and IV) were achieved in the same manner as described in (b).



b

Sample	Image I (no dust)				Image II & III (medium)		Image IV & V (heavy)	
	Diameter (mm)		Volume (mm ³)		Dust loads (ng)			
	Colony	Colony core	Colony	Colony core	Initial	Final	Initial	Final
Colony 1	1.2	0.2	0.852	0.007	111	74	1400	1973
Colony 2	0.8	0.2	0.247	0.006	410	120	3475	N/A
Colony 3	0.8	0.2	0.232	0.006	214	109	597	697
Colony 4	1.0	0.3	0.592	0.009	140	49	1538	723
Colony 5	1.0	0.2	0.502	0.006	96	33	1224	1036

Figure S2. An example of image analysis – estimation of dust loads on five Red Sea colonies from sedimentation experiments conducted on October 18th, 2020.

(a) The size of colony and colony core was obtained from Image I using DinoCapture 2.0 software. To determine medium dust-loads (Image II and III), individual dust-covered area was measured using polygon tools and was summed to obtain the total dust-covered area (μm^2). To determine heavy dust-loads (Image IV and V), since dust particles were clustered in the colony core, total dust-covered area was obtained through pixel counting using contrast mode in ImageJ software. Total dust volume (μm^3) was subsequently derived by multiplying dust-covered area (μm^2) with an assumed constant thickness of 10 μm for the dust layer. Similar analysis was also conducted on natural dust loads of Red Sea (Eilat, this study) and Atlantic colonies (as reported by Held et al., 2022). All scale bars shown in the graph are 200 μm .

(b) A summary table of basic colony parameters and calculated medium and heavy dust loads for the colonies shown in panel a. The volume of colony and colony core was determined using the equation for calculating the sphere volume ($V=4/3\cdot\pi\cdot r^3$). Dust loads were derived by multiplying total dust volume (μm^3) with a dust density of 2.5 $\text{g}\cdot\text{cm}^{-3}$. N/A means not available due to the colony loss during transfer.

Table S1. Image analysis of *in situ* dust loads for Red Sea and Atlantic *Trichodesmium* colonies; related to Fig. 1 in the main text.

Colony #	Collection date	Colony radius	Colony volume	Number of particles	Particle diameter	Total dust Volume	Calculated dust weight ^a
		mm	μL		μm	μm^3	ng
1	10-Oct-18	0.644	1.1	1	N/A	7.4E+03	18
2	11-Oct-18	1.282	8.8	1	68	3.6E+04	91
3	15-Oct-18	0.814	2.3	7	10-26	3.9E+04	97
4	18-Oct-18	0.731	1.6	2	8-18	3.0E+03	8
5	18-Oct-18	0.464	0.4	4	18-20	1.1E+04	29
6	18-Oct-18	0.501	0.5	4	16-30	1.7E+04	42
7	28-Oct-18	0.760	1.8	3	12	5.9E+04	148
8	29-Oct-18	0.587	0.8	2	18-22	6.3E+03	16
9	29-Oct-18	0.477	0.5	1	40	1.3E+04	31
10	31-Oct-18	0.927	3.3	5	30-38	6.7E+04	167
11	1-Nov-18	0.689	1.4	1	16	2.0E+03	5
12	1-Nov-18	0.606	0.9	2	30-48	2.5E+04	63
13	1-Nov-18	0.557	0.7	2	16	4.4E+04	111
14	1-Nov-18	0.479	0.5	1	N/A	3.3E+03	8
15	6-Nov-18	0.469	0.4	2	10-16	2.8E+03	7
16	6-Nov-18	0.442	0.4	1	30	7.1E+03	18
17	7-Nov-18	0.560	0.7	2	20	9.4E+03	23
18	15-Nov-18	0.602	0.9	1	16	2.0E+03	5
19	7-May-19	0.887	2.9	2	12-18	3.7E+03	9
20	15-May-19	0.937	3.4	1	48	1.8E+04	45
21	15-May-19	0.572	0.8	1	18	2.5E+03	6
22	22-May-19	0.454	0.4	1	12	1.1E+03	3
23	22-May-19	0.658	1.2	1	N/A	2.1E+04	53
24	22-May-19	0.479	0.5	2	12-26	6.4E+03	16
	Min.	0.442	0.4	1	8	1.1E+03	3
	Max.	1.282	8.8	7	68	6.7E+04	167
	Median.	0.595	0.9	2	18	8.4E+03	21
	Fig. 1c	0.776	2.0	-	-	5.4E+06	13461
Held et al.	Fig. 1d	0.763	1.9	-	-	6.0E+06	14999
(2021)	Fig. 1e	0.792	2.1	-	-	4.0E+06	9954
	Fig. 1f	0.776	2.0	-	-	1.8E+06	4486

a. Dust weight (ng) was derived by multiplying the volume of dust particles (μm^3) with a dust density of $2.5 \text{ g}\cdot\text{cm}^{-3}$.

b. N/A means not available because the particle diameter was too small to be measured.

Table S2. Data pairs of colony dust load and sinking velocity during sedimentation experiments (n=75). The data for six representative colonies (colored red) analyzed on October 18th and October 20th 2020 was plotted in Fig. 2 in the main text.

Data pairs	Exp. date	Colony ID	Colony radius mm	Treatments	Dust weight (ng)		Sinking velocity m·d ⁻¹	Floatation status at 15 min
					Initial	Final		
1	18-Oct-20	A	0.588	No dust	-	-	64	Floater
2				Medium	111	74	119	Sinker
3				Heavy	1400	1973	141	Sinker
4		B	0.389	No dust	-	-	64	Sinker
5				Medium	410	120	53	Floater
6				Heavy	3475	Colony lost	351	Sinker
7		C	0.381	No dust	-	-	38	Floater
8				Medium	214	109	47	Sinker
9				Heavy	597	697	75	Sinker
10		D	0.521	No dust	-	-	58	Floater
11				Medium	140	49	34	Sinker
12				Heavy	1538	723	38	Sinker
13		E	0.493	No dust	-	-	45	Floater
14				Medium	96	33	45	Sinker
15				Heavy	1224	1036	131	Sinker
16	20-Oct-20	F	0.502	No dust	-	-	22	Floater
17				Medium	649	512	198	Sinker
18				Heavy	4065	2752	479	Sinker
19		G	0.504	No dust	-	-	26	Floater
20				Medium	168	51	41	Floater
21				Heavy	4419	2221	211	Sinker
22	H	0.454	No dust	-	-	32	Floater	
23			Medium	114	38	66	Sinker	
24			Heavy	3045	133	83	Sinker	
25	I	0.433	No dust	-	-	37	Floater	
26			Medium	1405	648	114	Sinker	
27			Heavy	2721	1345	161	Sinker	
28	J	0.532	No dust	-	-	21	Floater	
29			Medium	1053	559	142	Sinker	
30			Heavy	1910	2747	277	Sinker	
31	21-Oct-20	K	0.376	No dust	-	-	42	Floater
32				Medium	16	20	144	Floater
33				Heavy	2442	39	220	Sinker
34		L	0.410	No dust	-	-	33	Floater
35				Medium	69	2	234	Sinker
36				Heavy	2997	40	251	Sinker

Supplementary Information

37			No dust	-	-	50	Sinker	
38		M	0.499	Medium	166	43	158	Sinker
39				Heavy	2621	56	180	Sinker
40				No dust	-	-	38	Floater
41		N	0.482	Medium	132	101	221	Floater
42				Heavy	4024	3128	351	Sinker
43				No dust	-	-	50	Floater
44		O	0.566	Medium	68	58	243	Sinker
45				Heavy	1872	1290	129	Sinker
46				No dust	-	-	37	Floater
47		P	0.399	Medium	53	7	216	Floater
48				Heavy	951	31	102	Sinker
49				No dust	-	-	20	Floater
50		Q	0.420	Medium	85	37	237	Floater
51				Heavy	2343	759	144	Sinker
52				No dust	-	-	36	Floater
53	22-Oct-20	R	0.393	Medium	38	74	65	Floater
54				Heavy	1021	1403	65	Sinker
55				No dust	-	-	25	Floater
56		S	0.373	Medium	50	5	198	Sinker
57				Heavy	497	61	65	Sinker
58				No dust	-	-	14	Floater
59		T	0.435	Medium	99	62	144	Sinker
60				Heavy	2561	1628	186	Sinker
61				No dust	-	-	53	Sinker
62		U	0.543	Medium	114	48	211	Sinker
63				Heavy	1089	84	16	Floater
64				No dust	-	-	37	Floater
65		V	0.445	Medium	82	18	138	Sinker
66				Heavy	2075	1155	23	Sinker
67				No dust	-	-	0	Floater
68	26-Oct-20	W	0.457	Medium	61	9	122	Floater
69				Heavy	334	174	52	Floater
70				No dust	-	-	36	Floater
71		X	0.399	Medium	55	5	113	Floater
72				Heavy	1508	765	59	Sinker
73				No dust	-	-	11	Floater
74		Y	0.689	Medium	153	210	156	Sinker
75				Heavy	409	675	23	Floater

Supplementary text S1. Modeling the sinking velocity of natural *Trichodesmium* colonies loaded with dust particles.

The sinking velocity of a *Trichodesmium* colony can be calculated according to Stoke's Law (Kromkamp & Walsby, 1990; White et al., 2006), using the following equation:

$$v = \frac{2gr^2(\rho_c - \rho_w)A}{9\phi\eta} \quad (eq. 1)$$

Where: v – colony sinking velocity ($m \cdot s^{-1}$); g – gravitational acceleration ($m \cdot s^{-2}$); r – colony radius (m); ρ_c and ρ_w – colony and seawater density, respectively ($kg \cdot m^{-3}$); A – cell volume to colony volume ratio; ϕ – coefficient of form resistance; η – molecular viscosity of the medium ($kg \cdot m^{-1} \cdot s^{-1}$). A is the ratio of cell volume to colony volume, since most of space within colony sphere is occupied by seawater. For instance, A was assigned a value of 0.05 in the study by White et al. (2006), indicating that the colony sphere consists of 5% cell volume and 95% seawater volume.

We considered the significant change of ρ_c and A for *Trichodesmium* colonies after interacting with dust particles. Assuming that dust volume did not exceed the colony volume, new ρ_c and A can be derived as follows:

$$\rho' = \rho_{colony+dust} = \frac{m_{cell} + m_{dust}}{V_{cell} + V_{dust}} \quad (eq. 2)$$

$$A' = \frac{V_{cell} + V_{dust}}{V_{colony}} \quad (eq. 3)$$

$$V_{colony} = \frac{4}{3}\pi r^3 \quad (eq. 4)$$

Where in eq.2: ρ' – the new density of a colony with dust ($kg \cdot m^{-3}$); m_{cell} and m_{dust} – cell and dust mass, respectively (kg); V_{cell} and V_{dust} – cell and dust volume, respectively (m^3). Where in eq.3: A' – cell and dust volume to colony volume ratio; V_{cell} , V_{dust} and V_{colony} are cell, dust and colony volume, respectively (m^3). Where in eq.4: V_{colony} – colony volume (m^3); r – colony radius (m). Substituting equation 2, 3 and 4 into equation 1 and performing integration, the sinking velocity of a colony with dust particles (v') is derived as follows:

$$v' = v_{colony+dust} = \frac{g}{6\pi r\phi\eta} [m_{dust} - \rho_w V_{dust} + m_{cell} - \rho_w V_{cell}] \quad (eq. 5)$$

Since:

$$V_{dust} = \frac{m_{dust}}{\rho_{dust}} \quad (eq. 6); \quad V_{cell} = \frac{m_{cell}}{\rho_{cell}} \quad (eq. 7)$$

Where: ρ_{dust} and ρ_{cell} – *Trichodesmium* dust density and cell density, respectively ($kg \cdot m^{-3}$). Substituting equation 6 and 7 into equation 5 derives equation 8:

$$v' = m_{dust} \cdot \frac{g \left(1 - \frac{\rho_w}{\rho_{dust}}\right)}{6\pi r \phi \eta} + m_{cell} \cdot \frac{g \left(1 - \frac{\rho_w}{\rho_{cell}}\right)}{6\pi r \phi \eta} \quad (eq. 8)$$

Where: v' – the sinking velocity of colony with dust particles ($m \cdot s^{-1}$); m_{dust} and m_{cell} – dust and cell mass, respectively (kg); g – gravitational acceleration ($m \cdot s^{-2}$); ρ_w , ρ_{dust} and ρ_{cell} – seawater, dust and cell density, respectively ($kg \cdot m^{-3}$); r – colony radius (m); ϕ – coefficient of form resistance; η – molecular viscosity of the medium ($kg \cdot m^{-1} \cdot s^{-1}$).

$$K = \frac{g \left(1 - \frac{\rho_w}{\rho_{dust}}\right)}{6\pi r \phi \eta} \quad (eq. 9); \quad v_0 = m_{cell} \cdot \frac{g \left(1 - \frac{\rho_w}{\rho_{cell}}\right)}{6\pi r \phi \eta} \quad (eq. 10)$$

Equation 8 predicts a linear increase of velocity (v') with increasing dust weight (m_{dust}). The slope (dust factor-K) is influenced by colony size (r), seawater (ρ_w) and dust density (ρ_{dust}). The intercept (sinking velocity when the colony is particle-free; herein defined as " v_0 ") is influenced by cell mass (m_{cell}), colony size (r), seawater (ρ_w) and cell density (ρ_{cell}). When dust load is zero, the intercept (v_0) can be converted to equation 1 using equation 3. Calculations and simulations of dust factor (K) and sinking velocity of particle-free colonies (v_0) are described in supplementary text S2.

Supplementary text S2. Calculations and simulations of dust factor (K) and sinking velocity of particle-free colonies (v_0).

Using python (Version 3.10.9) with a *linspace* function, we first simulated the range of dust factors (K) derived from equation 8, using parameter values obtained from this study and literatures (see Table S3). During the simulation, seawater and dust density and colony radius (ρ_{water} , ρ_{dust} and r) were set to be variants, while the remaining parameters were fixed to literature values. The simulated dust factor (K) ranged from 2.2-7.4 x 10⁵ m·s⁻¹·kg⁻¹ (0.02-0.06 m·d⁻¹·ng⁻¹). All python codes related to the calculation of dust factor (K) can be found in Github (<https://github.com/Zhanzhu1110/Trichobuoyancy.git>), as well as in Zenodo (<https://zenodo.org/records/10290901>; DOI:10.5281/zenodo.10290901)(Wang et al., 2023).

Table S3. The equation and parameter values for calculating dust factor (K)

Dust factor (K)	Para- meters	Definitions	Parameter range	Units	Source
$\frac{g \left(1 - \frac{\rho_w}{\rho_{dust}}\right)}{6\pi r \phi \eta}$	K	Dust factor	2.2 x 10 ⁵ to 7.4 x 10 ⁵	m·s ⁻¹ ·kg ⁻¹	Simulation results
	ρ_w	Seawater density	Variable ^a	kg·m ⁻³	Benaltabet et al. (2022)
	ρ_{dust}	Dust density	Variable ^b	kg·m ⁻³	McConnell et al. (2008); Schladitz et al. (2009)
	r	Colony radius	Variable ^c	m	This study (Table S2)
	g	Gravitational acceleration	9.81	m·s ⁻²	Wikipedia ^d
	Φ	Form resistance	1	-	White et al. (2006)
	η	Dynamic viscosity	9.60 x 10 ⁻⁴	kg·m ⁻¹ ·s ⁻¹	White et al. (2006)

a. The range of seawater densities (ρ_w) is from 1026.5 to 1029 kg·m⁻³ (Red Sea surface to ca. 700m).

b. The range of dust densities (ρ_{dust}) is from 2100 to 2600 kg·m⁻³.

c. The range of colony radius (r) is from 0.442 to 1.282 mm (measured on Red Sea colonies, see Table S2).

d. https://en.wikipedia.org/wiki/Gravity_of_Earth

Simulation of sinking velocity of particle-free colonies (v_0) requires the key parameter of cell mass (m_{cell}) or more specifically, the cell volume (V_{cell} ; see Table S4 for V_{cell} estimation). Using equation 7 and 10, the equation for calculating v_0 is derived as follows:

$$v_0 = \frac{g \cdot V_{cell} \cdot (\rho_{cell} - \rho_w)}{6\pi r \phi \eta} \quad (eq. 11)$$

Where: v_0 – the sinking velocity of particle-free colonies (m·s⁻¹); V_{cell} – cell volume (m³); ρ_{cell} and ρ_w – cell and seawater density, respectively (kg·m⁻³); r – colony radius (m); Φ – coefficient of form resistance; η – molecular viscosity of the medium (kg·m⁻¹·s⁻¹). During the simulation, four parameters (V_{cell} , ρ_{cell} , ρ_{water} and

r) were set to be variants, while the rest parameters were fixed to literature values (see Table S5). Using python, we obtained the sinking velocity of particle-free colonies ranged between 9.9×10^{-7} - $1.1 \times 10^{-4} \text{ m}\cdot\text{s}^{-1}$ (0 to 9 $\text{m}\cdot\text{d}^{-1}$). All python codes related to the calculation of v_0 can be found in Github (<https://github.com/Zhanzhu1110/Trichobuoyancy.git>) and Zenodo (<https://zenodo.org/records/10290901>; DOI:10.5281/zenodo.10290901)(Wang et al., 2023).

Table S4. Estimation of total cell volume (V_{cell}) in single Red Sea *Trichodesmium* colonies

<i>Trichodesmium</i>	Single cell volume	Cell number	Total cell volume ^a	Source
	μm^3	#	μm^3	
Tuft colonies	-	-	3.9×10^5	Benavides et al. (2022) - SI
Puff colonies (Eilat)	83-209 ^b	4708-11088	$3.9 -23 \times 10^5$	Basu and Shaked (2018) - Table SI-B

- a. Total cell volume (μm^3) was derived by multiplying the single cell volume (μm^3) with cell number (#).
b. Single cell volume (μm^3) was derived by considering the cell as a cylinder ($V=\pi r^2*d$). Cell radius (r) and cell length (d) used here ranged between 2.4-2.9 μm and 4.8-8.2 μm , respectively (Basu & Shaked, 2018). Calculated single cell volume is similar to the results of *Trichodesmium* IMS101 culture, as reported by Ho (2013).

Table S5. Equation and parameter values for calculating sinking velocity of particle-free colonies (v_0)

v_0	Para-meters	Definitions	Parameter range	Units	Source
$\frac{g \cdot V_{cell} \cdot (\rho_{cell} - \rho_w)}{6\pi r \phi \eta}$	v_0	Sinking velocity (particle-free)	9.9×10^{-7} to 1.1×10^{-4}	$\text{m}\cdot\text{s}^{-1}$	Simulation results
	V_{cell}	Cell volume	Variable ^a	m^3	Table S4
	ρ_{cell}	Cell density	Variable ^b	$\text{kg}\cdot\text{m}^{-3}$	White et al. (2006)
	ρ_w	Seawater density	Variable ^c	$\text{kg}\cdot\text{m}^{-3}$	Benaltabet et al. (2022)
	r	Colony radius	Variable ^d	m	This study (Table S2)
	g	Gravitational acceleration	9.81	$\text{m}\cdot\text{s}^{-2}$	Wikipedia ^e
	Φ	Form resistance	1	-	White et al. (2006)
	η	Dynamic viscosity	9.60×10^{-4}	$\text{kg}\cdot\text{m}^{-1}\cdot\text{s}^{-1}$	White et al. (2006)

- a. The range of cell volume is from $3.9 -23 \times 10^5 \mu\text{m}^3$ (see Table S4)
b. The range of a sinking cell density (ρ_{cell}) is from 1035 to 1065 $\text{kg}\cdot\text{m}^{-3}$, as reported by White et al. (2006).
c. The range of seawater density (ρ_w) is from 1026.5 to 1029 $\text{kg}\cdot\text{m}^{-3}$ (sea surface to ca. 700m).
d. The range of colony radius (r) is from 0.442 to 1.282 mm (measured on Red Sea colonies, see Table S2).
e. https://en.wikipedia.org/wiki/Gravity_of_Earth

Table S6. Calculation of dust loss on *Trichodesmium* colonies during sedimentation experiments.

Data pairs	Exp. date	Colony ID	Colony radius	Colony volume	Dust load			Dust loss
					ng			
					Treatments	Initial	Final	
1	18-Oct-20	A	0.588	0.852	Medium	111	74	37
2					Heavy	1400	1973	No loss
3		B	0.389	0.247	Medium	410	120	290
4					Heavy	3475	Colony lost	Colony lost
5		C	0.381	0.232	Medium	214	109	105
6					Heavy	597	697	No loss
7		D	0.521	0.592	Medium	140	49	90
8					Heavy	1538	723	815
9		E	0.493	0.502	Medium	96	33	63
10					Heavy	1224	1036	188
11	20-Oct-20	F	0.502	0.530	Medium	649	512	137
12					Heavy	4065	2752	1313
13		G	0.504	0.536	Medium	168	51	117
14					Heavy	4419	2221	2198
15		H	0.454	0.392	Medium	114	38	75
16					Heavy	3045	133	2912
17		I	0.433	0.340	Medium	1405	648	757
18					Heavy	2721	1345	1376
19		J	0.532	0.631	Medium	1053	559	494
20					Heavy	1910	2747	No loss
21	21-Oct-20	K	0.376	0.223	Medium	16	20	No loss
22					Heavy	2442	39	2403
23		L	0.410	0.289	Medium	69	2	67
24					Heavy	2997	40	2957
25		M	0.499	0.520	Medium	166	43	123
26					Heavy	2621	56	2564
27		N	0.482	0.469	Medium	132	101	31
28					Heavy	4024	3128	896
29		O	0.566	0.760	Medium	68	58	10
30					Heavy	1872	1290	582

Supplementary Information

31	22-Oct-20	P	0.399	0.266	Medium	53	7	46
32					Heavy	951	31	920
33	22-Oct-20	Q	0.420	0.310	Medium	85	37	48
34					Heavy	2343	759	1584
35	22-Oct-20	R	0.393	0.254	Medium	38	74	No loss
36					Heavy	1021	1403	No loss
37	22-Oct-20	S	0.373	0.217	Medium	50	5	45
38					Heavy	497	61	435
39	22-Oct-20	T	0.435	0.345	Medium	99	62	36
40					Heavy	2561	1628	932
41	26-Oct-20	U	0.543	0.671	Medium	114	48	65
42					Heavy	1089	84	1005
43	26-Oct-20	V	0.445	0.369	Medium	82	18	64
44					Heavy	2075	1155	920
45	26-Oct-20	W	0.457	0.400	Medium	61	9	52
46					Heavy	334	174	161
47	26-Oct-20	X	0.399	0.266	Medium	55	5	50
48					Heavy	1508	765	744
49	26-Oct-20	Y	0.689	1.370	Medium	153	210	No loss
50					Heavy	409	675	No loss

Treatments	Dust loss (ng)	
Medium	Min	10
	Max	757
Heavy	Min	161
	Max	2957

Supplementary text S3. Selection criterion for data pairs presented in Fig. 3, related to the main text - Section 3.1.3.

To illustrate the effect of dust loss on colony sinking velocity, we selected 20 out of 50 total data pairs obtained from sedimentation experiments and showed seven representative data pairs in Fig. 3 and the rest in Fig. S3 (n=13). The selected data pairs/colonies meet the following requirements: 1) calculation of dust loss was found to be positive values (42 out of 50 total data pairs) and 2) measured sinking velocities of these colonies against their initial dust loads plotted below the prediction line established in Fig. 2b ($y = 0.06 \text{ m}\cdot\text{d}^{-1} \cdot \text{ng}^{-1} \times \text{dust weight (ng)} + 53 \text{ m}\cdot\text{d}^{-1}$; 20 out of 42 data pairs).

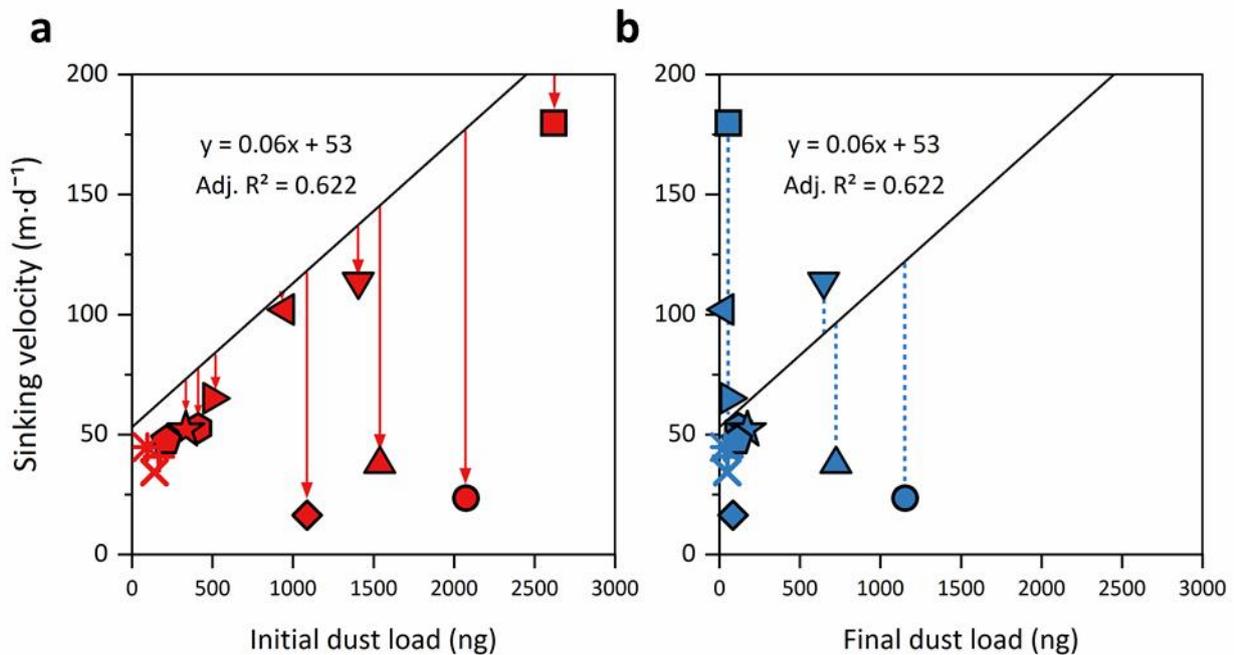


Figure S3. Effect of dust loss on colony sinking velocity. Measured sinking velocities of additional colonies (n=13, shown as different symbols) plotted against their initial (a) and final (b) dust loads, related to the main text – Fig.3. The equation (black line) is the linear relationship established in the main text - Fig. 2b. Arrows and dash lines indicate the mismatch of measured sinking velocities and expected velocities calculated from initial and final dust loads, respectively.

Supplementary text S4. Toxicity assays – incubation experiments on Red Sea *Trichodesmium* colonies with dust suspension, dust leachates and dissolved Cu (CuSO₄) and visual examinations of colony mortality during incubations.

To investigate the particle toxicity to *Trichodesmium*, we conducted incubation experiments on colonies with dust suspension and leachate for 24 hrs during the spring of 2022 (n=176; see main text – section 2.3). Simultaneously, similar incubation assays were conducted on Red Sea colonies with dissolved Cu (CuSO₄).

Primary CuSO₄ solutions were prepared daily in Milli-Q water (18.2 Ω) and diluted to final concentrations of 5, 10, 50, 200, 250, 500, 1000, and 3000 nM using filtered seawater (FSW). Two colonies per well were incubated in a 48-well plate containing 0.5 mL CuSO₄ solutions and were kept in a culture room (25 °C, ~80 μE m⁻²·s⁻¹, 10:14 h light-dark cycle) for up to 74 hrs. Visual examination of colony and filament shape, structure, and color was performed under a stereoscope (Fig. S4). Incubation of colonies without CuSO₄ addition served as control. Incubations with dissolved Cu were repeated thrice using freshly-collected Red Sea colonies (n=118).

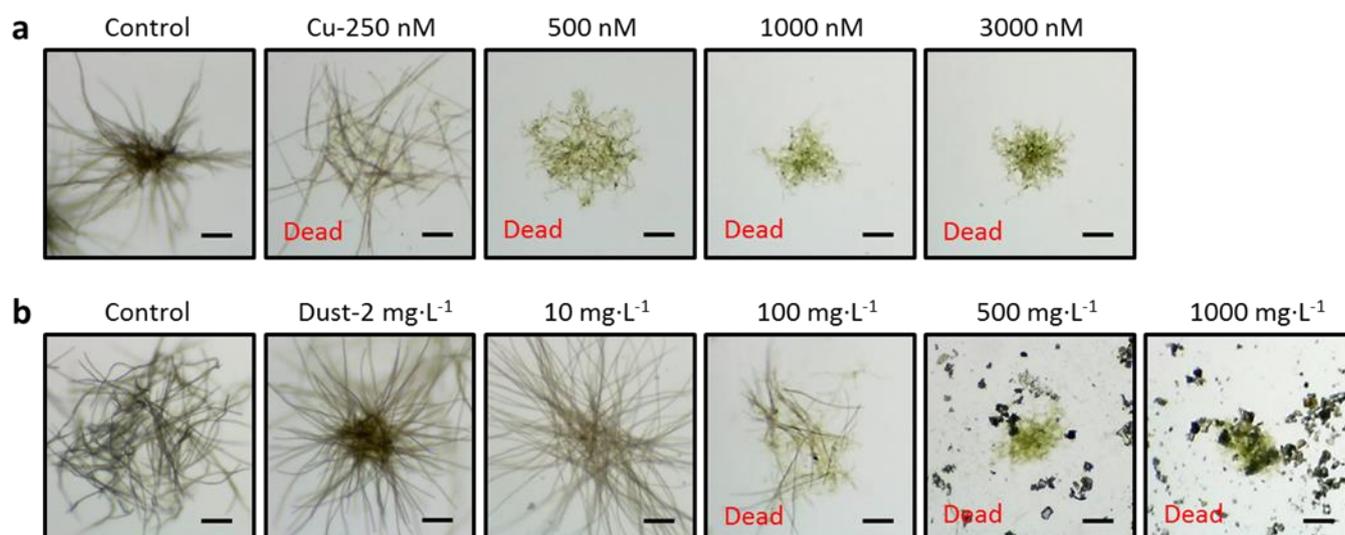


Figure S4. Stereoscopic observations of Red Sea *Trichodesmium* colonies when exposed to CuSO₄ (a) and dust suspensions (b) for 24 hrs. All scale bars are 200 μm. The mortality of *Trichodesmium* (%) was calculated by dividing the number of dead colonies to the total number of colonies used in each treatment. Colonies identified as "dead" colonies were marked accordingly in the images.

Addition of 3000 nM CuSO₄ induced an acute toxicity to *Trichodesmium*, with 100% of colonies dead in 2hrs. Moreover, no colonies survived when incubating with >200 nM CuSO₄ for 24 hrs. Incubating with 5-50 nM Cu for 24 hrs yields 30-50% mortality of colonies (Fig. S5).

Applying Chlorophyll *a* (Chl *a*) content measured on Red Sea colonies (~5 ng Chl *a* colony⁻¹; unpublished data), we determined the lethal dose 100 (LD100) of Cu as 0.6 μg total Cu · (μg Chl *a*)⁻¹ (when total [Cu] = 200 nM). It is important to note that we reported the toxicity threshold of Cu with a unit of total Cu per biomass in this study, yet the toxicity does not depend on the total Cu added but rather on free (non-complexed) Cu concentrations (Paytan et al., 2009; Sunda & Huntsman, 1998). The toxicity threshold of Cu for

Trichodesmium was comparable to the Cu threshold for *Synechococcus* WH8102 ($0.2 - 2 \mu\text{g Cu} \cdot (\mu\text{g Chl } a)^{-1}$), as reported by Paytan et al. (2009).

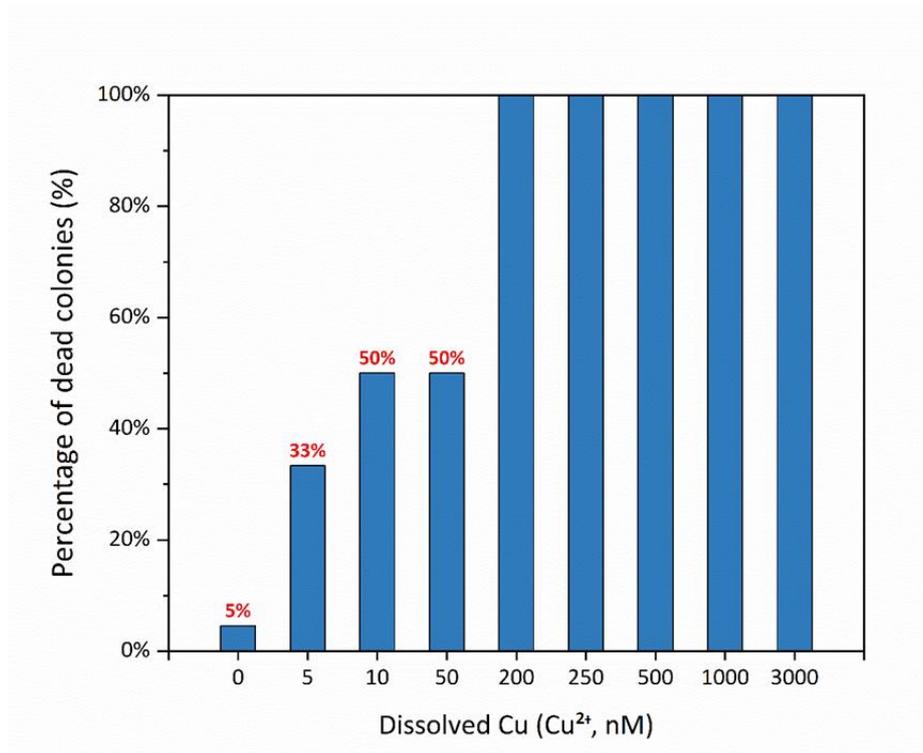


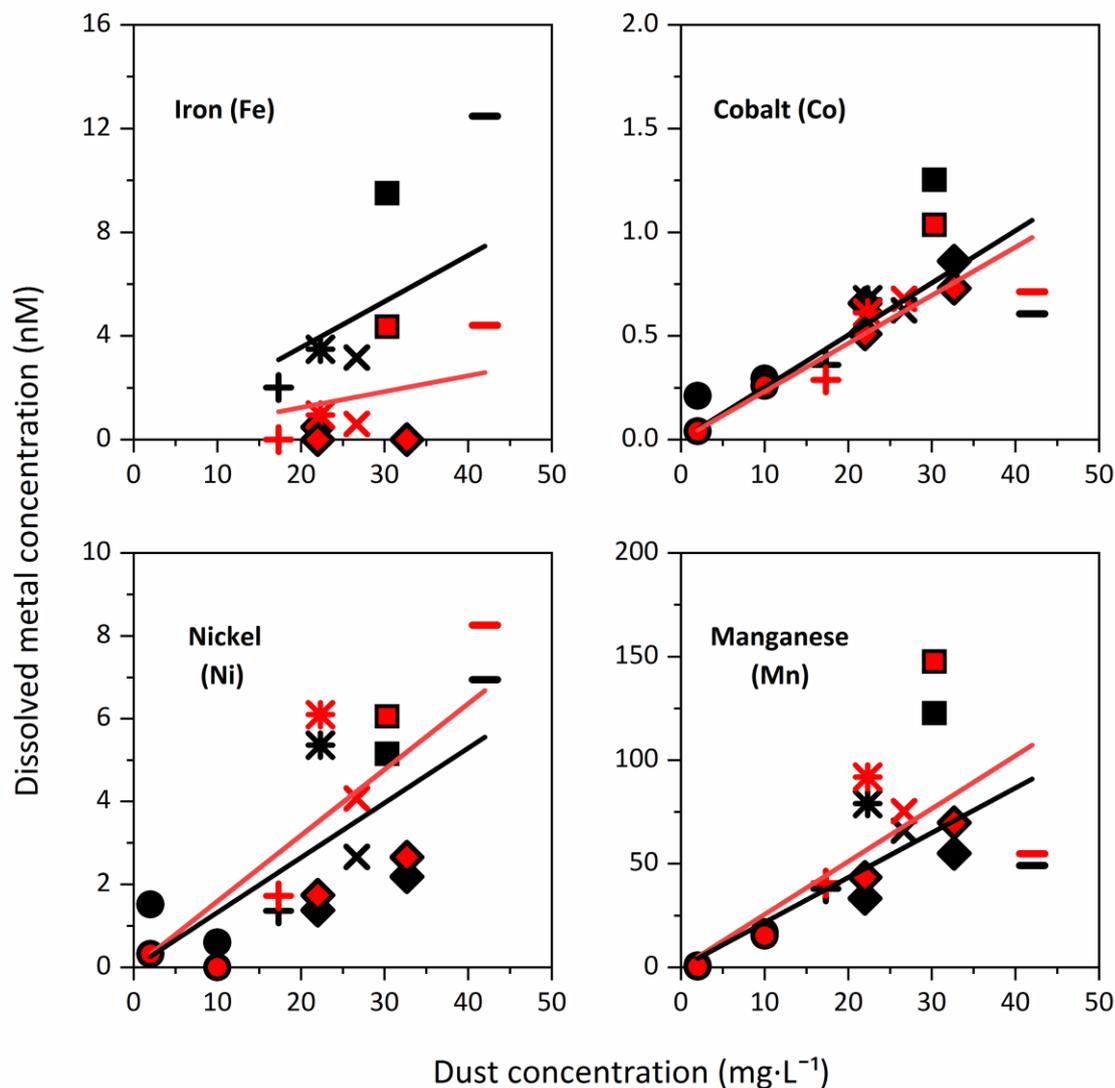
Figure S5. Percentage (%) death of Red Sea colonies after a 24-hour incubation with varying concentrations of dissolved Cu (CuSO₄) in seawater. The mortality was determined by dividing the number of dead colonies by the total colonies in each treatment prior to the incubation.

Table S7. Compilation data of seawater soluble aerosol metal in nM (aerosol concentrations = 2-42 mg·L⁻¹; data were obtained from this study and from Mackey et al., 2015 – Supplemental Table 2). Values were corrected using the average values of two operational blanks (seawater). Dissolution data were separated into rapid (<6 hrs) and gradual (1-7 days) dissolution and their median values were calculated. Boxes colored in green and red indicate dissolution of the same dust particles, respectively.

Data source		This study		Mackey et al. (2015)						
[Dust] mg·L ⁻¹		2	10	17	22	22	27	30	33	42
Metal	Dissolution time	[Metal] nM								
Ni	10min			0.1	4.3	0.7	2.5	4.2	1.1	5.5
	6h			2.6	6.4	2.1	2.9	6.1	3.3	8.4
	Rapid (Median)	1.5	0.6	1.4	5.4	1.4	2.7	5.1	2.2	6.9
	1d			1.3	5.3	1.1	3.4	5.1	2.2	7.6
	3d			1.7	6.1	1.7	4.1	6.0	2.7	8.3
	7d			2.5	7.4	2.3	4.7	6.6	3.8	9.1
	Gradual (Median)	0.3	0.0	1.7	6.1	1.7	4.1	6.0	2.7	8.3
	Zn	10min			42	82	27	59	201	54
6h				55	96	38	65	226	55	107
Rapid		0	33	49	89	32	62	214	54	103
1d				52	97	35	69	226	54	105
3d				50	97	36	71	221	54	106
7d				52	109	35	68	202	61	111
Gradual		0	40	52	97	35	69	221	54	106
Pb		10min			3.4	2.9	6.8	3.4	5.2	9.4
	6h			3.7	2.8	7.9	3.2	3.8	9.3	7.3
	Rapid	1.5		3.6	2.9	7.3	3.3	4.5	9.3	6.7
	1d			3.1	2.4	7.3	2.7	2.9	7.9	6.2
	3d			3.1	2.2	7.0	2.7	2.5	7.3	6.0
	7d			2.9	2.0	6.8	2.4	2.2	7.1	5.9
	Gradual	2.2		3.1	2.2	7.0	2.7	2.5	7.3	6.0
	Co	10min			0.4	0.7	0.4	0.7	0.8	0.5
6h				0.3	0.7	0.9	0.5	1.7	1.2	0.6
Rapid		0.2	0.3	0.4	0.7	0.7	0.6	1.3	0.9	0.6
1d				0.0	0.3	0.0	0.2	1.1	0.3	0.4
3d				0.3	0.7	0.5	0.7	0.8	0.7	0.7
7d				0.4	0.6	0.5	0.7	1.0	0.7	0.7
Gradual		0.0	0.3	0.3	0.6	0.5	0.7	1.0	0.7	0.7
Cu		10min			3.1	8.4	0.8	5.8	4.8	1.3
	6h			5.6	11.8	1.5	7.9	8.1	2.1	8.7
	Rapid	0.4	1.8	4.3	10.1	1.2	6.8	6.4	1.7	7.3
	1d			6.3	13.1	1.8	8.9	9.2	2.7	9.5
	3d			5.7	12.1	1.6	9.0	9.0	2.7	8.8
	7d			5.6	11.9	1.3	9.3	8.2	2.3	8.8
	Gradual	1.0	1.1	5.7	12.1	1.6	9.0	9.0	2.7	8.8

Supplementary Information

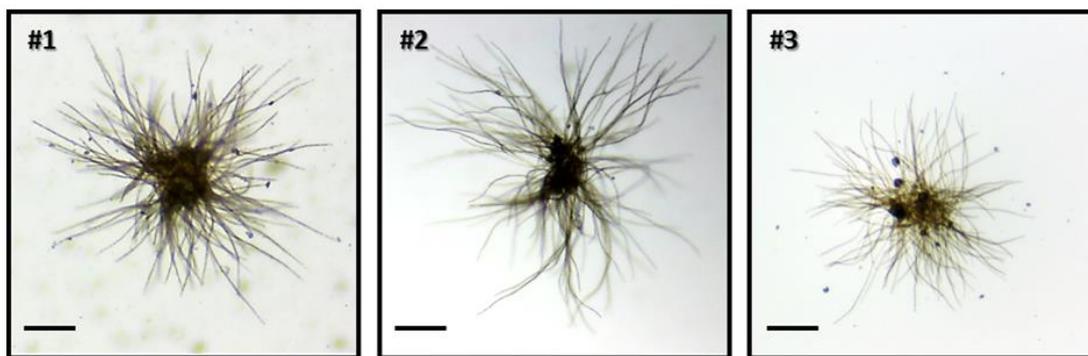
Cd	10min		0.4	0.5	0.1	0.5	0.5	0.1	0.3
	6h		0.4	0.4	0.0	0.4	0.5	0.1	0.3
	Rapid	0.0 0.1	0.4	0.4	0.1	0.5	0.5	0.1	0.3
	1d		0.4	0.4	0.0	0.4	0.5	0.0	0.3
	3d		0.4	0.4	0.0	0.4	0.5	0.1	0.3
	7d		0.4	0.5	0.0	0.4	0.5	0.1	0.3
	Gradual	0.1 0.3	0.4	0.4	0.0	0.4	0.5	0.1	0.3
Mn	10min		35	72	28	62	108	46	46
	6h		41	86	39	70	137	64	52
	Rapid	1 17	38	79	33	66	122	55	49
	1d		41	89	42	74	140	68	54
	3d		41	92	43	76	147	70	55
	7d		43	96	47	75	148	75	56
	Gradual	0 15	41	92	43	75	147	70	55
Al	10min		35	38	17	30	60	21	115
	6h		67	83	56	82	171	75	176
	Rapid		51	61	37	56	116	48	146
	1d		82	105	80	112	236	151	193
	3d		114	129	190	144	327	253	211
	7d		135	180	310	180	441	421	198
	Gradual		114	129	190	144	327	253	198
Fe	10min		3.2	4.7	1.0	5.3	10.6	0.0	8.2
	6h		0.8	2.3	0.0	1.1	8.4	0.0	16.7
	Rapid		2.0	3.5	0.5	3.2	9.5	0.0	12.5
	1d		0.4	0.9	0.0	0.6	4.2	0.0	8.1
	3d		0.0	4.7	0.0	0.0	5.9	0.0	4.4
	7d		0.0	0.0	0.0	4.1	4.4	6.1	0.0
	Gradual		0.0	0.9	0.0	0.6	4.4	0.0	4.4



Metal (nM)	Regression slopes (nmol · (mg dust) ⁻¹)			
	Fe	Co	Ni	Mn
Rapid diss.	0.18	0.025	0.13	2.16
Gradual diss.	0.06	0.023	0.16	2.55

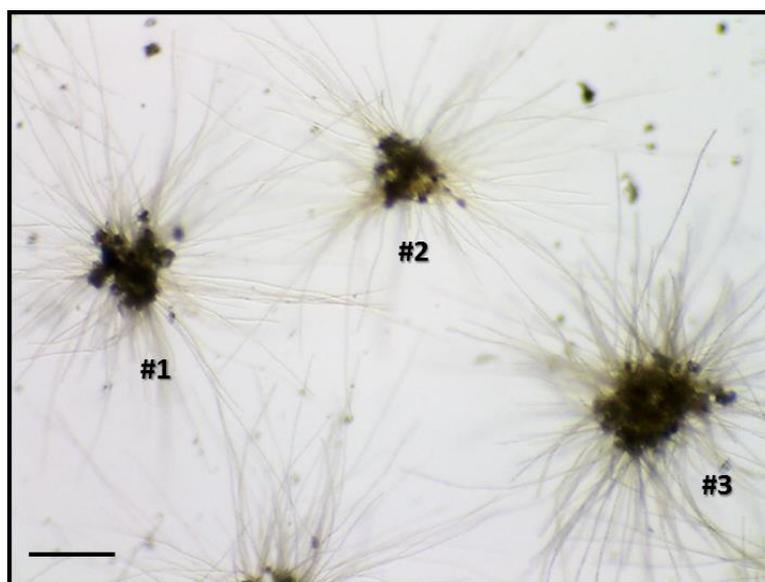
Figure S6. The release kinetics of four additional metals (Fe, Co, Ni and Mn) in dust dissolution experiments, related to the main text - Fig. 4.

The dataset combines new measurements (circles) and published data from Mackey et al., 2015, which includes seven dust samples plotted as different symbols. Dissolution kinetics is presented in two categories - rapidly released metals (black, up to 6hrs) and gradually released metals (red, up to 7 days). A summary table of regression slopes is shown below.



Colony	Colony radius	Colony volume	Dust load	Effective dust concn.
#	mm	mm ³ ; μ L	ng	mg·L ⁻¹
1	0.410	0.29	69	239
2	0.689	1.37	675	492
3	0.381	0.23	214	925

Figure S7. Effective dust concentrations calculated for three representative natural/freshly collected Red Sea colonies, related to the main text section 3.2.2. The concentration (mg·L⁻¹) was derived by dividing dust load (ng) by the colony volume (μ L). Scale bar = 200 μ m.



Colony	Incubation time	Colony radius	Colony volume	Dust load	Effective dust concn.
#	hours	mm	mm ³ ; μ L	ng	mg·L ⁻¹
1	24	0.53	0.62	2490	4039
2	24	0.49	0.48	1948	4051
3	24	0.43	0.33	4127	12391

Figure S8. Images of Red Sea *Trichodesmium* colonies following a 24-hour *in situ* incubation with dust particles (10 mg·L⁻¹). Effective dust concentrations within colony sphere were observed at levels exceeding 1000 mg·L⁻¹. Scale bar = 200 μ m.

Supplementary text S5. Characterizations of toxic particle removal via SEM-EDX analysis.

To investigate the ability of natural *Trichodesmium* colonies to remove toxic particles, incubation experiments were performed during the autumn of 2021, using 16 Red Sea colonies with Cu-containing mineral (malachite) and Fe-containing mineral (hematite). Briefly, 16 freshly collected colonies were first placed into a Nalgene bottle containing $2 \text{ mg}\cdot\text{L}^{-1}$ malachite and $2 \text{ mg}\cdot\text{L}^{-1}$ hematite (total particle concentration = $4 \text{ mg}\cdot\text{L}^{-1}$). The bottle was then incubated *in situ* (under the pier of Interuniversity of Marine Science in Eilat, Israel) for up to 24 hrs. 5-6 colonies were subsampled at 2h, 6h and 24h, placed on a PES membrane filter (Supor®), air-dried and frozen prior to SEM-EDX analysis at Environmental Molecular Sciences Laboratory (EMSL), USA (Fig. S9a). Stereoscopic images of each colony after the incubation were taken prior to (Fig. S9b) and after the air-drying procedure (Fig. S9c), before SEM-EDX analysis.

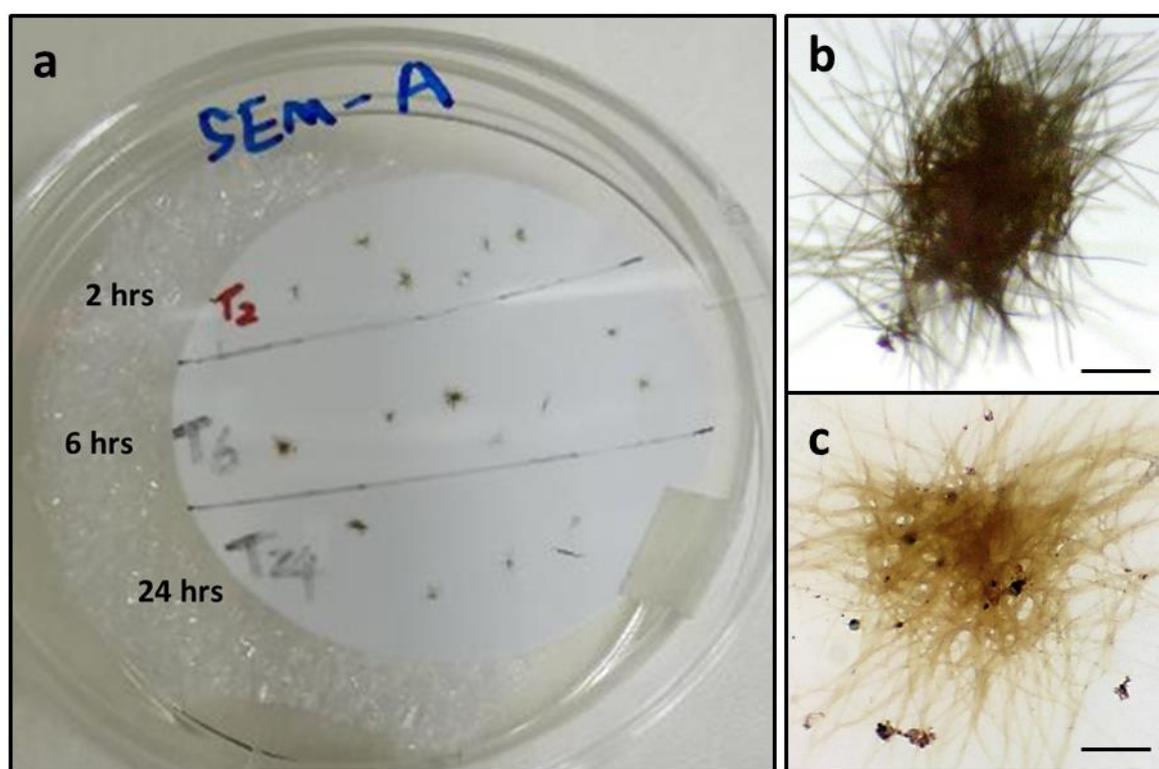


Figure S9. An illustrative figure of sample collection for SEM-EDX analysis (a), stereoscopic images of a colony prior to (b) and after the air-dried procedure (c). Scale bar = 200 μm .

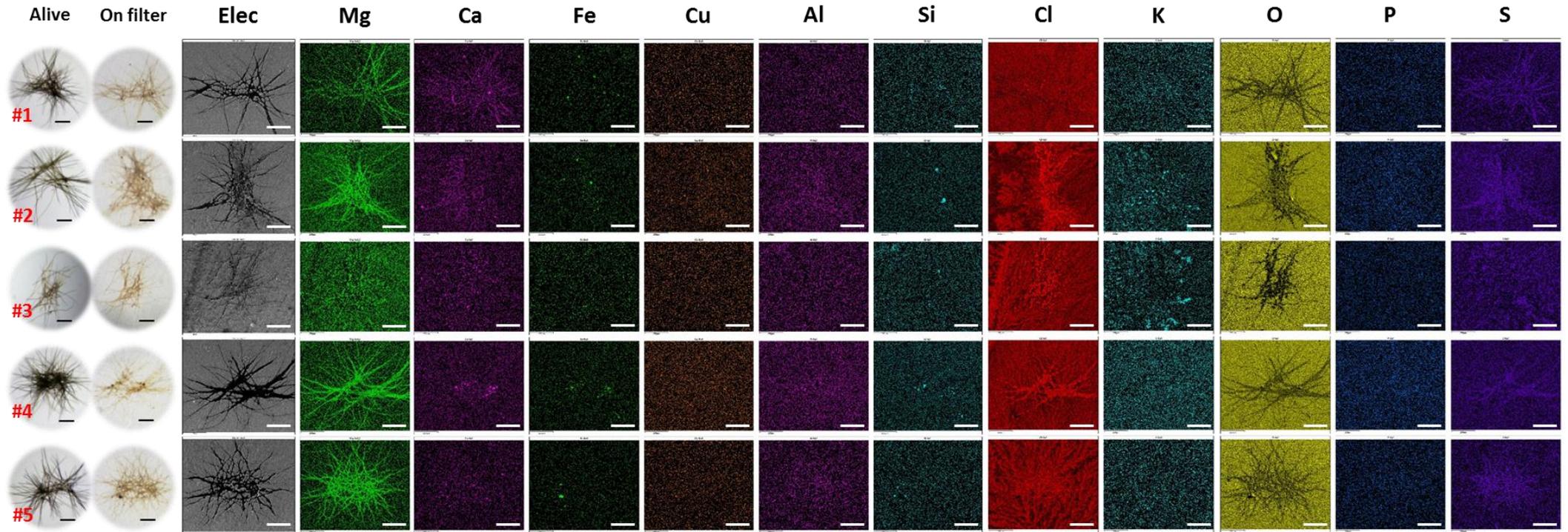
2h-incubation

Figure S10. SEM-EDX images of five natural *Trichodesmium* colonies incubated with Cu-minerals (malachite) and Fe-minerals (hematite) for 2 hrs, related to the main text - Section 3.3.2. Stereoscopic images taken prior to (alive, 1st column) and after the air-drying procedure (on filter, 2nd column). “Elec” means electron. Scale bars for stereoscopic (1st and 2nd columns) and SEM images (3rd to 14th columns) are 200 and 250 μm , respectively.

6h-incubation

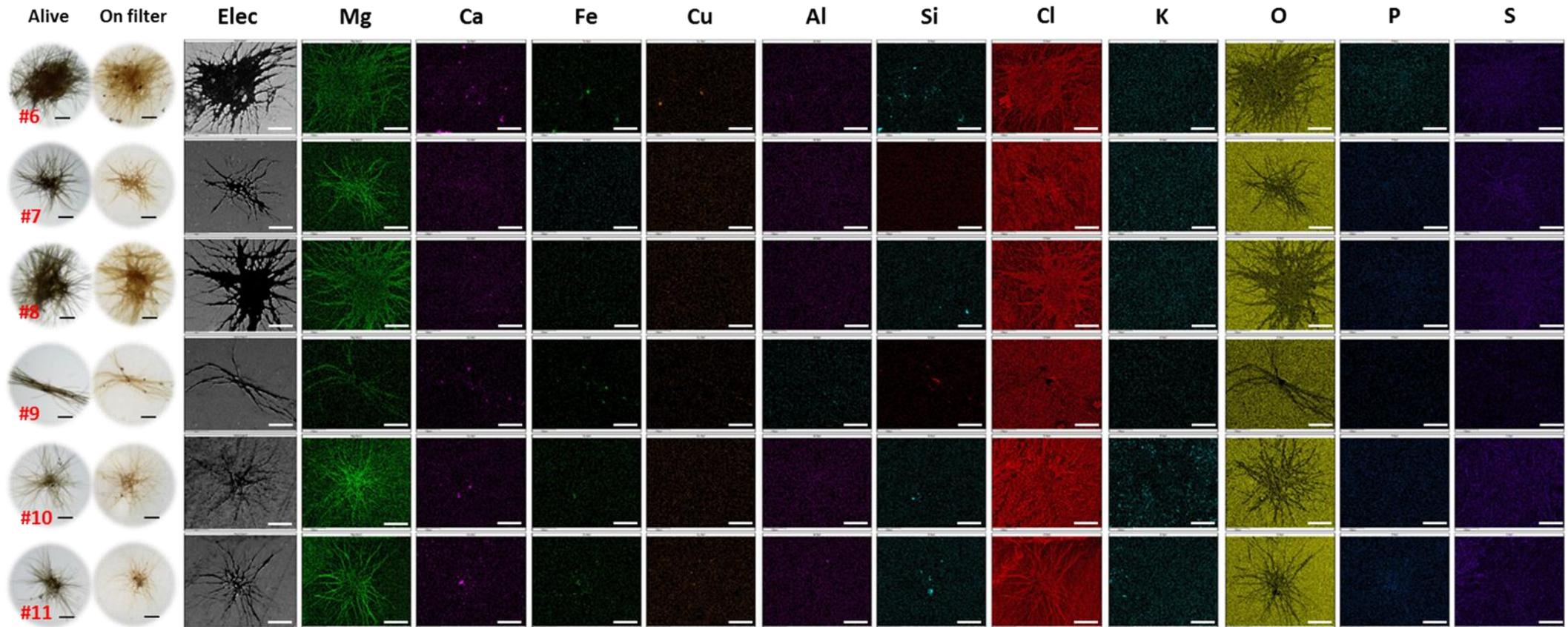


Figure S11. SEM-EDX images of five natural *Trichodesmium* colonies incubated with Cu-minerals (malachite) and Fe-minerals (hematite) for 6 hrs, related to the main text - Section 3.3.2. Stereoscopic images taken prior to (alive, 1st column) and after the air-drying procedure (on filter, 2nd column). “Elec” means electron. Scale bars for stereoscopic (1st and 2nd columns) and SEM images (3rd to 14th columns) are 200 and 250 μm , respectively. The element map (Mg, Ca, Fe and Cu) of colony (#11) was presented in the main text – Fig. 6 (top-left panel).

24h-incubation

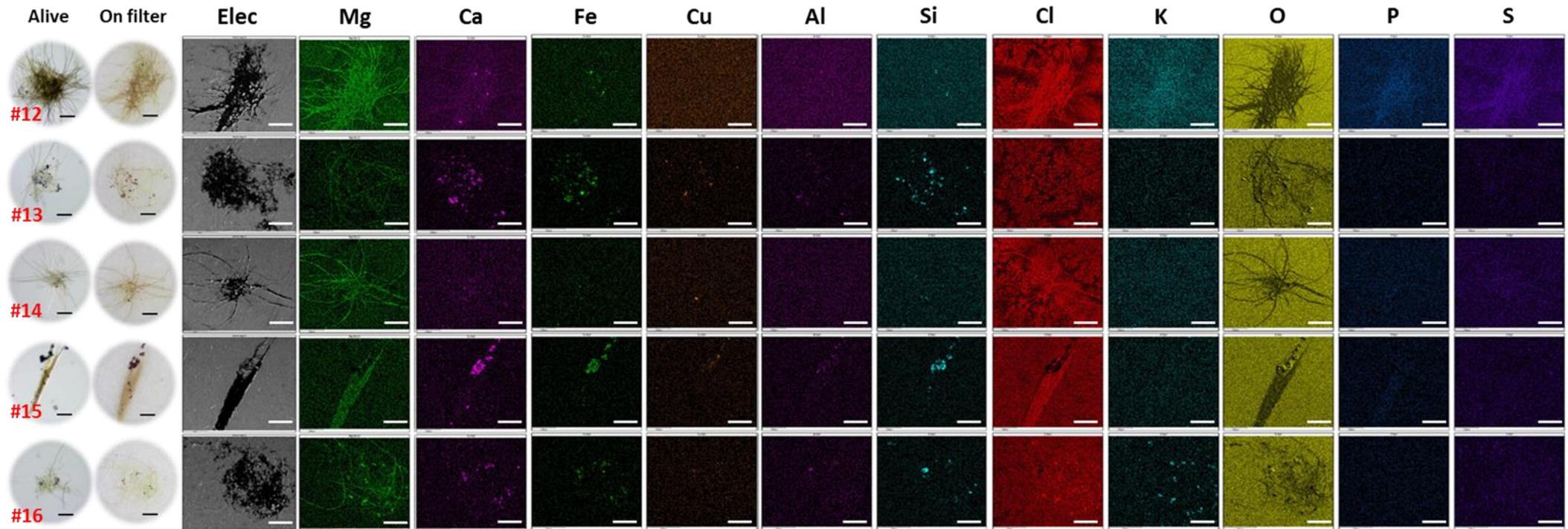


Figure S12. SEM-EDX images of five natural *Trichodesmium* colonies incubated with Cu-minerals (malachite) and Fe-minerals (hematite) for 24 hrs, related to the main text - Section 3.3.2. Stereoscopic images taken prior to (alive, 1st column) and after the air-drying procedure (on filter, 2nd column). “Elec” means electron. Scale bars for stereoscopic (1st and 2nd columns) and SEM images (3rd to 14th columns) are 200 and 250 μm , respectively. The element map (Mg, Ca, Fe and Cu) of colony (#13) was presented in the main text – Fig. 6 (top-right panel).

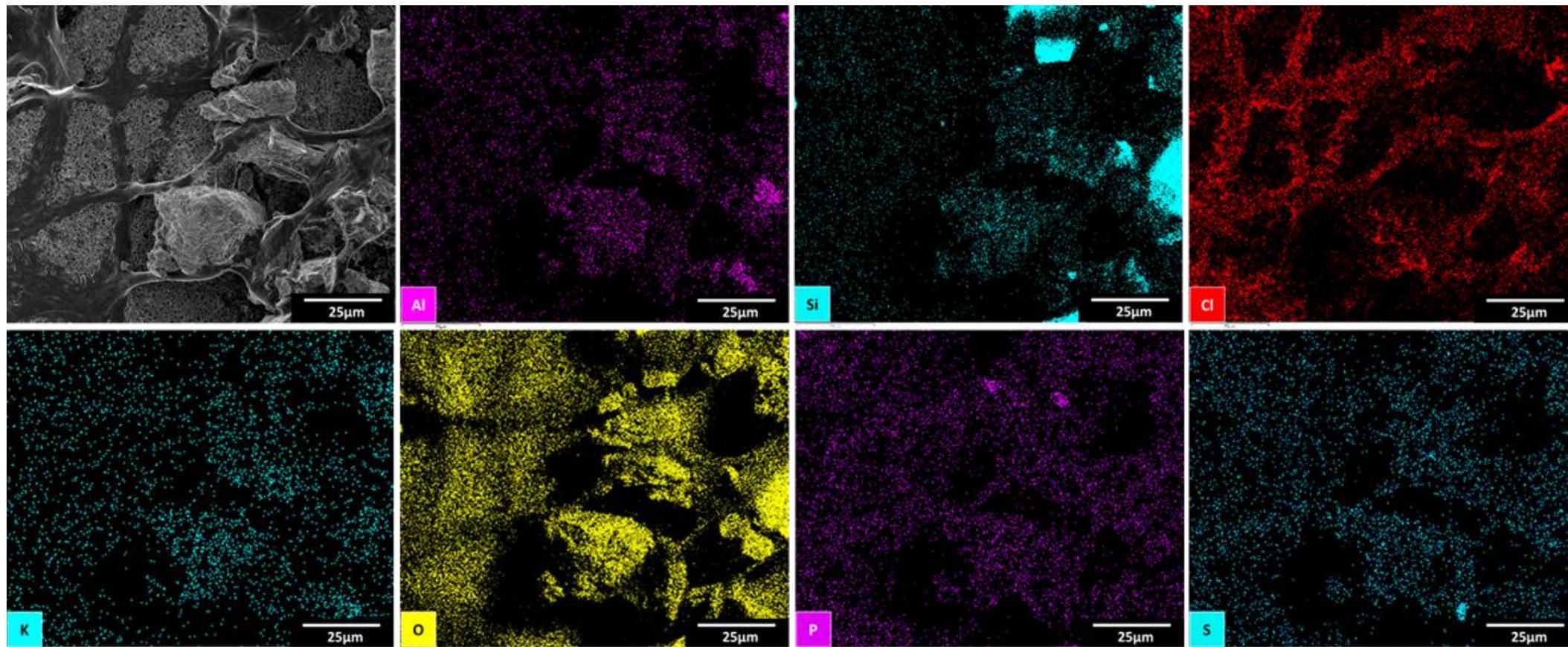


Figure S13. Additional element maps of a *Trichodesmium* colony (#13) incubated with Cu-minerals (malachite) and Fe-minerals (hematite) for 24 hrs, related to the main text - Section 3.3.2 (see Fig.6 – bottom panels). All scale bars = 25 μm .

References

- Basu, S., & Shaked, Y. (2018). Mineral iron utilization by natural and cultured *Trichodesmium* and associated bacteria. *Limnology and Oceanography*, *63*(6), 2307–2320. <https://doi.org/10.1002/lno.10939>
- Benaltabet, T., Lapid, G., & Torfstein, A. (2022). Dissolved aluminium dynamics in response to dust storms, wet deposition, and sediment resuspension in the Gulf of Aqaba, northern Red Sea. *Geochimica et Cosmochimica Acta*, *335*, 137–154. <https://doi.org/10.1016/j.gca.2022.08.029>
- Benavides, M., Bonnet, S., Le Moigne, F. A. C., Armin, G., Inomura, K., Hallstrøm, S., et al. (2022). Sinking *Trichodesmium* fixes nitrogen in the dark ocean. *ISME Journal*, *16*(10), 2398–2405. <https://doi.org/10.1038/s41396-022-01289-6>
- Held, N. A., Sutherland, K. M., Webb, E. A., McIlvin, M. R., Cohen, N. R., Devaux, A. J., et al. (2021). Mechanisms and heterogeneity of *in situ* mineral processing by the marine nitrogen fixer *Trichodesmium* revealed by single-colony metaproteomics. *ISME Communications*, *1*(1), 1–9. <https://doi.org/10.1038/s43705-021-00034-y>
- Held, N. A., Waterbury, J. B., Webb, E. A., Kellogg, R. M., McIlvin, M. R., Jakuba, M., et al. (2022). Dynamic diel proteome and daytime nitrogenase activity supports buoyancy in the cyanobacterium *Trichodesmium*. *Nature Microbiology*, *7*(2), 300–311. <https://doi.org/10.1038/s41564-021-01028-1>
- Ho, T. Y. (2013). Nickel limitation of nitrogen fixation in *Trichodesmium*. *Limnology and Oceanography*, *58*(1), 112–120. <https://doi.org/10.4319/lno.2013.58.1.0112>
- Kromkamp, J., & Walsby, A. E. (1990). A computer model of buoyancy and vertical migration in cyanobacteria. *Journal of Plankton Research*, *12*(1), 161–183. <https://doi.org/10.1093/plankt/12.1.161>
- Mackey, K. R. M., Chien, C. Te, Post, A. F., Saito, M. A., & Paytan, A. (2015). Rapid and gradual modes of aerosol trace metal dissolution in seawater. *Frontiers in Microbiology*, *6*(JAN), 1–11. <https://doi.org/10.3389/fmicb.2014.00794>
- McConnell, C. L., Highwood, E. J., Coe, H., Formenti, P., Anderson, B., Osborne, S., et al. (2008). Seasonal variations of the physical and optical characteristics of saharan dust: Results from the dust outflow and deposition to the ocean (DODO) experiment. *Journal of Geophysical Research*, *113*, 1–19. <https://doi.org/10.1029/2007JD009606>
- Paytan, A., Mackey, K. R. M., Chen, Y., Lima, I. D., Doney, S. C., Mahowald, N., et al. (2009). Toxicity of atmospheric aerosols on marine phytoplankton. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(12), 4601–4605. <https://doi.org/10.1073/pnas.0811486106>
- Schladitz, A., Müller, T., Kaaden, N., Massling, A., Kandler, K., Ebert, M., et al. (2009). *In situ* measurements of optical properties at Tinfou (Morocco) during the Saharan Mineral Dust Experiment SAMUM 2006. *Tellus, Series B: Chemical and Physical Meteorology*, *61*(1), 64–78. <https://doi.org/10.1111/j.1600-0889.2008.00397.x>
- Sunda, W. G., & Huntsman, S. A. (1998). Processes regulating cellular metal accumulation and physiological effects: Phytoplankton as model systems. *Science of the Total Environment*, *219*(2–3), 165–181. [https://doi.org/10.1016/S0048-9697\(98\)00226-5](https://doi.org/10.1016/S0048-9697(98)00226-5)
- Wang, S., Zhang, F., Koedooder, C., Qafoku, O., Basu, S., Krisch, S., et al. (2023). Calculations and simulations of dust factor (K) and sinking velocity of particle-free *Trichodesmium* colonies (v0). *Zenodo*. <https://doi.org/10.5281/zenodo.10290901>
- White, A. E., Spitz, Y. H., & Letelier, R. M. (2006). Modeling carbohydrate ballasting by *Trichodesmium* spp. *Marine Ecology Progress Series*, *323*(Oliver 1994), 35–45. <https://doi.org/10.3354/meps323035>