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

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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.

Plain Language Summary

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

Key Points

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

1. Introduction

Trichodesmium spp. is a filamentous, N_2-fixing, and bloom-forming cyanobacterium inhabiting subtropical and tropical oligotrophic ocean regions and contributing ~40% of the annual global marine nitrogen fixation (Capone et al., 1997; Tang et al., 2020; Zehr & Capone, 2020). *Trichodesmium* spp. appear both as individual filaments (trichomes) and as colonies containing hundreds to thousands of trichomes organized in millimeter-sized tuft- or puff-shaped aggregates (Eichner et al., 2023). In the Red Sea, puff-shaped colonies are primarily composed of *Trichodesmium thiebautii* while tuft-shaped colonies are typically comprised of *Trichodesmium erythraeum* (Koedooder et al., 2022). The different colony morphologies also serve as micro-habitats for diverse microbes including bacteria, phytoplankton and even zooplankton, all exchanging nutrients and carbon throughout the colony life cycle from growth to demise (Anderson, 1977; Frischkorn et al., 2018; Lee et al., 2017; Rouco et al., 2016).

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

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

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

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

2. Material and methods

2.1 Colony & dust collection

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

2.2 Effect of dust load on colony buoyancy

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

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

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

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

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

2.3 Metals in dust and toxicity to *Trichodesmium*

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

~1.7 with ultra-clean HNO_3 prior to analysis of metals. Metals were analyzed by inductively coupled plasma mass spectrometry after preconcentration (SeaFAST pico) following the method of Rapp et al. (2017) and were quantified by standard addition (Krisch et al., 2022) at GEOMAR, Helmholtz Centre for Ocean Research, Kiel, Germany. Extending our experiments we also included dissolution measurements of local Red Sea dust samples from Mackey et al. (2015). We then split the dissolution data to two groups: 1) rapid dissolution (10 min and 6 h), and 2) gradual dissolution (1, 3 and 7 days).

Toxicity assays – Dust toxicity was investigated by incubating ~180 individual natural *Trichodesmium* colonies for 24 h in 48 well-plates with either dust suspension or dust leachate. Primary dust suspension was prepared daily in FSW and diluted to final concentrations of 2, 10, 100, 500, and 1000 $mg \cdot L^{-1}$. Dust leachates were obtained after 10 min by filtering the dust suspensions through 0.22 µm syringe-filters (PC membrane). Colonies were incubated in wells of a 48-well plate containing 0.5 mL dust suspension or leachate and were kept in a culture room (25 ^{o}C, ~80 $\mu E\ m^{-2}\ s^{-1}$, 10:14 h light-dark cycle). Visual changes of the colony and filament shape, structure, and color were monitored under a stereoscope at 2, 5, and 24 h (supplementary text S4). Incubations were repeated twice during spring 2022 and included controls without dust additions. Probing specifically for Cu toxicity, colonies were also incubated with dissolved Cu (5-3000 nM $CuSO_4$, supplementary text S4).

2.4 Removal of Cu-containing minerals

Hypothesizing that colonies may remove toxic minerals as a detoxification mechanism, 16 Red Sea colonies were incubated with the Cu mineral malachite ($Cu_2CO_3(OH)_2$). To ensure optimal colony-mineral interactions, malachite was mixed with hematite (α-Fe_2O_3), which is typically preferred by *Trichodesmium*. Individual colonies were sampled at different time points, placed on filters and probed for the presence of malachite via light microscopy and scanning electron microscopy with energy dispersive X-Ray analysis (SEM-EDX). Experiments were repeated for three days in autumn 2021. Malachite was obtained from Timna National Park (Eilat, Israel), crushed and sieved (<38µm), while hematite (<38µm) was obtained from the Mineral Collection at the National Natural History Collections at the Hebrew University of Jerusalem. Colonies were incubated in eppendorf vials under the IUI pier up to 24 hrs. At three time points, randomly selected colonies were imaged and

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

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

3. Results and discussion

3.1 Dust loads and buoyancy control

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

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

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

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

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

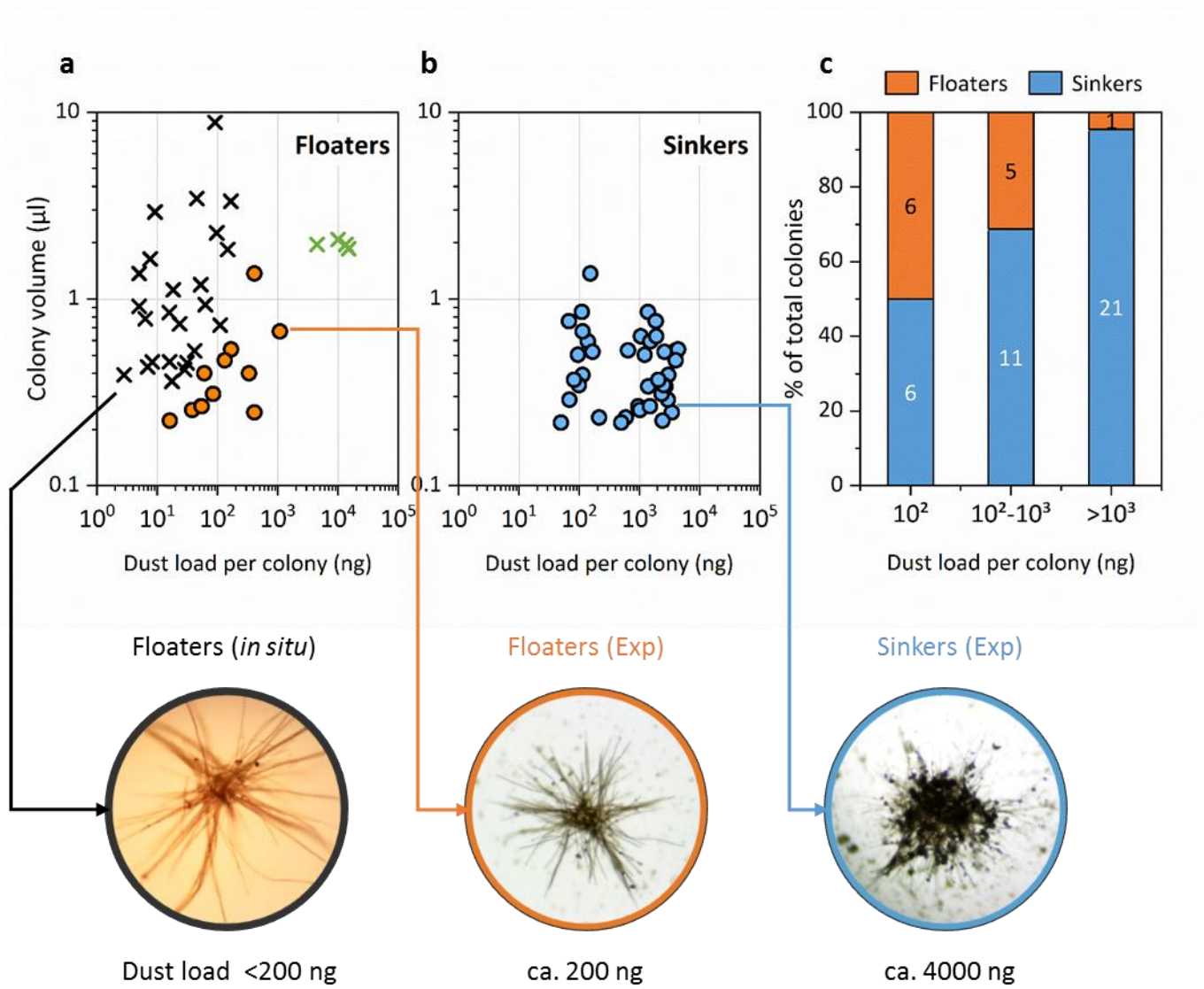


Figure 1. Effect of dust load on the buoyancy of natural *Trichodesmium* colonies.

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

(a) Range of dust loads associated with "floater" colonies tested in sedimentation experiments (n=12, orange circles) and freshly collected from the Red Sea (n=24, black crosses) and the Atlantic Ocean (n=4, green crosses, images from Held et al., 2021).

(b) Range of dust loads associated with "sinker" colonies tested in sedimentation experiments (n=38, blue circles).

(c) Fraction of experimentally determined "floaters" and "sinkers" as a function of dust load per colony. Pictures show typical dust loads as quantified through image analysis.

3.1.2 Effect of dust on colony sinking velocity

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

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

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

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

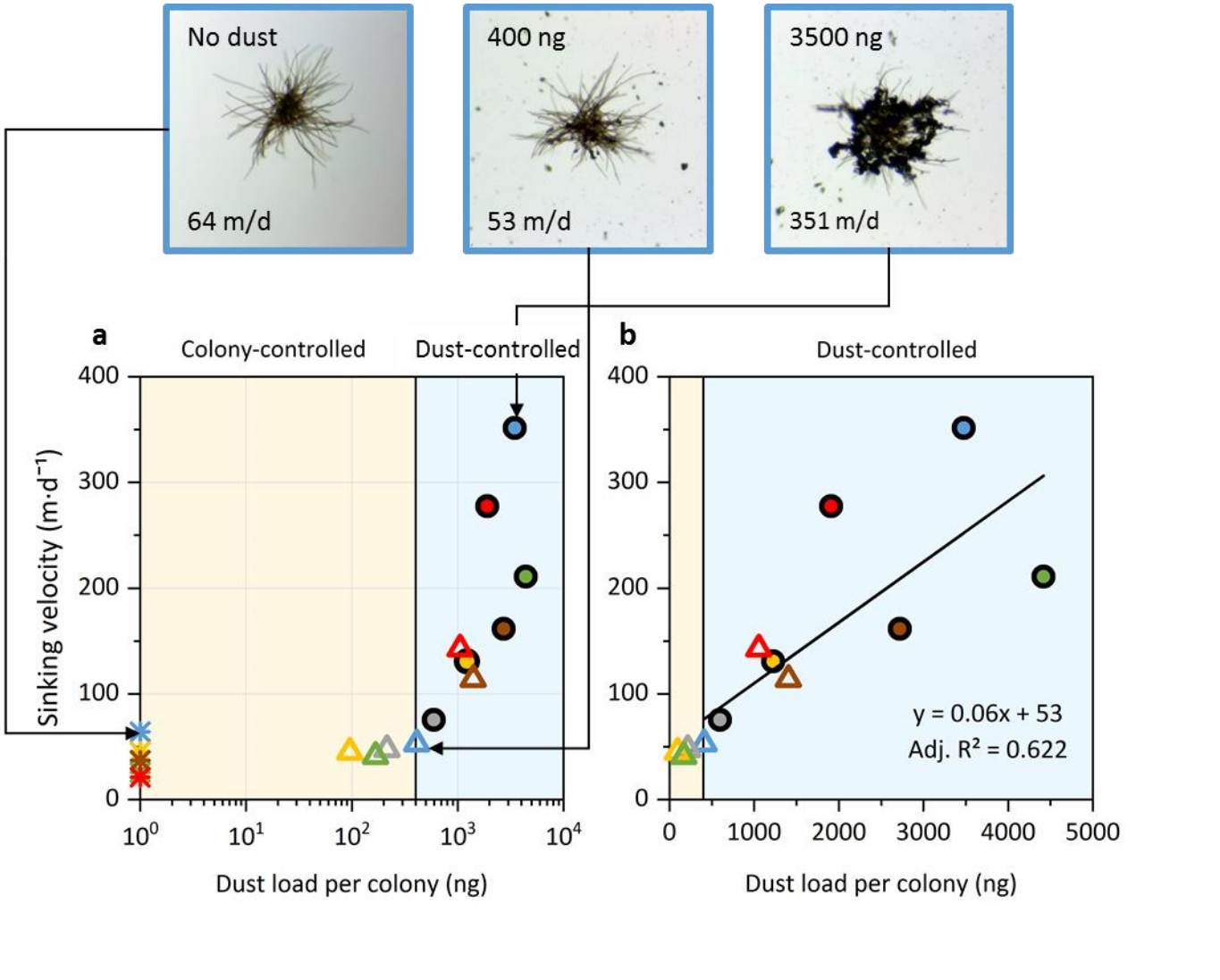


Figure 2. Effect of dust load on sinking velocities of Rea Sea *T. thiebautii* colonies.

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

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

3.1.3 Effect of dust loss on colony sinking velocity

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

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

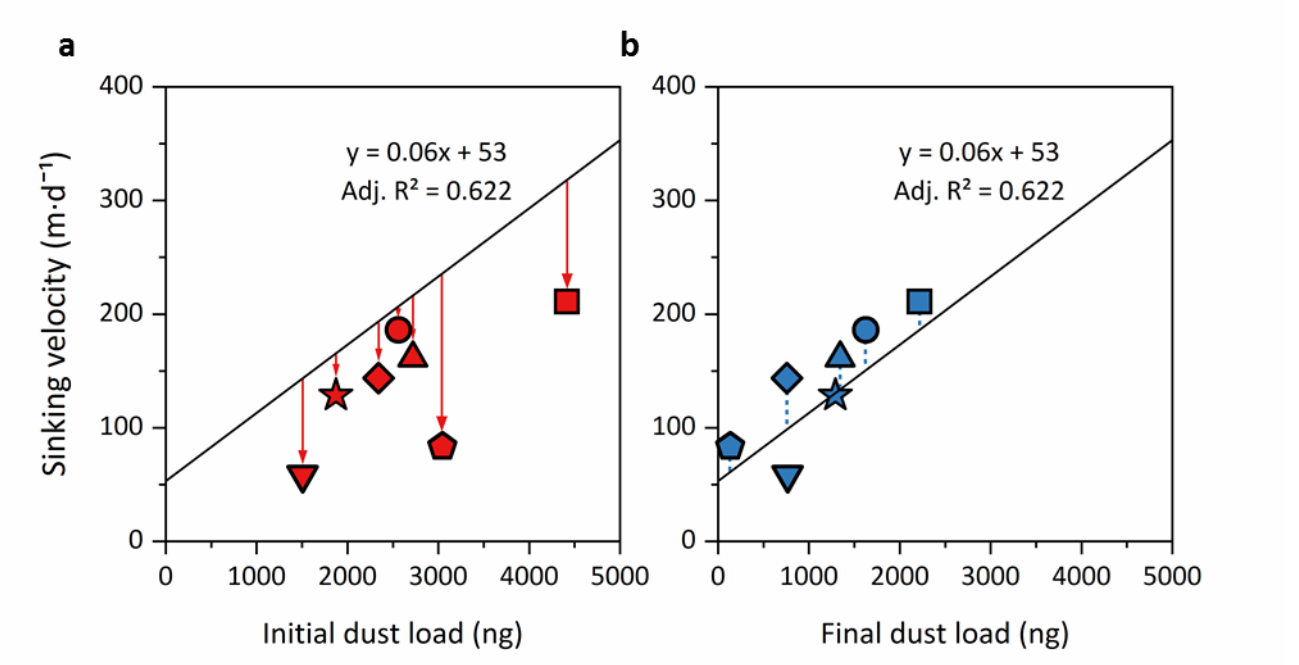


Figure 3. Effect of dust loss on colony sinking velocity.

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

3.2 Toxic effects of dust on *Trichodesmium*

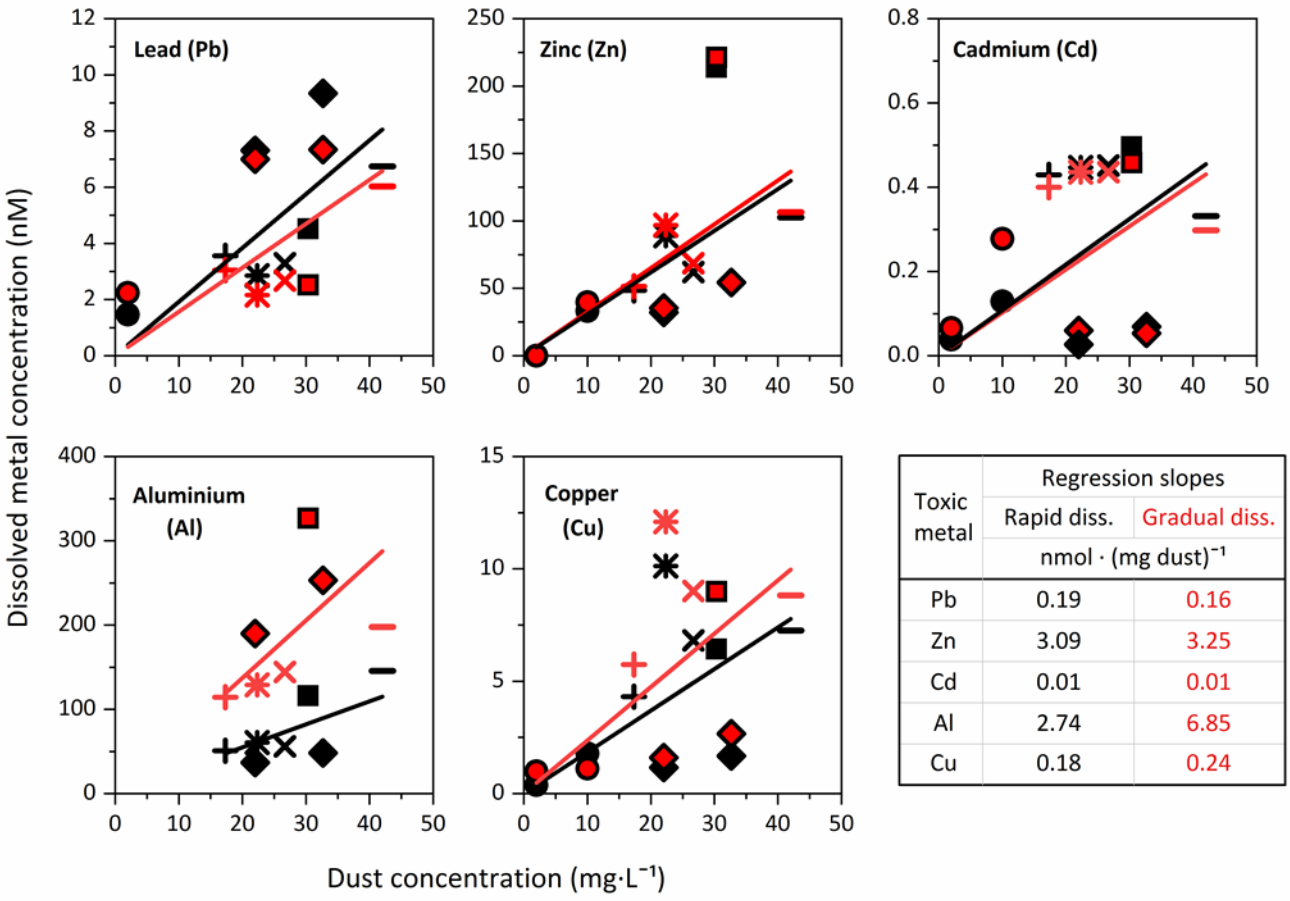
Dust and other aerosols contain an array of toxic elements (Bozlaker et al., 2013). Upon dust deposition on the surface ocean, some elements are rapidly released and may induce toxicity to positively buoyant *Trichodesmium* blooms that accumulate at the surface. Seeking to evaluate the toxicity of dust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



Toxic metal	Regression slopes	
	Rapid diss.	Gradual diss.
	nmol · (mg dust)⁻¹	
Pb	0.19	0.16
Zn	3.09	3.25
Cd	0.01	0.01
Al	2.74	6.85
Cu	0.18	0.24

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

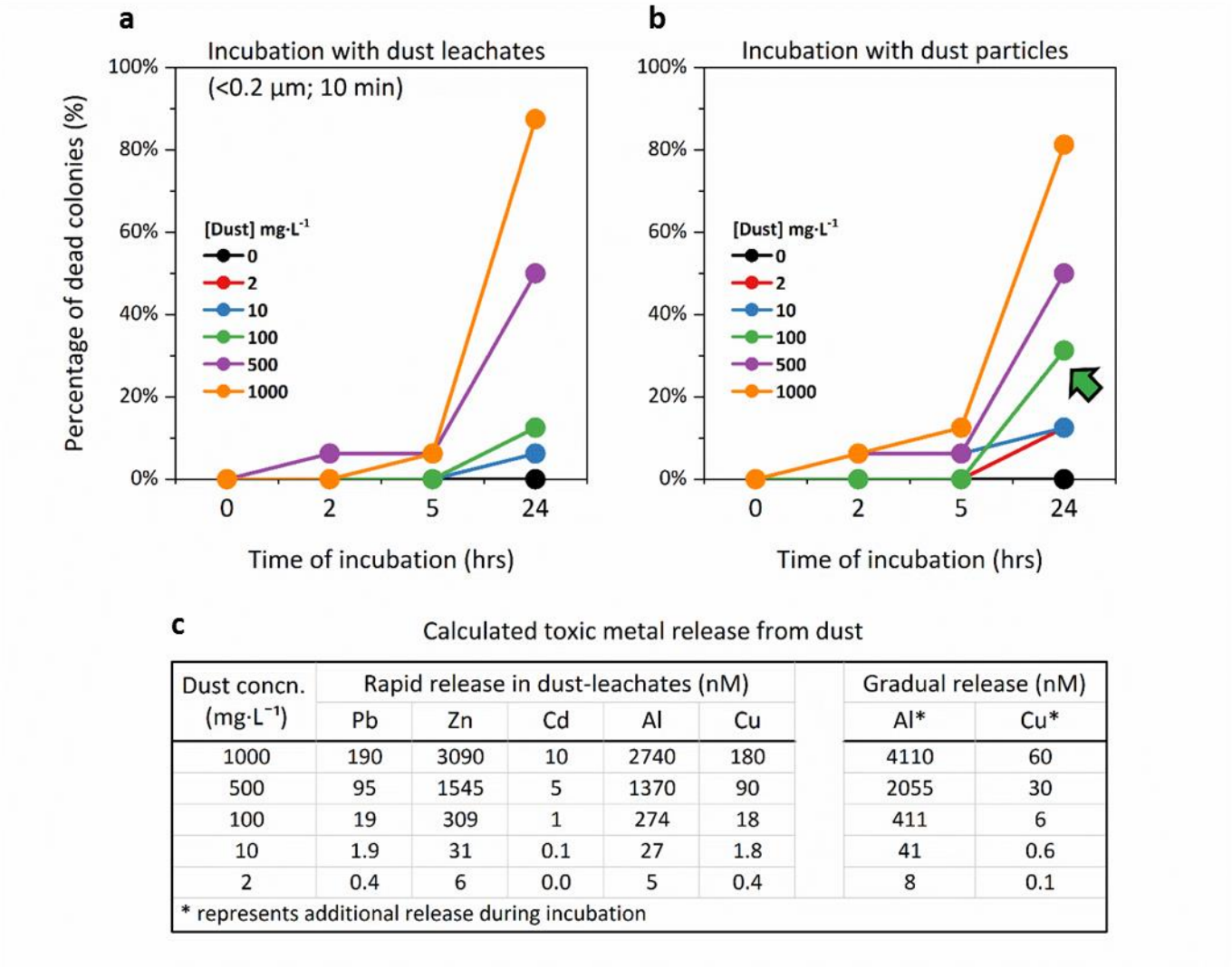
The dataset combines new measurements (circles) and published data from (Mackey et al., 2015) and includes seven dust samples plotted as different symbols. Metal release kinetics is presented by two categories - rapidly released metals (black, up to 6hrs) and gradually released metals (red, up to 7 days).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

3.2.2 Dust toxicity to Trichodesmium – fractions and doses

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

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

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



c Calculated toxic metal release from dust

Dust concn. ($mg \cdot L^{-1}$)	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

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

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

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

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

3.2.3 Selective removal of Cu minerals

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

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

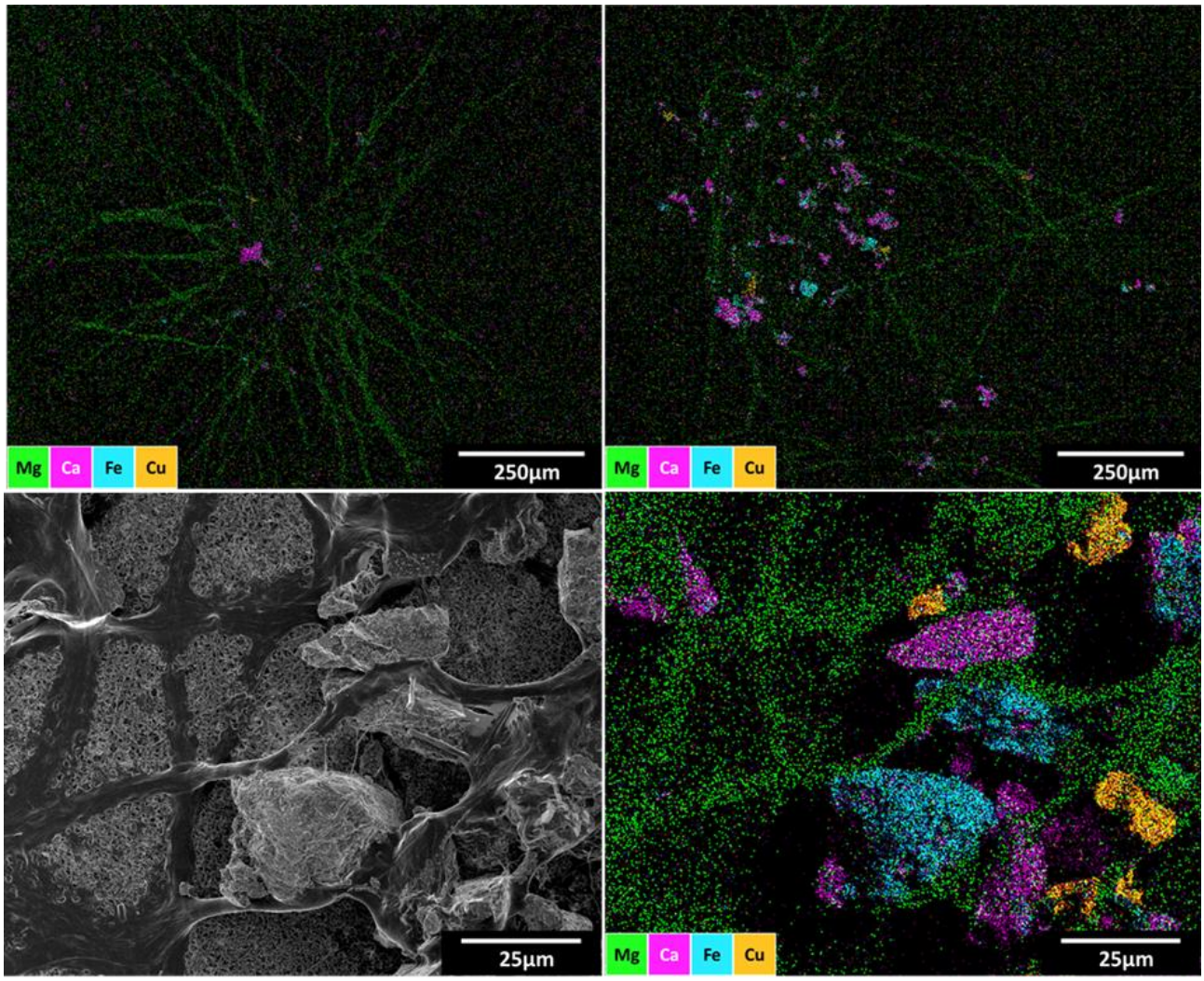


Figure 6. SEM-EDX images of natural *Trichodesmium* colonies incubated with Cu-minerals (malachite) and Fe-minerals (hematite).

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

4. Summary

Having studied the potential negative effects of dust on natural *Trichodesmium* colonies, we predict that in a typical open-ocean setting, the potential benefit of dust as a nutrient source outweighs the risks of buoyancy loss and toxification. In the Gulf of Aqaba, puff-shaped *T. thiebautii* colonies collected *in situ* were usually observed to contain less than 200 ng of dust per colony, which is below the threshold where sinking velocity becomes dust-controlled (Fig. 1) and is insufficient to induce toxicity through metal release (Fig. 5). In other environments (e.g. coastal seas, Mackey et al., 2012), however, *Trichodesmium* may encounter more toxic aerosols and the concepts laid here may facilitate the evaluation of those risks. With regards to buoyancy, accelerated sinking velocities due to interactions with dust may be significant to C export, and may help explain recent measurements of active N_2 fixation by *Trichodesmium* at 1000 meters (Benavides et al., 2022). If indeed colonies can modulate their particle load, the dust-induced sinking may benefit *Trichodesmium* and expand its ecological niche.

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

Supervision: Yeala Shaked

Writing – original draft: Siyuan Wang, Yeala Shaked

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

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Conflict of interest

The authors declare that they have no conflict of interest.

Data availability statement

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

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