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# Spread of a sea urchin disease to the Indian Ocean causes widespread mortalities—Evidence from Réunion Island

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Over the past four decades, the emergence and spread of infectious diseases have led to significant declines in biodiversity and species abundance across marine ecosystems (Weil et al., 2006). Notably, there has been a global increase in the frequency of sea urchin mortality outbreaks, leading to episodic mass mortality events (MME), which, in turn, drive shifts in their population structure and overall health (Hewson et al., 2023; Lessios et al., 1984; Zirler et al., 2023). Sea urchins are benthic herbivores that play a crucial role in maintaining the intricate balance between rapidly growing macroalgae and the slow growing scleractinian corals. In tropical regions, sustainable sea urchin populations play a vital role in reducing algal proliferation through grazing, thus preventing coral overgrowth, and facilitating coral recruitment (Birkeland & Randall, 1981). Recovery from these large-scale sea urchin die-offs can be slow (Pusack et al., 2023), and may lead to detrimental ecological consequences such as phase shifts from coral-dominated to algae-dominated reefs (Knowlton, 2001).

Sea urchins of the family Diadematidae, known for their distinct morphological features, characterized by long, slender spines that radiate from their spherical bodies, are largely recognized as some of the most prominent herbivores on Indo-Pacific coral reefs (Bronstein & Loya, 2014; Lawrence & Sammarco, 1982; Muthiga & McClanahan, 2020). These large-bodied echinoids are also some of the most motile extant sea urchins, allowing them easy access to new algal patches when local food supply is depleted, making them efficient grazers across large reef areas. As net herbivory is tightly linked to the size of consumer populations, reefs with flourishing diadematoid communities will benefit from controlled and much-reduced algal proliferation (Sammarco, 1982). For example, studies from the western Indian Ocean (WIO) off the coast of Zanzibar Island, showed that net herbivory may reach 1.44 kg algae $m^{-2}$ $year^{-1}$ for *Diadema setosum* and 3.87 kg algae $m^{-2}$ $year^{-1}$ for *Echinothrix diadema* (Bronstein &

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Jean-Pascal Quod and Mathieu Séré contributed equally to this study.

Loya, 2014). Echinoids are considered prominent grazers on coral reefs even when compared with other herbivores such as fish, mollusks, crustaceans, reptiles, and mammals. Poore et al. (2012) preformed a global synthesis of marine herbivory patterns and showed that sea urchin grazing was higher on filamentous algae and articulated calcareous algae than all other taxa, higher than fish grazing (but second to mollusks) on leathery macrophytes and crustose coralline algae, and comparable to mollusks and reptile herbivory on seagrasses.

An extensive MME of diadematoid sea urchins in the WIO was recently reported by Roth et al. (2024), however, the cause of mortalities or their full extent, were so far not established. First signs of mortalities appeared on July 24, 2023, at Cap la Houssaye (21°1′6.04″ S; 55°14′19.65″ E) off the coast of Réunion Island. We conducted surveys using both SCUBA and snorkeling between July and December 2023 at 33 sites, following a north–south gradient from Cap la Houssaye (21°1′6.04″ S; 55°14′19.65″ E) on the eastern side of the Island (the site of the first mortality observation in the WIO), to Sainte-Rose (21°7′28.69″ S; 55°47′14.04″ E) on the western side. The surveys covered three habitat types where diadematoids are known to be present: (1) the outer reef slope (depth 5–30 m), which is exposed to high turbulence and characterized by a basaltic substratum with alternating spurs and grooves, mostly covered by massive and encrusting corals; (2) the inner reef (depth 0.5–1 m), which is largely composed of branching corals, and (3) rock pools, naturally formed volcanic rock basins at the intertidal zone (Figure 1).

We documented dead and moribund diadematoids ranging between 0.002 and 0.2 individuals/m$^2$. Most

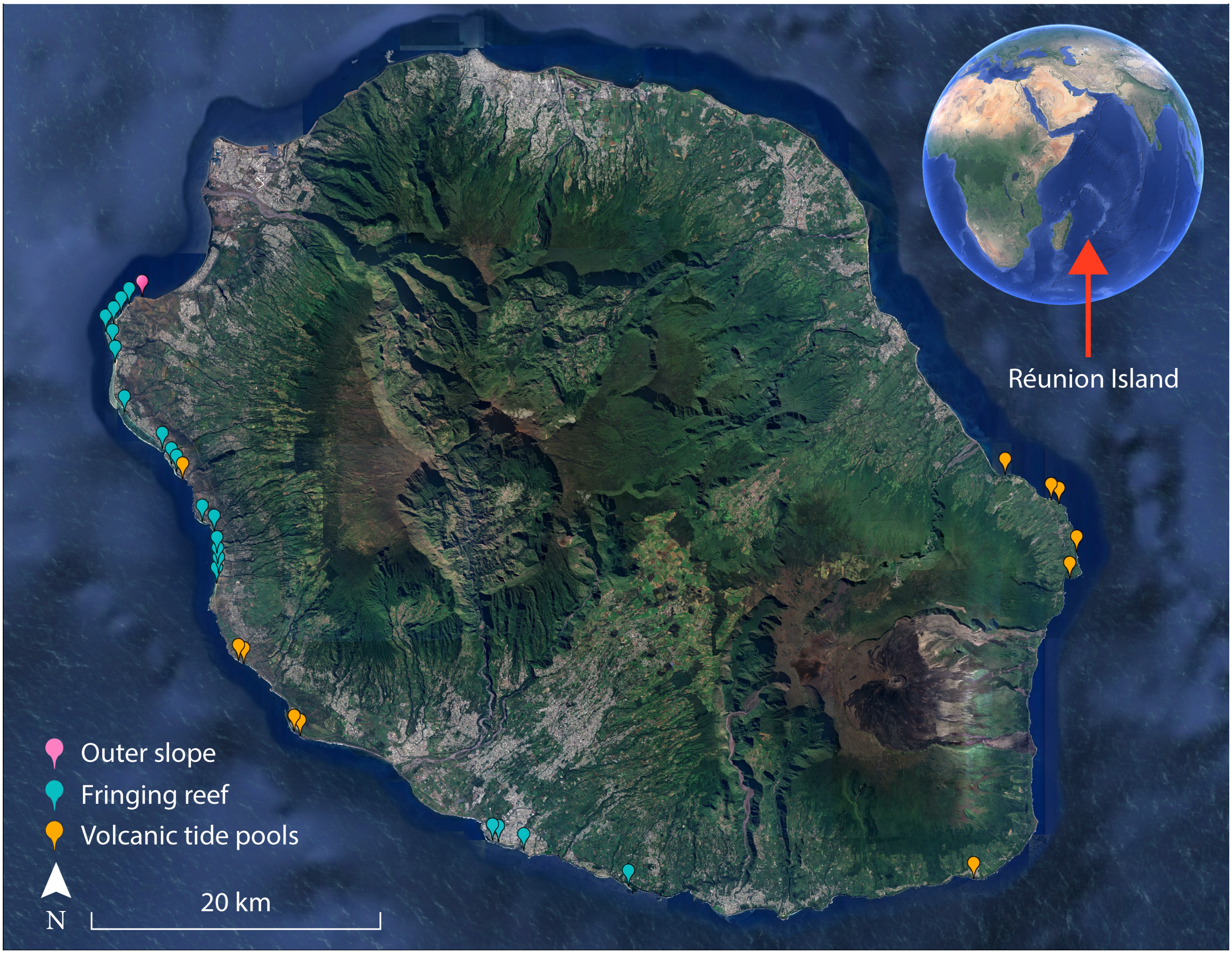

**FIGURE 1** Map of Réunion Island indicating surveyed sites where sea urchin mortalities were observed. Site locations are indicated by pins. Pin colors correspond to habitat type: Pink—outer slope; blue—fringing reef; orange—volcanic tidal pools. Map was created via Google Earth Pro.

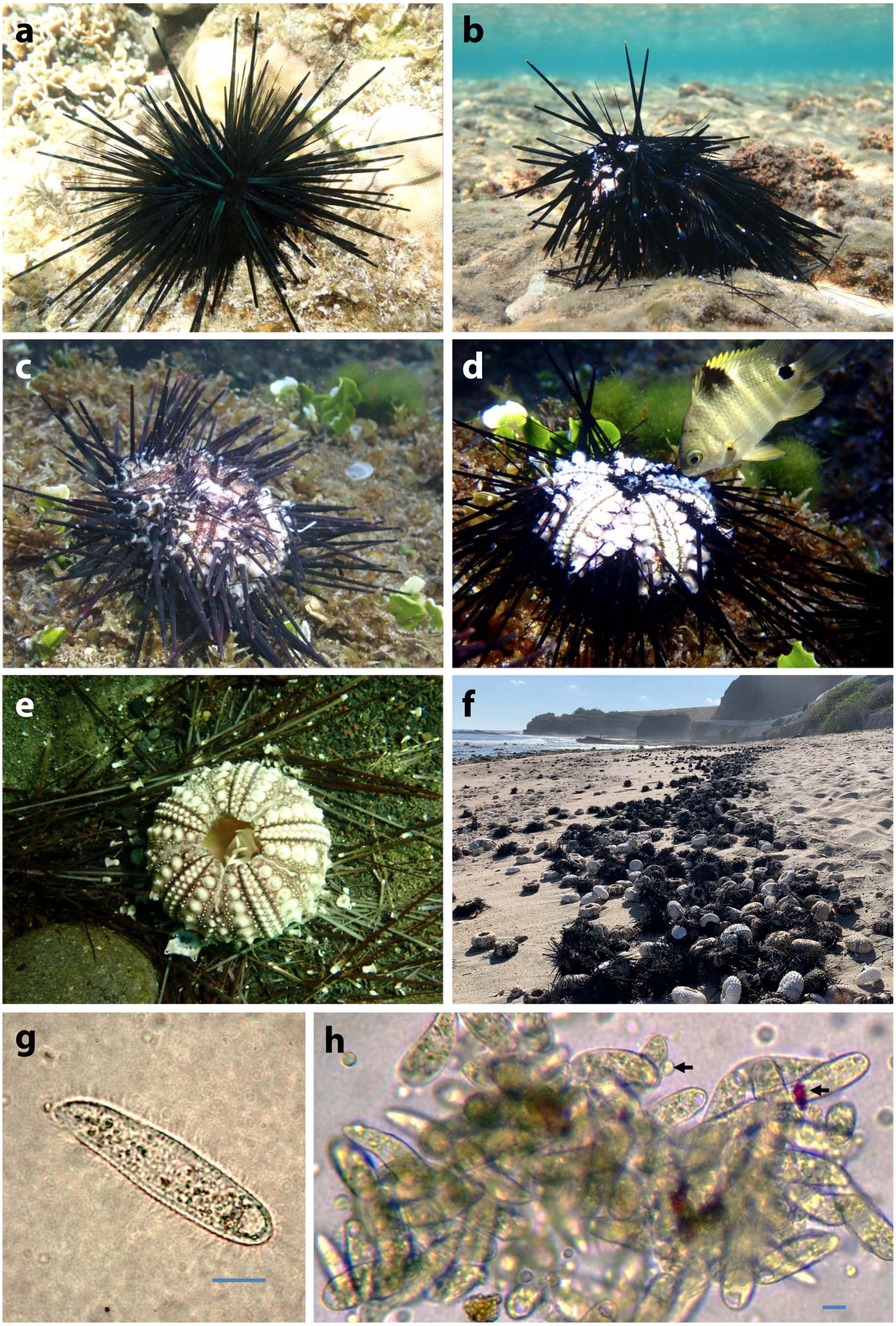

**FIGURE 2** Legend on next page.

diadematoid MMEs reported to date highlight the susceptibility of the genus *Diadema*, namely *Diadema antillarum* (Hewson et al., 2023) and *D. setosum* (Ritchie et al., 2024; Roth et al., 2024), to mortalities. However, while *D. setosum* and *Diadema savignyi* were similarly showing susceptibility to mortalities, the majority of affected echinoids at Réunion Island were members of the genus *Echinothrix* (both *E. diadema* and *Echinothrix calamaris*). Moribund individuals exhibited signs of infection similar to those recently observed in mass mortalities of *D. setosum* and *E. calamaris* from the Red Sea (Roth et al., 2024). Symptoms first become evident following the loss and paralysis of tube feet that impedes the individuals' capacity to adhere to the substrate as spine movement becomes slow and less responsive. Subsequently, distinctive lesions emerge in areas of tissue loss along the apical ambulacrum, and spines detach, revealing clearly visible bare areas (Figure 2a–e). Ultimately, the sea urchin succumbs, leaving behind skeletal remains: vacant tests, detached spines, and scattered Aristotle lanterns (Figure 2e). At sites of high wave energy, such as on the east coast of Réunion Island, carcasses were piled in thousands on the shoreline (Roth et al., 2024; Figure 2f).

Microscopic analyses of coelomic fluid, sampled from both healthy and moribund individuals, revealed high densities of protozoan ciliates of the phylum *Ciliophora* (Figure 2g,h) only in individuals exhibiting disease symptoms. Samples of these putative pathogens were cultured, isolated, and genetically tested following Vilanova-Cuevas et al. (2023) for the presence of *D. antillarum* scuticociliatosis (DaSc)-associated *Philaster* sp., the causative agent of the recent 2022 tropical western Atlantic (TWA), and 2023 Red Sea MMEs. Analysis of sequences derived from isolated cells, coelomic fluid, and cultivated ciliates from moribund individuals revealed that all specimens were identical to the TWA DaSc-associated *Philaster* (Figure 3), providing first identification of the pathogen in the genus *Echinothrix* and first genetic evidence of the disease in the WIO.

This disease now seems to be spreading throughout the WIO, with sightings in Zanzibar, Madagascar, and the Seychelles (O. Bronstein, unpublished data). Diadematoid mass mortality outbreaks have recently been reported from the Mediterranean Sea (2022; Zirler et al., 2023), the Red Sea (2023; Roth et al., 2024), and most recently, from the Gulf of Oman (2023; Ritchie et al., 2024). Although the presence of DaSc-associated *Philaster* is currently not confirmed for the Mediterranean Sea, a clear south-bond trajectory in its spread, from the Red Sea to the Gulf of Oman, and the greater Indian Ocean, is evident. Consequently, diadematoid mortalities now span over 4300 km across some of the world's most pristine coral reefs.

Still, the source of the pathogen affecting such distant populations as the TWA, Red Sea, and WIO, remains elusive. The mechanisms contributing to the spread of this waterborne pathogen are similarly elusive, although several conceptual mechanisms, such as local pathogen transport by currents, or opportunistic fish predation of infected individuals, have previously been suggested (Zirler et al., 2023). We consequently suggest two alternative hypotheses: (1) the pathogen, originating from the Caribbean Sea was transported to the Red Sea and WIO, likely along international shipping routes, ensuing mortalities, and spreading further locally (by direct contact with infected individuals, or transported by predators of moribund sea urchins) and regionally (by currents), the "pathogen transport" hypothesis. Alternatively, (2) the pathogen natively inhabits all sites, and virulence is triggered by changing environmental conditions (Burge & Hershberger, 2020), or the reduced echinoid immunity (Salazar-Forero et al., 2022), the "pathogen outbreak" hypothesis.

Although the presence of DaSc-associated *Philaster* is now confirmed for Réunion Island and, thus, the WIO, further investigations are warranted to elucidate the complex interactions between sea urchins and their associated microbial communities. Validating the role of this pathogen in diadematoid mortalities by fulfilling Koch's postulates (Koch, 1876) for the Diadematidae species beyond *D. antillarum* and *D. setosum*, is similarly essential.

Across diverse marine habitats, sea urchin grazing plays a fundamental ecological role in herbivory and bioerosion, capable of altering the trajectories of entire marine ecosystems (Steneck, 2013). For example, in the cold waters of the Aleutian kelp forests, hyperabundance of *Strongylocentrotus polyacanthus* is known to have

**FIGURE 2** Sea urchin mortality on Réunion Island. (a) A healthy *Echinothrix diadema*. (b) Lethargic behavior and initial tissue and spine loss. (c) Moribund individual with weakly moving spines and growing areas of exposed test. (d) Extensive spine loss and tissue necrosis. Apical side showing large areas of exposed test. (e) Bare *E. diadema* skeleton following mortality and complete tissue loss. (f) Massive stranding of dead sea urchins on Réunion Island's western beaches on August 14, 2023. (g) DaSc-associated *Philaster* clade ciliate. (h) Cluster of DaSc-associated *Philaster* clade isolated from *E. diadema* during the early stage of the disease, feeding on coelomic elements, showing vibratile cells from the coelom and red spherule cells. DaSc, *Diadema antillarum* scuticociliatosis. Photo credit: Jean-Pascal Quod.

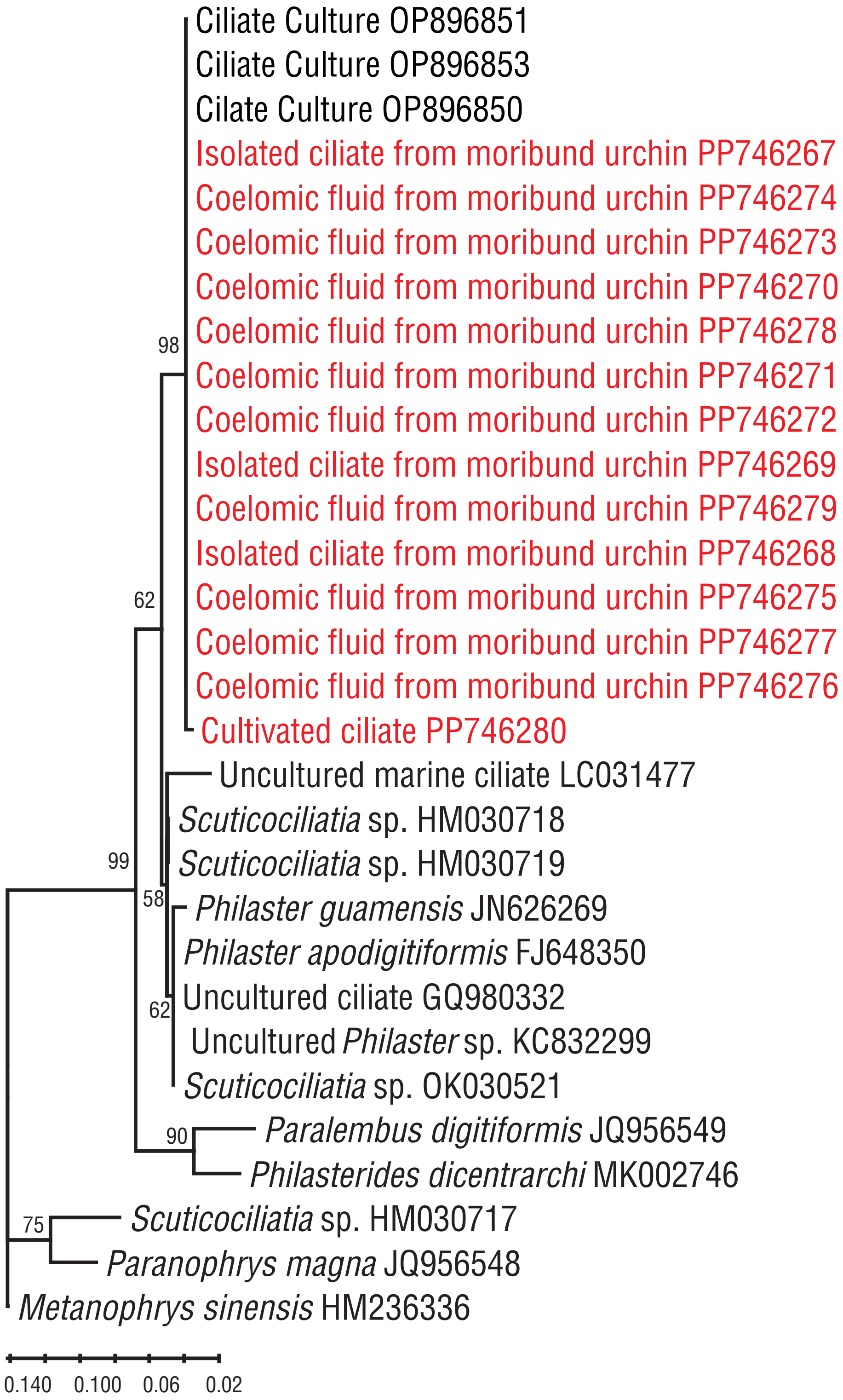

**FIGURE 3** Phylogenetic reconstruction of moribund urchin associated ciliates in the Philasteridae. The tree was constructed using MEGAX (Kumar et al., 2018) based on a 313 nt region that was aligned by MUSCLE (Edgar, 2004). Bootstrap support values are based on 1000 iterations. Tree topology was based on Maximum Likelihood following the Tamura 3 parameter model with gamma distributed sites and the nearest neighbor interchange heuristic model. Red colored sequences indicate sequences generated in the present study that fall within the *Diadema antillarum* scuticociliatosis *Philaster* clade (Vilanova-Cuevas et al., 2023). GenBank accession numbers are given after taxon names.

caused vast destruction of both kelp, and the underlying red alga *Clathromorphum nereostratum*, that forms the massive limestone structures of the entire region (Estes & Duggins, 1995). The later authors clearly demonstrated a three-trophic-level cascade between predators (sea otters; *Enhydra lutris*), invertebrate herbivores (sea urchins; *S. polyacanthus*), and macroalgae. When top-down control of sea urchins is removed (following collapse of their sea otter predators), their populations proliferate, and lead to overgrazing that drive the formation of "urchin barrens," areas devoid of kelp and associated biodiversity. In contrast, where sea urchin populations are greatly reduced, regardless of the drivers of decline, being natural or anthropogenic, rapid algal growth may occur, leading to equally destructive consequences (Carpenter, 1990; Steneck, 2013). Particularly, on coral reefs, sea urchins are known to reduce and control algal cover, enabling coral settlement and facilitating coral survival and growth (Birkeland & Randall, 1981; Carpenter & Edmunds, 2006).

Consequently, while maintaining balanced sea urchin populations at intermediate abundances is key for habitat stability (Bronstein & Loya, 2014), the future of habitats following major trophic cascades alternations is largely dependent on the intensity and duration of disturbance. Just as sea otters exert top-down trophic control over *S. polyacanthus* populations in the Aleutian kelp forests (Rasher et al., 2020), so does DaSc-associated *Philaster* exert bottom-up control on diadematoid sea urchins in coral reefs. As current data show that the intensities of recent diadematoid mortalities in the Red Sea and WOI are severe, often reaching 100% and surpassing the intensity of mortalities reported from the Caribbean (Roth et al., 2024), it remains to be seen whether these mortalities are transitional or mark the onset of a new era of coral-algal competition in affected regions.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Sequences used for the phylogenetic analysis are available in the National Center for Biotechnology Information GenBank database (https://www.ncbi.nlm.nih.gov/genbank/) under accession numbers PP746267–PP746280.

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