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Polyp loss and mass occurrence of sea urchins on bamboo corals in the deep sea: an indirect effect of fishing impact?

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The ability of corals to detach their polyps (leaving behind a naked skeleton) in times of stress, allows polyps to escape from a local source of hostility (Sammarco 1982). In situ observations of this behavior (referred to as "polyp bailout") were first documented in tropical reef-building corals. Later it was observed in some cold-water corals of *Acanthogorgia* (Braga-Henriques 2014), and *Acanella arbuscula* (Rakka et al. 2019) in aquaria. To the best of our knowledge, field observations of polyp bailout in the deep-sea have not been made, and triggering factors are unknown. Here, we describe massive tissue and polyp loss (potentially polyp bailout) on bamboo corals Keratoisidinae (family Isididae) photographed on Discovery seamount southwest of Cape Town, South Africa (South East Atlantic Ocean) at 850–960 m depth, and at 1,135–1,160 m depth on Mongrel seamount off the coast of Tasmania, Australia (Southwest Pacific Ocean; Fig. 1). Perched atop these naked colonies were large numbers of the deep-sea urchins (family Echinidae) *Dermechinus horridus* at Discovery and Mongrel seamounts and two instances of *Gracilechinus multidentatus* at Mongrel seamount. At Discovery seamount, 31% of the naked colonies contained *D. horridus.* All observations were from areas historically exposed to extensive fisheries: demersal longlining (southeast Atlantic; Bensch et al. 2009) and bottom trawling (southwest Pacific; Williams et al. 2010). Unfavorable environmental conditions are believed to cause polyp bailout and subsequent death of colonies (see references in Rakka et al. [2019]). For tropical corals, low food availability, competitive interactions with macroalgae, as well as rapid changes in temperature, salinity, and pH have been listed as the main stressors. However, in the deep sea, low food availability, and stable temperature, salinity, and pH is typical. Thus, deep-sea ecosystems are predominantly structured by species interactions rather than by physical factors and are known to be more stable and less stressful (Ashford et al. 2018). We discuss possible triggering factors that may explain massive tissue and polyp loss of Keratoisidinae corals. To compare *D. horridus* occurrence on various substrates, a linear model and post hoc test were performed on their densities using R version 3.6.2 for Mac OS X (Hothorn and Bretz 2008, R Core Team 2019). Significance was determined at $P < 0.05$. Visual inspection of standard model validation graphs was used to verify model assumptions. A log transformation, plus offset of 1, was used to meet the assumption of normality. The substrate categories of hosts for *D. horridus* were (1) dead coral (dead *Keratoisis*, attached to substrate, broken or intact, 0% live tissue), (2) partly dead coral (*Keratoisis*, attached to substrate, broken or intact, >0 to <90% live tissue), (3) live coral (*Keratoisis*, attached to substrate, only minor injuries, >90% live tissue), (4) coral fragments (dead or partly alive loose fragments), and (5) sponge (live sponge of various species and sizes).

In 2019, R/V *Dr Fridtjof Nansen* surveyed 14 locations across five seamounts in the SEAFO (South East Atlantic Fisheries Organization) sub area D, at 400–1,800 m depth with an ROV (Buhl-Mortensen, 2020). Some of these seamounts are currently closed to fishing whereas others are being fished for Patagonian toothfish (Bensch et al. 2009). Abundant bamboo corals (*Keratoisis* sp.) were only observed on Discovery seamount, where high abundance of sea urchins and naked colonies were also

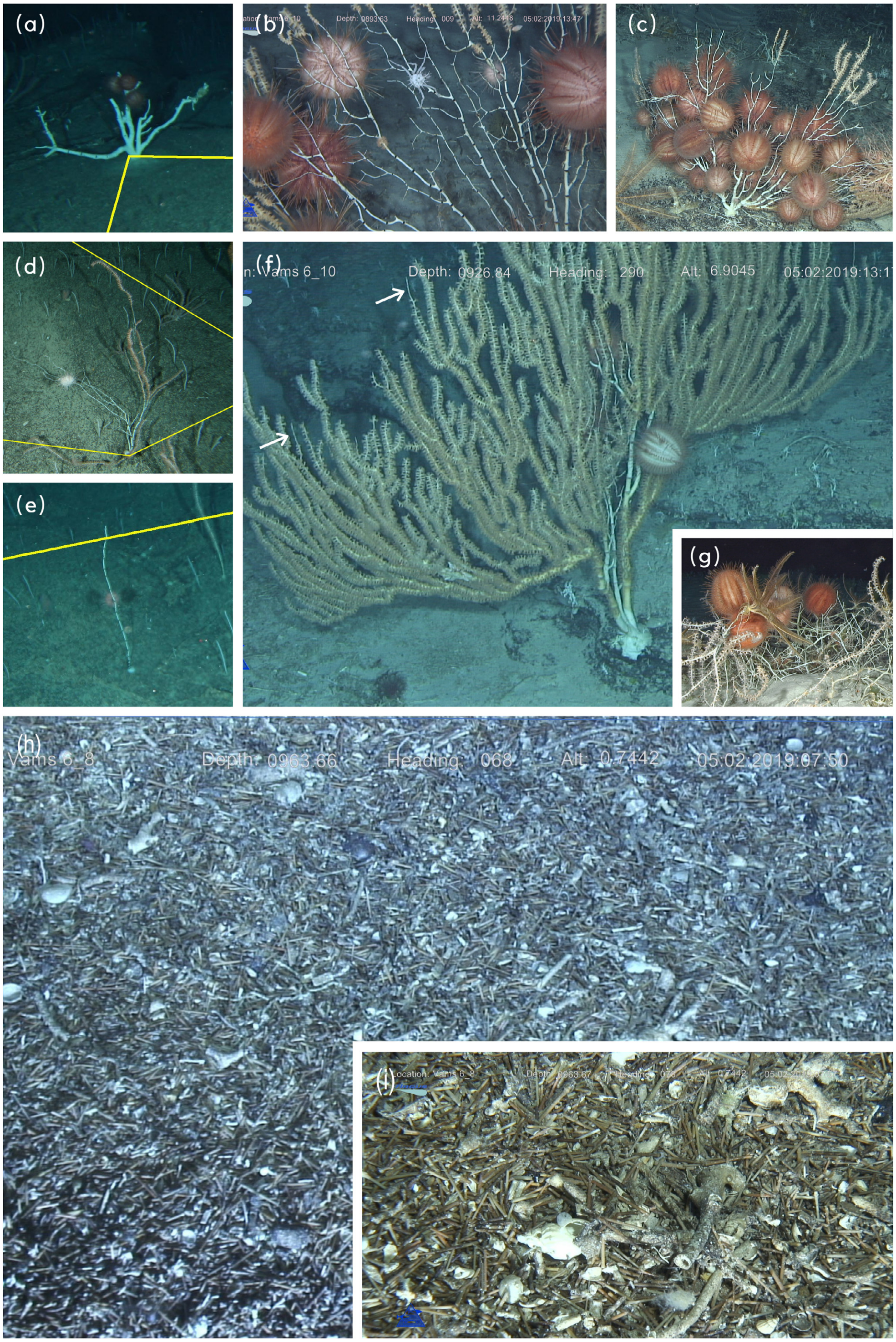

Fig. 1. (a, b, c, f, g) *Dermechinus horridus* and (d, e) *Gracilechinus multiradiatus* perched on dead and partly dead bamboo coral Keratoisidinae on Mongrel seamount, in Tasmania, Southwest Pacific Ocean (a, d, e), and on *Keratoisis* sp on Discovery seamount, in the South East Atlantic Fisheries Organization (SEAFO) Convention Area (b, c, f, g). (h) "Fragments" (pieces of the colony branches) found on the seafloor (some with coenenchymal tissue and polyps and others without). Large quantities of old (bioeroded and manganese coated) *Dermechinus horridus* spine rubble on Discovery seamount (h–i).

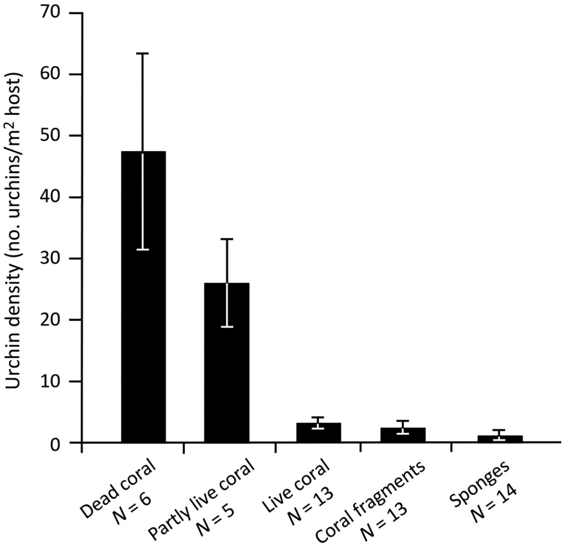

FIG. 2. Average urchin density (*Dermechinus horridus*; number per host area) for three categories of bamboo corals (*Keratoisis* sp.) and for sponges, estimated from a sample of 23 video frames (total area = 63 m^2) containing coral and/or urchins from depths between 846 and 946 m at Discovery seamount. Vertical lines are 95% confidence limits (Student *t* distribution). No urchins were observed on the surrounding seabed in these images.

observed. Similar interactions were noticed previously during a research expedition onboard the R/V *Southern Surveyor* in 2006. Here, 17 adjacent seamounts were surveyed across two areas (Tasman Fracture and Huon areas) south of Tasmania, using a towed camera system (Williams et al. 2010). Naked bamboo coral populated by *D. horridus* and *G. multidentatus* were observed on Mongrel seamount in the Huon area between 1,135 and 1,160 m depth. Deep-sea fisheries in the area started in the early 1990s, and were still actively trawled at the time of the study (Williams et al. 2010).

At Discovery Seamount, there were significantly more *D. horridus* on dead and partly dead coral than on sponges ($P < 0.001$ for both), live coral ($P < 0.01$, for both), and coral fragments ($P < 0.001$, for both) (Fig. 2). There were no significant differences between densities of *D. horridus* on dead compared to partly dead coral, and on sponges vs. live coral vs. coral fragments. The few intact colonies were not populated with sea urchins. Sea urchins were never observed over live polyps or coral tissue.

We present three possible causes for massive bamboo coral damage. First, we consider sea urchin bioerosion and/or corallivory.

Large-scale habitat impacts as a consequence of sea urchin gluttony has not been reported in the deep sea. However, gut content analyses suggest deep-sea urchins may erode and/or consume reef-forming scleractinian corals (Stevenson and Rocha 2013). These analyses revealed bioerosion and corallivory of deep-sea reef-building corals *Desmophyllum pertusum* and *Madrepora oculata* by several sea urchin taxa, including other members of family Echinidae (*Gracilechinus elegans* and *Gracilechinus alexandri*) from the Northeast Atlantic Ocean (Stevenson and Rocha 2013). While bioerosion or consumption of non-reef building corals have not been reported for sea urchins, other echinoderms have been found to feed on antipatharians and octocorals, including bamboo corals (Mah and Nizinski 2010).

The jaw mechanism of *D. horridus* is less extensive than those of other Echinidae species, but bamboo corals are more fragile than reef-building corals because of their partly organic joint-like nodes. It is possible that *D. horridus* and *G. multidentatus* are bioeroding the axes, non-retractile polyps, and/or the coenenchyma of the bamboo coral.

Second, it may be a colony stress response to sea urchin perching on the coral branches, leading to polyp bailout.

The weak jaw mechanism of *D. horridus,* in combination with the pronounced vertical elongation of the corona and its modified secondary spines has led some to propose a suspension feeding mode (Fell 1976). While this remains undocumented, suspension feeding has been described in four other sea urchin taxa (e.g., *Dendraster*, *Echinostrephus*, *Echinometra*, and *Evechinus*). Consistent with this feeding mode, and as seen in Fig. 1, *D. horridus* is commonly observed atop living coral structures (as opposed to low-lying and less complex habitats like sediment, coral rubble, or bedrock) (Stevenson et al. 2018). Placement atop coral (Fig 1a–g), above the seafloor and into swifter currents facilitate the capture of organic particles and reduce sediment clogging. This position in strong currents implies that *D. horridus* needs to hold firmly to the coral branches in order to feed. Physical damage may thus be a consequence of *D. horridus* grasping the fragile coral branches rather than bioerosion or corallivory. However, initial tissue (coenosarc) withdrawal was evident in some branch tips (see arrows in Fig. 1f), which could not have been due to the physical presence of the urchins in these parts of the colony. Naked tips are a typical feature of polyp bailout and indicate that the colony is stressed (e.g., by the presence of *D. horridus)*. We propose that polyp bailout progress from tips (Fig. 1f) as well as from near the urchins, resulting in polyp loss along the entire skeleton (see newly naked skeleton in Fig. 1a, e).

Corals attached to a substrate with different health status (dead, partly dead, and live) were within the same height range but differed with respect to density of urchins. However, we do not believe that *D. horridus* prefer dead vs. live coral and propose the higher density of *D. horridus* on dead and partly dead coral branches is a consequence of the sea urchins colonizing a live colonies, causing coenenchymal tissue and polyp mortality (through physical contact), then a bailout response (via stress to the whole colony), and eventually, coral death, rather than a preference for dead corals.

Selective removal of predatory fish by deep-water longline fishing may cause long-term shifts in species composition, trophic cascades, and changes in predation levels (Daskalov et al. 2007). It is possible that longlining and trawling in the southeast Atlantic and southwest Pacific, could indirectly damage these vulnerable marine ecosystems (VMEs) by removing demersal predators that regulate sea urchin populations, like *D. horridus.* We found large amounts of old (bioeroded and manganese coated) *D. horridus* spines along ~30% of the transect on Discovery seamount in the rubble among the bamboo corals at this seamount, suggesting high levels of predation on *D. horridus* in the past (Fig. 1h–i). While we are not aware of predators on *D. horridus*, the fishes *Molva molva*, *Mora moro*, *Lepidion* spp., and *Trachyscorpia* spp., as well as several shark, octopus, and decapod species (*Chaceon affinis and Bathynectes*) have been observed feeding on sea urchins off Tasmania, Australia, or sea urchin material was found in their guts (Stevenson et al. 2015). One of these species and another closely related one (*Chaceon* cf. *affinis* and Moridae fishes [*Antimora rostrata*]) were observed at the Discovery seamount (Buhl-Mortensen et al. 2020). Previous analyses suggest predators like fish and decapods drive sea urchin population structure in deep-sea coral habitats by influencing how sea urchins use space and resources in these locations when in proximity of such predators (Stevenson et al. 2015).

The third possible explanation to the observed coral damage could be polyp loss from mechanical damage caused by fishing gear. Deep-sea fishing activities have the potential to impact benthic communities by removing habitat forming organisms (and also inducing mechanical damages such as abrasion, breakage, or partial mortality; see Braga-Henriques et al. 2013) or in/directly applying pressure on demersal predators that regulate benthic populations, as described above. The former has been shown to be an influential factor in shaping deep-sea urchin community composition (Stevenson et al. 2018), with certain taxa being more resistant to fishing impacts and/or favoring early colonizers (Clark and Rowden 2009). Dead bamboo coral branches found in the observed areas and naked/broken tips of intact coral colonies are consistent with this hypothesis, indicating longline fishing impact. It is possible that the monofilament lines of the longline gear could damage branching coral during hauling operations. However, no evidence of human footprint was found in the southeast Atlantic area and longline gear could not be responsible for the damage observed in sites surveyed in the southwest Pacific (e.g., bare skeleton in bottom/midsections of Keratoisidinae in Fig. 1b–d, g). Also, the light manganese coating on the skeletal elements in Fig. 1h–i suggest the pieces are very old (Edinger and Sherwood 2012).

Of the three proposed hypotheses, the second is the most likely, i.e., to enhance suspension feeding efficiency, *D. horridus* perches high above the seafloor on the bamboo coral to elevate itself into swifter currents to facilitate feeding and prevent sediment obstructions, but during exposure to swifter currents it must firmly hold the fragile branches of the coral to maintain its position. In the process, the sea urchins may damage the polyps and stress the colony, which starts to release polyps (bailout) at the tip/base and locations near the sea urchin. Are we observing a periodic event, or possibly an alternate stable state (a tipping point) caused by overfishing top predators (see Scheffer et al. 2001)? The gluttony of sea urchins has marked this taxon as a powerful structuring force in coastal ecosystems with the potential to cause catastrophic shifts in ecosystems when predators are removed (e.g., kelp forests [Pearse et al. 1970], tropical coral reefs [McClanahan and Kurtis 1991]). Similar shifts have not yet been documented in the deep sea, and much still remains unknown about the intimate community dynamics, predator–prey relationships, and their structuring force for these organisms here. However, community interactions should be considered when assessing the health status of the system as its resilience may depend on a healthy balance between predators (e.g., fish) and their prey (e.g., sea urchins). In this case, it would be prudent to further probe into the effect of demersal fish predator shifts on sea urchin populations, and indeed on the benthic community as a whole.

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Data (Buhl-Mortensen, Braga-Henriques and Stevenson 2021) are accessible and permanently archived in the Norwegian Marine Data Centre at https://doi.org/10.21335/NMDC-181814768.