Sea Urchin Massacre Is a Natural Experiment

Major influences on community composition are often difficult to determine, but a massive natural experiment in the Caribbean has thrown some light on one case

In February 1983 a wave of death swept through the Caribbean, virtually obliterating the populations of *Diadema antillarum*—a spiny sea urchin—that thrived there. The cause of this massive 95 to 99% population crash is still a mystery, although some form of bacterial infection is strongly suspected. Be that as it may, the effect of the crash on the coral reef communities where the urchins lived has been dramatic and illuminating.

"It was a Caribbean-wide natural experiment," says Robert Carpenter of the National Undersea Research Program at Fairleigh Dickinson University in St. Croix. "For 20 years biologists have been doing small-scale experimental manipulations of reef communities. This massive die-off has confirmed a lot of the predictions that were made previously."

The urchins were part of a complex ecological web that includes carnivorous fish that prey on them, herbivorous fish with which they compete, and a great diversity of algae on which they subsist. The question is, what part, if any, do the urchins play in shaping the overall balance of the community. According to Carpenter, data from the aftermath of the die-off "suggest that *D. antillarum* has an important role in structuring both the producer and consumer components of the Caribbean coral reef ecosystems."

Most notable are the changes in abundance, composition, and productivity of the reef algae following the disappearance of the urchins. Before the crash 80% of the reef surfaces were covered with algal turf, a 1- to 2-millimeter-thick mat composed of as many as 60 species of filamentous and crust algae. Within 5 days of the crash the turf had begun to thicken, testimony to the previously intense grazing pressure of the urchins. Very soon canopy height reached 20 to 30 millimeters, and larger, macroalgae became prominent among the community where previously they had been virtually absent.

Before the crash about 90% of the algal community were short, turf varieties; after 2 months this was down to 50%; and 2 years later the figure was 40%. The macrophytes, meanwhile, expanded from near zero to 40% of the community. "Species composition of the community is therefore clearly effected by *D. antillarum*" says Carpenter.

This burgeoning of the algal communities occurred in spite of increased grazing from herbivorous fish, which presumably were benefiting from the absence of competition from the urchins. Clearly, although the fish competed with the urchins, the fish were unable to replace the urchins in their effect on the algal community.

The thickening of the algal turf was, however, accompanied by a decrease in productivity, both per unit area and per unit of biomass: the figures are 37% and 61%, respectively. "Part of the explanation is that as they grow taller the algae shade each other, which inevitably cuts down productivity," says Carpenter.

In addition, however, he suspects that algal metabolism was modified. Specifically, while the urchins are highly effective in consuming biomass from the algal turfs, they also pour out large quantities of nitrogen-containing excreta. The nitrogen in the fecal pellets is made available to the algae by disintegration and bacterial decomposition. "The importance of such nutrient pulses would be great for tropical algae communities due to the extremely low ambient nutrient concentrations in the oceanic water surrounding most coral reefs."

In other words, the urchins provided a rich supply of fertilizer as they grazed, just as resting schools of reef fish are thought to do in other circumstances. An alternative explanation, Carpenter acknowledges, is linked to the change in species balance within the algal community. "Removal of urchin grazing could lead to domination by other algal species with lower [productivity to biomass] ratios," he notes. Although not completely excluded, this possibility is not thought to be likely.

The removal of a predator from a community frequently has a dramatic effect on that community, usually in maintaining a wider diversity of potential prey species than would otherwise coexist: this is known as the keystone predator concept. In the case of *D. antillarum*, although there is some indication that species diversity is higher in its presence than in its absence, the greater effect appears to be in boosting community productivity. Again, there are parallels in this respect with other systems, specifically in terrestrial plant-herbivore interactions. "The data presented here provide confirmation that this benthic marine herbivore has a positive effect on the rate of algal primary productivity," concludes Carpenter. ■

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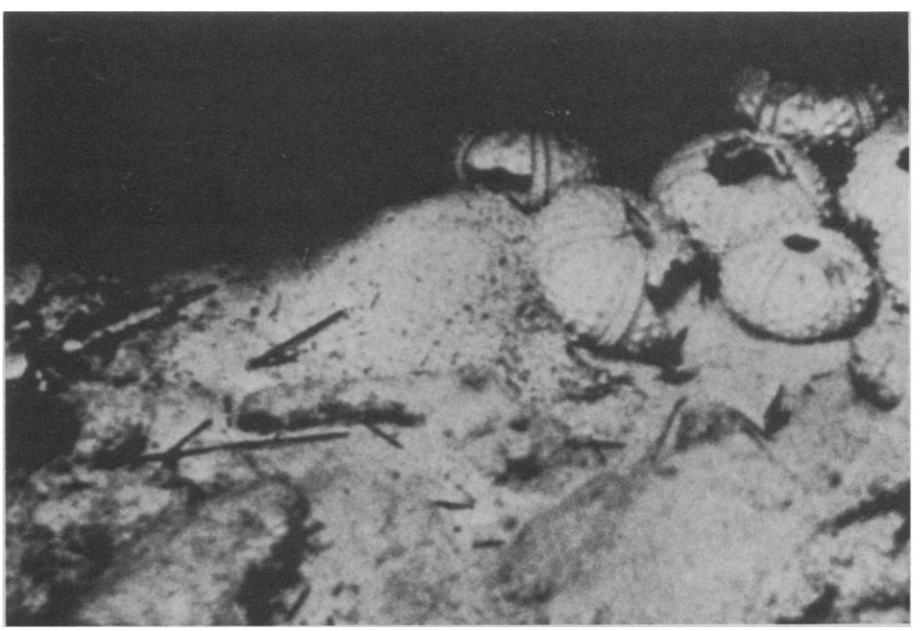

It's an ill wind: *Some form of water-borne pathogen is thought to have devastated sea urchin populations throughout the Caribbean in February 1983. This visitation of death was soon followed by a burgeoning algal community.* [*R. C. Carpenter,* Proc. Natl. Acad. Sci. U.S.A. ***85****, 511 (1988)*]