NOTE

Densities of the sea urchin *Diadema antillarum* before and after mass mortalities on the coral reefs of Curaçao

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ABSTRACT: The sea urchin *Diadema antillarum* commonly occurs on Caribbean reefs in densities sufficiently high to influence characteristics such as community composition and reef growth. We observed an outbreak of mass mortality in this species reducing population densities by 98 to 100 %. Mortality spread from the Curaçao harbour mouth along the coast, most rapidly advancing in the down-current direction. Our calculations show a pronounced effect on the carbonate budget of the reef. Recovery of *Diadema* populations may be facilitated by parthenogenesis. There is continuing recruitment on affected reefs, a possible location of the parent population being up-current unaffected reefs of Bonaire.

The sea urchin *Diadema antillarum* Philippi is a key factor in biological and geological processes on Caribbean reefs. Although it occurs in varying densities, *D. antillarum* is generally abundant with common densities ranging from 3 up to 71 m^{-2} (e.g. Ogden, 1977; Bauer, 1980; Sammarco, 1980; Hawkins and Lewis, 1982). The urchins forage in the late afternoon and at night (Ogden et al., 1973) feeding on a variety of food items (Lewis, 1964; Quinn, 1965; Bak and van Eys, 1975; Ogden, 1976). Commonly they scrape off the outer layers of various bottom components, mostly coral rock, grazing on the abundantly present thin algal turf, endolithic algae and crustose corallines. Often the dominant herbivores of the reef (Hawkins and Lewis, 1982), the urchins are of crucial importance in the development of the reef flora (Sammarco et al., 1974; Carpenter, 1981). *D. antillarum* preys on living coral (Bak and van Eys, 1975) contributing to the control of the coral community as predators on coral recruits (Sammarco, 1980, 1982). They also control survival of larger colonies through erosion of the dead colony base (Bak, in prep.). *D. antillarum* erodes much

larger quantities of coral rock than other common bio-eroders such as excavating sponges, Clionidae (Rützler, 1975; Bak, 1976; MacGeachy and Stearn, 1976) and parrot fishes, Scaridae (Ogden, 1977; Frydl and Stearn, 1978). In the delicate balance between growth and erosion of a reef, *D. antillarum* accounts for a major portion of the calcium carbonate budget (Scoffin et al., 1980).

Diadema antillarum population density data on the fringing reefs along the southeast, leeward, coast of Curaçao are available for different sites and for a number of years. Population densities have shown a decrease at some reefs, e.g. on Carmabi Buoy III Reef (Fig. 1), depth 3 to 12 m, densities decreased from
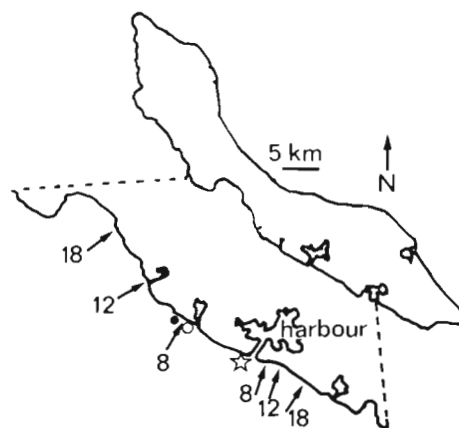

Fig. 1. *Diadema antillarum*. Distribution of mass mortalities through time along the southwest coast of Curacao. Asterisk: location of first mortalities, 6 October, near the harbour mouth. Arrows: position of borderline 100 % living/infested populations at 8, 12 and 18 October 1983. Pre- and post-mortality densities recorded for Holiday Beach (asterisk), Carmabi Buoy I (open dot), Carmabi Buoy III (closed dot). Note the relatively rapid spread of mortalities down-current from the site of the original outbreak (current direction: northwest)

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$12 \, \text{m}^{-2}$ in summer 1975 to $7 \, \text{m}^{-2}$ in summer 1979 to $4 \, \text{m}^{-2}$ in summer 1983 (van Eys, unpubl.; Geerlings, unpubl.; this paper; surveyed transects 183 to 457 m^2). We interpret these as natural fluctuations. Populations consisted of healthy urchins; dead or dying urchins have never been observed.

An abrupt change was first observed on 6th October 1983, when we found approximately 50 % of the population at the reef 800 m down-current of the harbour mouth (Holiday Beach) to be dead or dying. On succeeding days this mass mortality spread along the coast. The distribution of the mortality at successive dates is shown in Fig. 1. Affected *Diadema antillarum* show the following sequence of symptoms: accumulation of detritus on spines, disappearance of epidermis around the mouth and at spots over the test, loss of spines resulting in exposure of tubercles and finally of the whole skeleton, decomposition of remaining tissue (Fig. 2). A healthy population in which very few individuals show the first symptoms at Day X will be significantly affected ($\pm$ 20 % of population) at Day X + 2. More than 50 % of the population will be dying at Day X + 4. The size of the pre- and postcatastrophe population for 3 areas (locations see Fig. 1) is shown in Table 1.

Similar mass mortalities in *Diadema antillarum* populations have been reported since January from other areas in the Caribbean (Lessios et al., 1983; G. D. Oliver, Florida, pers. comm.). The causative agent(s) are yet unknown but hypotheses include pollution and bacterial disease. The sequential distribution of outbreaks of mortality appears to be related with (1) the location of the first outbreak, the entrance to the Panama Canal, and (2) the direction of the main Caribbean currents: down the coast of Panama towards Colombia, and north and north-west (Costa Rica, Jamaica, Cayman Islands, Florida). On a local scale the current effect is demonstrated in Curaçao. Mass mortalities spread rapidly along the coast down-current, while up-current urchin populations at similar distance from the harbour were affected much later (Fig. 1).

The original location of the mortality at the harbour mouth strongly suggests human activity as the source of the catastrophe in Curaçao. There appear to be 2 possibilities. Firstly, pollutants are the cause of the mortality. Mass mortality occurred first at the Atlantic mouth of the Panama Canal, an extremely busy shipping route, and affected localities down-current throughout the Caribbean. Curaçao is 750 km up-current from the affected localities and possibly a similar pollutant was released in the busy port of Willemstad, Curaçao. An argument against pollution is the relatively slow spread, even down-current, of the observed mortalities. A polluted body of water would be transported down-current along the coast in 1 or 2 d causing nearly simultaneous mortalities along the reefs. A second possibility is that the causative agent is a water-borne disease which was brought in from a heavily affected area by ship to Curaçao and released, e.g. with ballast or bilge water. A strong argument in favour of this possibility is the species specificity of the mortality: no other species are visibly affected.
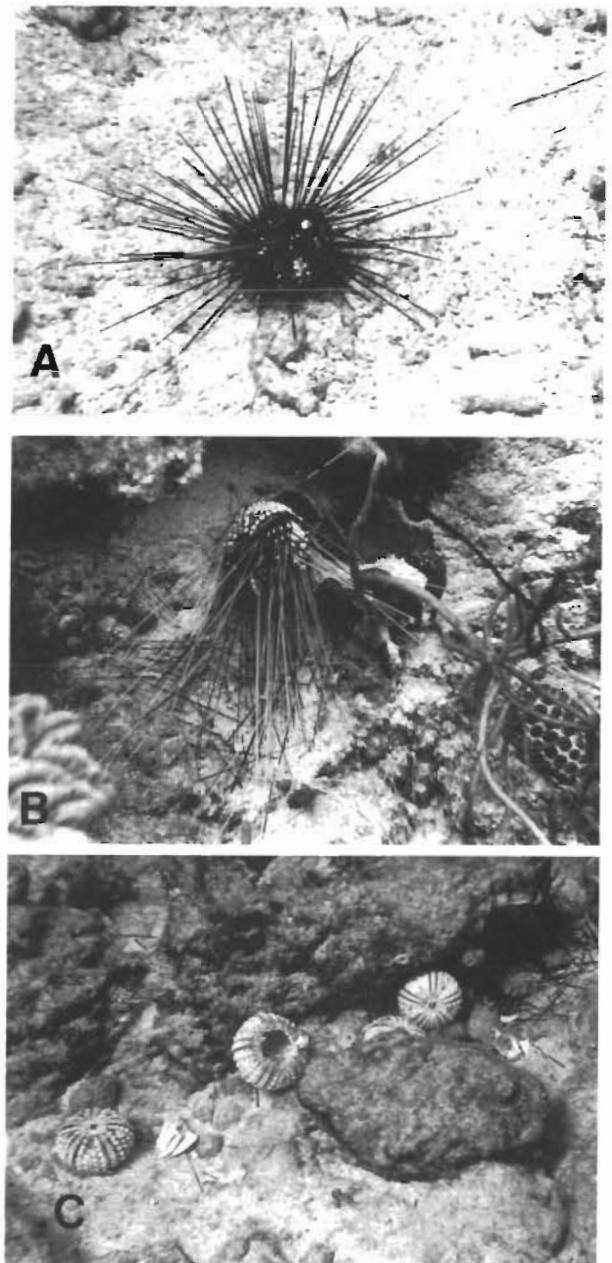

Fig. 2. *Diadema antillarum*. Mortality (A) Loss of spines and tissue results in exposure of test (test diameter, 3.5 cm; depth, 6 m). (B) Urchin in final stage of dying (test diameter, 4 cm; depth, 18 m). (C) Remains of urchin population: empty tests, loose spines and Aristotles lanterns (test diameter, 4 cm; depth 7 m)

Table 1. *Diadema antillarum*. Densities of populations /m² at various depths on the reef terrace (0 to 12 m) and reef slope (> 12 m) in 3 locations. Dates of surveys: Holiday Beach, May/June and 26/27 October 1983; Carmabi Buoy I, May/June and 26/27 October 1983; Carmabi Buoy III, July/August and 28 October 1983. Transect area (m²) indicated for each survey in parentheses. For locations see Fig. 1

Location	Depth (m)	Mean pre-mortality density	Mean post-mortality density	% decrease
Holiday Beach	3	3.97 (120 m²)	0.01 (100 m²)	99.7
	12	0.39 (66 m²)	0.0 (100 m²)	100
	9–30	0.26 (97 m²)	0.0 (112 m²)	100
Buoy I	3	2.93 (114 m²)	0.01 (100 m²)	99.7
	12	2.49 (55 m²)	0.0 (100 m²)	100
	9–36	0.73 (97 m²)	0.02 (112 m²)	97.3
Buoy III	3–16	4.16 (183 m²)	0.05 (226 m²)	98.8

The disappearance of dense *Diadema antillarum* populations from the reefs has various effects. Within 1 wk of the first signs of mortality on a reef we saw the ubiquitous filamentous algae increase significantly in length and density. Possible future changes in bottom cover between various algal species and sessile invertebrates are being studied. A major effect is the immense decrease in bioerosion. Using data accumulated for the Carmabi study area (depth 5 to 10 m) on coral cover (30 %; van Duyl, ms), coral growth rates (10 kg m^{-2} yr^{-1}; Bak, 1976), cover of crustose coralline algae (15 %; de Groot and de Ruyter van Steveninck, ms), and growth of corallines (0.53 kg m^{-2} yr^{-1}, Bak 1976), the production of carbonate rock by corals is 3 kg m^{-2} yr^{-1}, by algae 0.08 kg m^{-2} yr^{-1}, giving a total of nearly 3.1 kg m^{-2} yr^{-1}. Similar data on the most important destructive factors such as excavating sponges (cover 5.5 %; de Groot and de Ruyter van Steveninck, ms; erosion rate: 3 kg m^{-2} yr^{-1}; Bak, 1976), parrot fishes (erosion rates vary from 0.49 to 0.034 kg m^{-2} yr^{-1}; Ogden, 1976: Panama; Frydl and Stearn, 1978: Barbados, with intermediate values of 0.25 and 0.21 kg m^{-2} yr^{-1}; Bardach, 1961: Bermuda; Gygi, 1975: Bermuda) and *D. antillarum* (1976 population density 12 m^{-2}; erosion: 2.9 kg m^{-2} yr^{-1}; van Eys, ms) yield a total erosion of 3.3 kg m^{-2} yr^{-1}. The calcium budget of this reef appears to be slightly negative for this period; this is confirmed by the dominance of small (< 1 m) eroded coral colonies. The disappearance of the *D. antillarum* as the most effective bioeroder could result in a net accumulation of calcium carbonate of 2.7 kg m^{-2} yr^{-1}. Of course, actual future changes in calcium budget will be influenced by overgrowth of crustose corallines and possibly corals by filamentous algae (Wanders, 1977; Sammarco, 1980).

Recovery of the *Diadema antillarum* populations depends on survivorship of the remnants of the original populations and reproduction/recruitment patterns. *D. antillarum* is reported to be dioecious (Hyman, 1955), but there are indications that parthenogenesis (known to take place in other urchins: Harvey, 1956) occurs. On 21st July 1983 we found the gonads of 2 individuals (sample: 25 individuals; test size: > 4 cm diameter) to be packed with blastulae (Fig. 3). Under conditions of extremely low population density – e.g. after the mass mortality – successful parthenogenesis
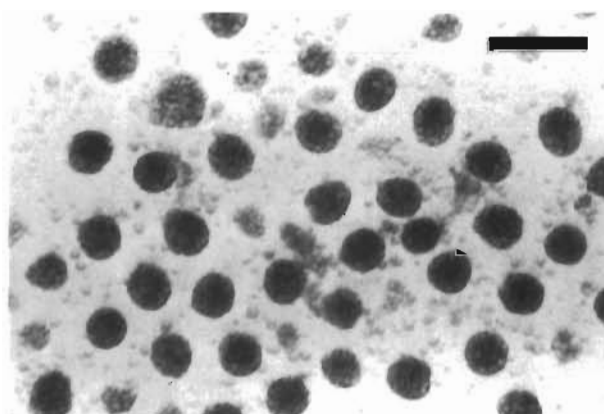

Fig. 3. *Diadema antillarum*. Gonad smear showing abundant blastulae. Bar: 10.3 µm

could facilitate recovery. Urchins with ripe gonads occur during most of the year in Curaçao (Bak, unpubl.). Also recruits, ≤ 1 mm test diameter, settle throughout the year (Bak, unpubl.). Crucial knowledge on the life history between spawning and settlement is not available, but there is supposedly a pelagic stage of a few weeks. Whether the larvae remain largely trapped within a reef system or in a stable eddy system or whether there is interchange between islands on a sufficiently large scale will be one of the deciding factors in the recovery of the *D. antillarum* populations. At this time (28th Oct 1983) urchin recruits (≤ 1 mm) are still settling on the affected reefs of Curaçao. It may be of importance that no *D. antillarum* mass mortality yet occurs on the island of Bonaire, 52 km up-current of Curaçao.

LITERATURE CITED

Bak, R. P. M. (1976). The growth of coral colonies and the importance of crustose coralline algae and burrowing sponges in relation with carbonate accumulation. Neth. J. Sea Res. 10: 285–337

Bak, R. P. M., van Eys, G. (1975). Predation of the sea urchin *Diadema antillarum* Philippi on living coral. Oecologia (Berl.) 20: 111–115

Bardach, J. E. (1961). Transport of calcareous fragments by reef fishes. Science, N. Y. 133: 98–99

Bauer, J. C. (1980). Observations on geographical variations in population density of the echinoid *Diadema antillarum* within the Western Atlantic. Bull. mar. Sci. 30: 509–514

Carpenter, R. C. (1981). Grazing by *Diadema antillarum* Philippi and its effects on the benthic algal community. J. mar. Res. 39: 749–765

Frydl, P., Stearn, C. W. (1978). Rate of bioerosion by parrotfish in Barbados reef environments. J. sedim. Petrol. 48: 1149–1158

Gygi, R. A. (1975). *Sparisoma viride* (Bonneterre), the stoplight Parrotfish a major sediment producer on coral reefs of Bermuda? Eclog. geol. Helv. 68: 327–359

Harvey, E. B. (1956). The American *Arbacia* and other sea urchins. Princeton University Press, Princeton

Hawkins, C. M., Lewis, J. B. (1982). Ecological energetics of the tropical sea urchin *Diadema antillarum* Philippi in Barbados, West-Indies. Estuar. coast. Shelf Sci. 15: 645–669

Hyman, L. H. (1955). The invertebrates: Echinodermata. McGraw-Hill, New York

Lessios, H. A., Glynn, P. W., Robertson, D. R. (1983). Mass mortalities of coral reef organisms. Science, N. Y. 222: 715

Lewis, J. B. (1964). Feeding and digestion in the tropical sea urchin *Diadema antillarum* Philippi. Can. J. Zool. 42: 549–557

MacGeachy, J. K., Stearn, C. W. (1976). Boring by macro-organisms in the coral *Montastrea annularis*, on Barbados reefs. Int. Revue ges. Hydrobiol. 61: 715–745

Ogden, J. C. (1976). Some aspects of herbivore-plant relationships on Caribbean reefs and seagrass beds. Aquat. Bot. 2: 103–116

Ogden, J. C. (1977). Carbonate-sediment production by parrot fish and sea urchins on Caribbean reefs. In: Frost, S. H., Weiss, M. P., Saunders, J. B. (ed.) Reefs and related carbonates – ecology and sedimentology. Stud. Geol. 4. AAPG Tulsa, p. 281–288

Ogden, J. C., Brown, R., Salesky, N. (1973). Grazing by the echinoid *Diadema antillarum* Philippi: formation of halos around West Indian patch reefs. Science, N. Y. 182: 175–171

Quinn, B. G. (1965). Predation in sea urchins. Bull. mar. Sci. 15: 259–264

Rützler, K. (1975). The role of burrowing sponges in bioerosion. Oecologia (Berl.) 19: 203–216

Sammarco, P. W. (1980). *Diadema* and its relationship to coral spat martality: grazing, competition, and biological disturbance. J. exp. mar. Biol. Ecol. 45: 245–272

Sammarco, P. W. (1982). Echinoid grazing as a structuring force in coral communities: whole reef manipulations. J. exp. mar. Biol. Ecol. 61: 31–55

Sammarco, P. W., Levinton, J. S., Ogden, J. C. (1974). Grazing and control of coral reef community structure by *Diadema antillarum* Philippi (Echinodermata: Echinoidea): a preliminary study. J. mar. Res. 32: 47–53

Scoffin, T. P., Stearn, C. W., Boucher, D., Frydl, P., Hawkins, C. M., Hunter, I. G., MacGeachy, J. K. (1980). Calcium carbonate budget of a fringing reef on the west coast of Barbados. Bull. mar. Sci. 30: 475–508

Wanders, J. B. W. (1977). The role of benthic algae in the shallow reef of Curaçao (Netherlands Antilles) II: The significance of grazing. Aquat. Bot. 3: 357–390