

# Mass Mortality of *Diadema antillarum* on the Caribbean Coast of Panama

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Accepted 11 September 1984

**Abstract.** The ecologically important sea urchin *Diadema antillarum* suffered mass mortalities in 1983, first noted in Panama and then reported from the rest of the Caribbean. We documented the effects of this mortality at two localities on the Atlantic coast of Panama, Punta Galeta and the San Blas Archipelago. At Punta Galeta, affected by the mortality in January 1983, the numbers of *D. antillarum* changed from an estimated 14,000 per ha in June 1982 to 0.5 per ha in May 1983; by February 1984 they had increased to 38 per ha. In the San Blas, where mass mortality started in April 1983, the number of *D. antillarum* in permanent quadrats on 8 reefs was reduced by an average of 94.2%. The average reduction in population density measured in transects on nine reefs was 98.9%. Data taken in permanent quadrats on four reefs in 1978, 1979 and 1980 indicate that population fluctuations of *D. antillarum* are normally much smaller, justifying the labeling of the 1983 event as “mass mortality”. Size structure of the San Blas populations was also affected; mean test diameter of *D. antillarum* on four reefs was reduced from 48.6 mm to 25.0 mm. Other echinoids (*Echinometra viridis*, *E. lucunter*, *Lytechinus variegatus*, *L. williamsi*, *Eucidaris tribuloides*, *Tripneustes ventricosus*, *Clypeaster rosaceus* and *Echinoneus cyclostomus*) suffered no ill effects at either Galeta or the San Blas; their population densities remained stable or increased. Density determinations of *Diadema mexicanum* at the island of Taboguilla on the Pacific side of Panama indicate that *Diadema* mass mortality did not extend to the eastern Pacific. Sea surface temperatures, tidal levels, rainfall and salinity showed no abnormal fluctuations during the time of *D. antillarum* mass mortality at Galeta, suggesting that mortality was not due to physical stress. The wide geographical spread and species-specificity of the mortality suggest a water-borne pathogen as the most likely causative agent. Recovery of *D. antillarum* populations is likely to be slow because there are few, if any, unaffected populations in the Caribbean to contribute larvae for the recolonization of depleted areas. The absence of *D. antillarum* will probably be reflected by changes in the algal,

coral and echinoid communities, and by altered patterns of bioerosion.

## Introduction

The long-spined sea urchin *Diadema antillarum* Philippi is normally very abundant on Caribbean coral reefs, *Thalassia* beds, mangroves, and sand habitats (Randall et al. 1964). Its feeding activity affects the geomorphology and ecology of coral reefs. *Diadema* is believed to erode more calcium carbonate from reef framework than any other organism (Stearn and Scoffin 1977; Scoffin et al. 1980), to eat live coral (Bak and van Eys 1975; Carpenter 1981), to compete with other sea urchins (Williams 1981) and herbivorous fishes (Randall 1961; Williams 1979, 1980, 1981; Sammarco and Williams 1982), to cause bare halos in *Thalassia* beds around coral reefs (Ogden et al. 1973), to determine algal cover and diversity (Carpenter 1981; Sammarco 1982a, b), and to affect coral community composition by grazing on juvenile corals (Sammarco 1980, 1982a).

In 1983 *Diadema antillarum* experienced mass mortalities, first noted at Punta Galeta, near the entrance of the Panama Canal, and then reported from the rest of the Caribbean (Lessios et al. 1983; Lessios et al. 1984). The causative agent of these mortalities remains unidentified. Here we describe the effects of mass mortality on *D. antillarum* populations on the Caribbean coast of Panama and its initial effects upon populations of other species of sea urchins.

## Materials and Methods

We made observations along the Caribbean coast of Panama, from the entrance of the Panama Canal to the Colombian border. We collected quantitative data at Punta Galeta and in the San Blas Archipelago, two areas for which we had data on sea urchin population densities previous to the mass mortality.

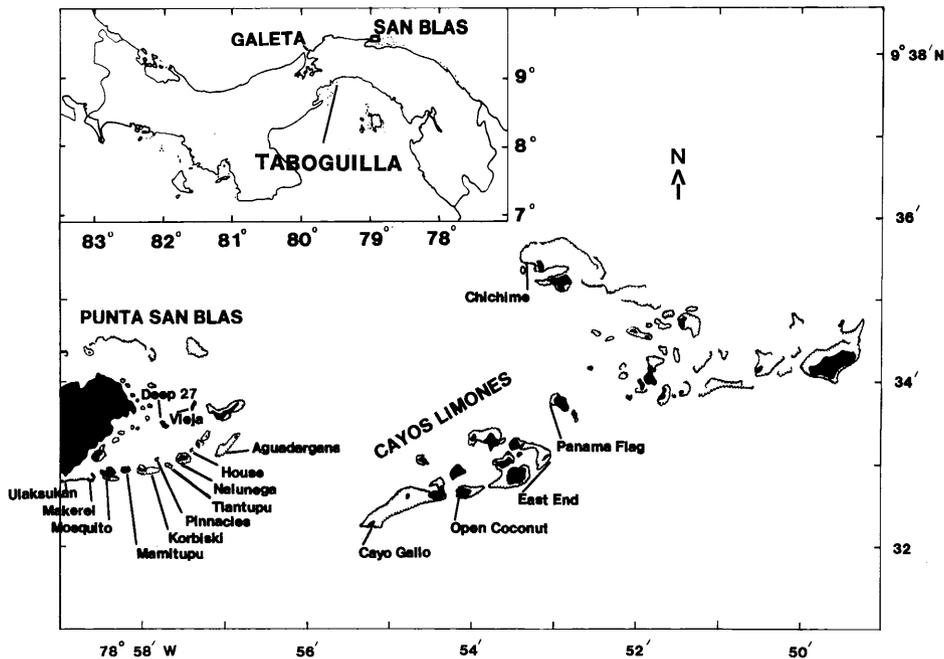


Fig. 1. Punta San Blas and Cayos Limones areas of the San Blas Archipelago. Local names are used where available; names were coined by researchers at the San Blas facility of the Smithsonian for previously unnamed reefs. *Insert*: Identification of study areas along the Atlantic and Pacific coasts of Panama

### Punta Galeta

Our principal study area at this site was on the eastern side of Punta Galeta (Fig. 1), where an intertidal reef flat encloses a lagoon and channels. Before January 1983, *Diadema* were concentrated in the lagoon and channels along the inner edges of the reef flat to a depth of approximately 1.5 m. The area of this shallow, subtidal habitat is approximately 2.9 ha. The total study site, including lagoon, channels, and reef flat, encompasses an area of 12 ha.

On 3 June 1982, six months before the mass mortality of *D. antillarum*, a census was made at the eastern end of the lagoon. *Diadema* were counted in 200 quadrats of 1 m<sup>2</sup> each placed around the edge of the lagoon. On 4 May 1983, after mass mortality of *Diadema* had occurred at Galeta, we searched the entire 12 ha area for *D. antillarum* to determine the extent of population reduction. This census was repeated on 24–25 February 1984 to assess the degree of recovery of *D. antillarum* populations.

Physical parameters have been measured on the Galeta reef for the past ten years by the Environmental Sciences Program of the Smithsonian Institution (Meyer and Birkeland 1974; Meyer et al. 1975; Hendler 1976, 1977 a). We examined rainfall, salinity and tidal level data collected between October 1982 and May 1983 for abnormal fluctuations which might have caused *D. antillarum* mortality. Sea-surface temperatures of the area adjacent to Panama were obtained from the United States National Weather Service. The Environmental Sciences Program has also been censusing populations of echinoids on the intertidal reef flat at Galeta for the past ten years. These data are taken at approximately monthly intervals in three permanent transects, each 20 m long and 1 m wide. One transect is located on the seaward edge of the reef flat, one on the central reef flat, and one in a *Thalassia* bed which occurs in an area of sand accumulation on top of the reef flat. *Diadema* was seasonally abundant in these transects until 1976 (Hendler 1977 b); however, as a probable result of the fall in mean sea level in more recent years, the reef flat habitats have become too shallow for *D. antillarum*, which cannot survive in areas of frequent subaerial exposure (Cubit, in preparation). We examined echinoid counts taken between October 1982 and May 1983 to determine whether other species of echinoids suffered from the same malady that caused *D. antillarum* mortality.

### San Blas Archipelago

Our observations in this area were concentrated on the reefs close to Punta San Blas and at the Cayos Limones (Fig. 1). To assess the impact

of mass mortality on *D. antillarum* populations, we set up permanent quadrats on 8 reefs and determined numbers of healthy-looking and diseased *Diadema* at 3 to 9 day intervals while the die-offs were in progress and at monthly or bimonthly intervals thereafter. Diseased individuals were recognized by characteristic symptoms displayed by many animals during the mass mortality (see below). In the vicinity of Punta San Blas we established three 1 m<sup>2</sup> quadrats on each of three reefs after the symptoms of the presumed disease had already appeared. In the Cayos Limones we were able to overtake the mortality front and start monitoring a single 25 m<sup>2</sup> quadrat on each of five reefs before the die-offs became widely spread. Thus the quadrats at Cayos Limones provide a record of population densities before the mass mortality event, of the time of first appearance of symptoms in each reef, of the duration of mass mortality, and of the population densities of the surviving *D. antillarum*.

In four reefs at Cayos Limones (Open Coconut, East End, Panama Flag, and Chichime, see Fig. 1 for locations) we also measured the test diameter of living *D. antillarum*, both healthy and diseased, in each 25 m<sup>2</sup> quadrat. These measurements were made on 24 May 1983, when populations were declining but had not yet reached their lowest levels, and again on 8 July 1983, and on 7 August 1983, after most affected sea urchins had died. We were thus able to assess the changes in population size structure associated with mass mortality.

We had also collected data on population densities of *D. antillarum* on nine reefs in 1980 and 1982, before the mortality appeared in the San Blas. These data were obtained from five to ten transects per reef. Each transect was 1.8 m wide and started at the shallowest depth at which *Diadema* was encountered and extended to a depth of 17 m, or to the deepest edge of the reef if it occurred at less than 17 m. In July 1983, after the occurrence of mass mortality, population densities were reassessed on the same reefs in the same manner.

To compare changes in population density caused by mass mortality to changes resulting from "normal" population fluctuations, we also present data of *D. antillarum* densities obtained from permanent 1 m<sup>2</sup> quadrats at various reefs in the San Blas in years previous to the mass mortality. Twelve quadrats were situated on Nalunega reef, 14 on Tiantupu, and 36 on Korbiski (Fig. 1). On all reefs the quadrats were spread between the low tide mark and a depth of 1.5 m. The numbers of *Diadema* in these quadrats were determined during the day once a month from February 1978 through November 1979. *Diadema* were also counted in the same quadrats during December 1983, seven months after the die off. In January 1980, 11 quadrats of 25 m<sup>2</sup> each, were established at depths of 3 to 10 m at Makereel reef, and three quadrats of the same

size at a comparable depth at Korbiski reef. *D. antillarum* were counted in these quadrats during the day once a month in January, February, April, June, July and September 1980, and during the night in February and June 1980.

To find out whether other species of echinoids in the San Blas were affected by the causative agent of *D. antillarum* mortality, we compared population density data from House reef for *Lytechinus variegatus*, *L. williamsi*, *Tripneustes ventricosus*, *Clypeaster rosaceus*, *Echinometra viridis*, *E. lucunter*, and *Eucidaris tribuloides* gathered before and after the *Diadema* demise. Individuals of each species were counted on the reef flat, reef slope and surrounding *Thalassia* beds between July and September 1982 in 1.8 m wide transects stretching from the shallowest point of each habitat to the habitat end, or (in *Thalassia* beds) to a distance of 30 m. In August 1983, four months after the *Diadema* mass mortality, population densities of these species were determined in the same manner at the same locality.

### Pacific Coast of Panama

In June 1983, two months after mass mortality of *Diadema* was first observed in the San Blas, many corals in the same area lost their zooxanthellae, and a few of them subsequently died (Lessios et al. 1983, Glynn 1984), a phenomenon which had been previously noted on a much larger scale on the Pacific coast of Panama (Glynn 1983). To examine the possibility that coral and echinoid mortality might be due to the same general causes and to see if *D. antillarum* mass mortality had also occurred in the eastern Pacific, we assessed population densities of *Diadema mexicanum* at the island of Taboguilla, in the Bay of Panama on 30 September 1983. We compared these data to population density values determined in the same area between 6 October and 4 November 1982, before coral mortality had occurred in the eastern Pacific. Corals at Taboguilla and the surrounding islands had suffered extensive bleaching and mortality in June 1983 (Glynn 1984; Lessios, personal observations). *Diadema* densities at Taboguilla were determined in 2 m wide transects extending from the intertidal zone to the deepest end of the rocky substrate.

### Results

Mass mortality of *D. antillarum* was first noted at Punta Galeta in mid-January 1983 (J. Burgett, personal communication) and at the San Blas islands in early April (J. Crisp, personal communication). It is possible that it started earlier than these dates in each locality and that it went unnoticed until moribund *Diadema*, spines, and tests were abundantly evident. The first symptom of the presumed disease was accumulation of sediment on the spines and sloughing off of the spine ectoderm. This was followed by loss of pigment by the skin covering the spine muscles, the peristome, and the anal cone. Spines became brittle, and some broke, while others fell off completely, exposing areoles and tubercles. Tube feet became flaccid, no longer retracted fully, and were apparently unable to cling to the substrate; many individuals at this stage were found on their sides or being moved to and fro by the surge. In advanced stages large patches of skin fell off the test, the peristome and the anal cone lost practically all pigmentation, and the muscles at the base of the spines became so soft that spines could be pulled off their tubercles with little force. Sick *Diadema* abandoned their day-time cryptic habits. They were attacked by fishes that do not normally prey upon healthy individuals. We observed the wrasses, *Thalassoma bifasciatum* and *Halichoeres bivittatus*, the parrotfish *Sparisoma aurofrenatum*, and the damselfishes *Microspathodon chrysurus*,

*Stegastes planifrons*, *S. dorsopunicans*, and *S. leucostictus* attacking moribund *D. antillarum*, and feeding on external and internal tissues. In June 1983 we observed in the San Blas apparent survivors in the process of recovering as evidenced by regenerating distal ends of spines and healing skin lesions on the test surface.

### Punta Galeta

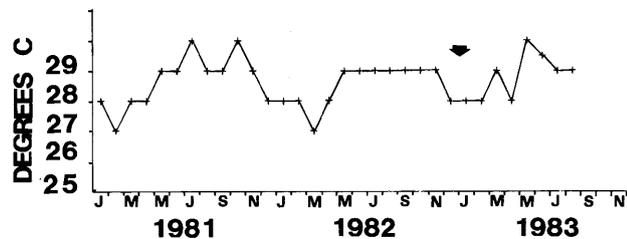
*D. antillarum* densities, measured in 200 quadrats on the edge of the reef flat at the eastern end of the lagoon on 3 June 1982, averaged 1.38 individuals per m<sup>2</sup> (range 0 to 5 individuals per m<sup>2</sup>). If this is extrapolated to the 2.9 ha of similar habitat at the study site, approximately 40,000 *Diadema* (not counting those on the reef flat) were present at this time. On 4 May 1983 only six individuals were found in the entire 12 ha site (lagoon, edge, channels, and reef flat), five of them within one 4 m<sup>2</sup> area on the reef flat. On 24 and 25 February 1984, about 13 months after the *Diadema* mortality, a total of 458 *Diadema* were counted in a similar search of the 12 ha study site.

The permanent transects on the reef flat indicate that mass mortality did not occur in species other than *Diadema* (Table 1). *Diadema* was absent from these shallow areas both before and after the mass mortality event. Population densities of *Echinometra lucunter*, *E. viridis*, and *Eucidaris tribuloides* increased in March, April and May, a normal phenomenon for this time of year (Hendler 1977a; Cubit et al., in preparation). Populations of *L. variegatus* declined after January, probably as a result of exposure to physical stress and predation by shore birds during low tides that began in mid-January and continued to occur in the following months. Unlike *Echinometra* and *Eucidaris*, *Lytechinus* does not hide under rocks. It is, therefore, more susceptible to desiccation and to predation by birds.

Mortality of echinoids (including *Diadema*) has been observed at Galeta in previous years during extreme low tides coincident with either daytime absence of cloud cover or heavy rains (Hendler 1977b; Cubit, personal observations). Such mortality has been limited to animals inhabiting the intertidal reef flat. Unlike these past mortality events, the mass mortality of *Diadema* cannot be linked with fluctuations in temperature, tidal level or rainfall. *Diadema* mass mortality was first observed in Galeta in mid-January 1983; however, because of rough and turbid conditions, observations on the reef flat had not been made since mid-November 1982; we, therefore, have to assume that it could have begun as early as this date. Sea surface temperatures between November 1982 and January 1983 were normal for this time of the year (Fig. 2). In records from 1972 to 1983, the average rainfall for November at Galeta has been approximately 45 cm (range 17–98 cm) and for December 35 cm (range 6–87 cm). Rainfall during these months in 1982 was lower than average, and salinities remained normal (Table 2). From mid-November to mid-January minimum daytime tidal levels remained higher than the reef crest (Cubit et

**Table 1.** Sea urchin populations on the reef flat at Punta Galeta before and after the mass mortality of *Diadema antillarum* in January 1983 (\* = no data)

Transect	Species	Month of census							
		1982			1983				
		October	November	December	January	February	March	April	May
Number of sea urchins per 20 m <sup>2</sup> transect									
Reef edge	<i>Echinometra lucunter</i>	56	85	*	193	201	517	574	707
	<i>Echinometra viridis</i>	0	3	*	3	4	15	6	1
	<i>Echinoneus cyclostomus</i>	0	3	*	4	8	9	0	4
	<i>Eucidaris tribuloides</i>	3	2	*	5	5	5	8	9
	<i>Lytechinus variegatus</i>	0	3	*	3	4	15	6	1
	<i>Tripneustes ventricosus</i>	0	1	*	2	0	2	0	0
Central reef	<i>Echinometra lucunter</i>	4	6	*	10	17	17	25	34
	<i>Echinometra viridis</i>	0	1	*	1	1	5	8	22
	<i>Lytechinus variegatus</i>	1	21	*	11	9	0	0	1
Thalassia bed	<i>Echinometra lucunter</i>	39	38	*	38	28	28	32	30
	<i>Echinometra viridis</i>	1	3	*	6	6	11	7	13
	<i>Lytechinus variegatus</i>	140	117	*	62	22	35	0	0
	<i>Tripneustes ventricosus</i>	10	6	*	1	5	4	0	1

**Fig. 2.** Monthly mean sea surface temperature on the Caribbean coast of Panama. Arrow indicates the time of *Diadema antillarum* mortality. Data were extracted from National Weather Service Maps, based on buoy, ship and satellite observations

al., unpublished data). Northerly tradewinds, which maintain water flow over the reef, blew consistently each day. Between 8 November 1982 and 15 January 1983, the lowest average daily windspeed recorded for daylight hours was 16 km/h. It is unlikely, therefore, that physical fluctuations could have caused mass mortality of *Diadema* on the intertidal reef flat; it is even less likely that they could have done so in subtidal habitats.

### San Blas Archipelago

Mass mortality probably came to the San Blas on the shore current that flows eastward past Galeta (Lessios et al. 1984). The quadrats we established on various reefs to monitor the progress of the mortality (Figs. 3, 4) show that its front generally continued moving from west to east, though its advance on the local scale was far from uniform. Sick sea urchins were already present at Vieja and House reefs (Fig. 1), on 1 May 1983, when we began monitoring these areas. The peak number of sick *D. antillarum* and the concomitant sharp decrease in population size occurred in the vicinity of Punta San Blas (Fig. 3) before appearing in the Cayos Limones (Fig. 4). However, as the early mortality at Panama Flag reef indicates, some pockets of mortality started in advance of the general front. The time period between first appearance of symptoms in a population and the disappearance of all sick animals was variable and ranged from 7 days (Open Coconut, Chichime) to over a month and a half (House Reef). There is no correlation between pre-mortality population density and duration of the epidemic in each reef

**Table 2.** Rainfall and salinity at Punta Galeta during the period of sea urchin censuses

	October 1982	November	December	January 1983	February	March	April	May
Rain (cm)								
Monthly total	39.3	16.8	1.6	3.5	0.5	0.3	17.2	17.5
Daily average	1.6	0.6	0.06	0.1	0.02	0.01	0.7	0.9
max.	3.8	1.2	0.1	0.9	0.1	0.1	2.7	3.8
min.	0	0	0	0	0	0	0	0
Salinity (ppt)								
Daily average	32.4	32.1	33.6	33.2	34.9	35.2	34.8	33.8
max.	35	33	34	35	35.5	36	36	34.5
min.	26	31	32	32	34	35	31.5	33

(Spearman rank correlation coefficient = 0.063,  $N = 8$ ,  $P > 0.5$ ).

The one consistent feature between all quadrats is the drastic decline in numbers of individuals. Population densities were reduced by 94.2% on the average (range 88.1% to 100%). In two additional 36 m<sup>2</sup> quadrats at Aguardargana, where we monitored numbers of *D. antillarum* (but not percentage of sick animals) the number of individuals went from 260 to 0 between 1 May and 23 May. On Deep 27, a patch reef measuring approximately 20 m by 53 m, we counted 759 dead *Diadema* tests on 2 May 1983 and only 4 healthy and 5 sick individuals on the entire reef. Four days later no live *Diadema* could be found. On 13 August 1983 we censused this reef once again; 19 adult and 5 juvenile (< 1.5 cm in diameter) *D. antillarum* were observed. This population appears to have received no recruitment since then; on 24 February 1984, in a similar census we found 18 adults, and no juveniles. The pattern observed in Deep 27 of complete disappearance of adult *Diadema* immediately after the mortality event, and subsequent reappearance of a few survivors, probably hidden deep in the reef crevices, was noted on many other reefs.

A drastic decline in *D. antillarum* population densities is also evident in our pre- and post-mortality transects in nine reefs around Punta San Blas (Table 3). Densities on these reefs were reduced by an average of 98.9% (range 94.6% to 100%). Since two years elapsed between some pre- and post-mortality density determinations, part of the observed population decline may have been due to causes unrelated to the mass mortality. However, the general agreement between decreases in abundance as measured in transects and quadrats, and comparisons to our observations of "normal" population fluctuations (see below) leave little doubt that the bulk of this decrease was in fact due to the presumed epidemic.

Population densities determined in quadrats or transects can vary due to movement of the animals, "normal" mortality, or recruitment. It is, therefore, useful to compare the population decline ascribed to mass mortality with fluctuations resulting from usual causes. Our 1978–1980 permanent quadrats at Nalunega, Tiantupu, Korbiski, and Makerel reefs (Figs. 5, 6) show that previous fluctuations in density were much smaller than what we observed in May and June 1983. The largest population density reduction ever observed in these quadrats was 59.8% between October 1978 and January 1979 at Korbiski. The largest decline between two adjacent months was 45.7% between July and August 1978 at Tiantupu (Fig. 5). In all cases population densities declined temporarily (probably due to movement of the animals) and soon increased, while in the quadrats we monitored after the die-offs little recovery was evident from June to October 1983 (Fig. 3). In December 1983 we once again counted *D. antillarum* in the same quadrats at Nalunega, Tiantupu, and Korbiski. Nalunega quadrats had a mean density of 1.2 individuals per m<sup>2</sup>, a 90% reduction from the November 1979 value, Tiantupu 0.21 individuals per

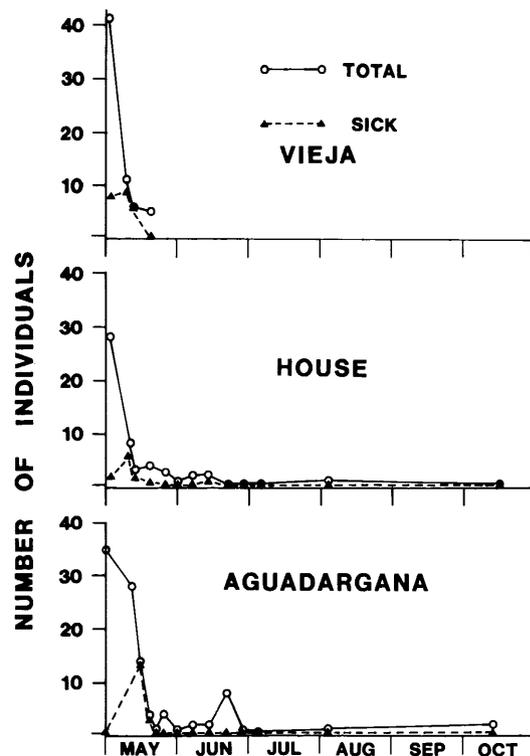


Fig. 3. *Diadema antillarum*. Total numbers of healthy and sick animals over time in three 1 m<sup>2</sup> quadrats per reef in the Punta San Blas area. Data taken in 1983. See Fig. 1 for locations

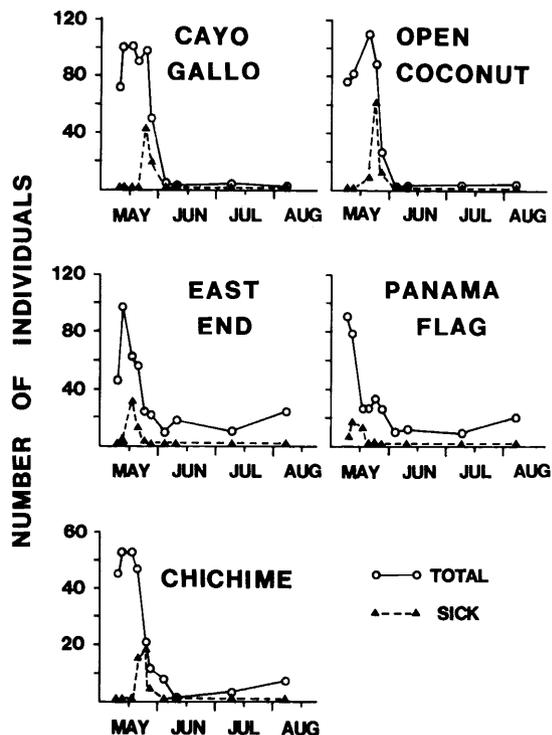
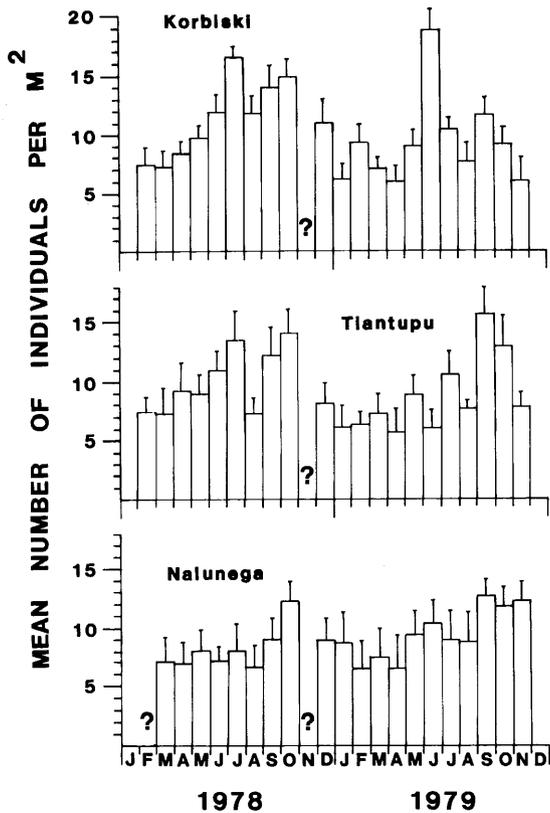


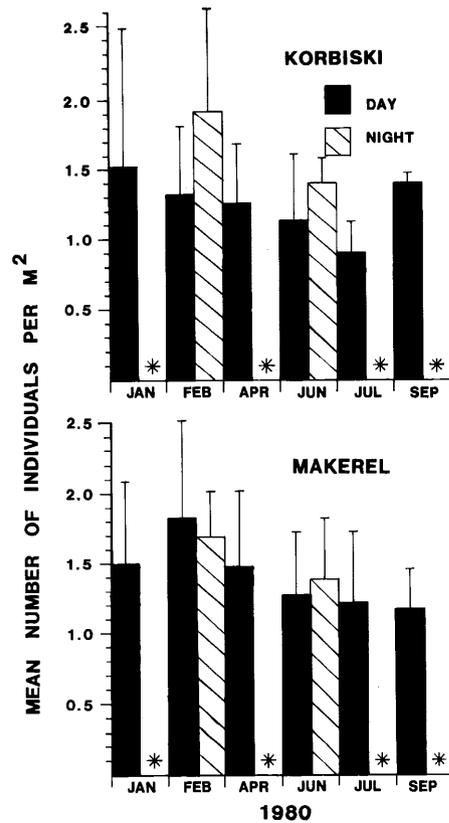
Fig. 4. *D. antillarum*. Numbers of healthy and sick animals over time in a 25 m<sup>2</sup> quadrat on each reef at Cayos Limones. Data taken in 1983. See Fig. 1 for locations

**Table 3.** *Diadema antillarum*. Population densities determined in transects before and after mass mortality in the San Blas. Probabilities for comparisons between pre- and post-mortality densities refer to Mann-Whitney U tests in which density in each transect was considered as a datum point. See Fig. 1 for reef locations

Reef	Before <i>D. antillarum</i> mortality					After <i>D. antillarum</i> mortality					P
	Date	Number of transects	Area covered (m <sup>2</sup> )	Mean density (N/m <sup>2</sup> )	Standard deviation (N/m <sup>2</sup> )	Date	Number of transects	Area covered (m <sup>2</sup> )	Mean density (N/m <sup>2</sup> )	Standard deviation (N/m <sup>2</sup> )	
Aguadargana	May 21–24, 1982	5	282	1.30	0.60	July 6–18, 1983	9	472	0.07	0.08	<0.001
Mamitupu	April 2, 1982	5	302	0.88	0.40	July 4–23, 1983	10	471	0.01	0.01	<0.001
Makerel West	April 5, 1982	5	259	0.53	0.10	July 20, 1983	10	208	0.00	0.00	<0.001
Makerel Est	April 1, 1982	5	229	0.49	0.22	July 20, 1983	10	133	0.00	0.00	<0.001
Mosquito	April 4, 1982	5	235	0.81	0.42	July 24, 1983	10	358	0.00	0.00	<0.001
House Reef	September 20, 1982	9	94	10.98	3.31	July 24, 1983	10	108	0.43	0.39	<0.001
Korbiski East	May 23, 1982	5	177	1.06	0.34	July 21, 1983	10	653	0.00	0.00	<0.001
Korbiski West	December 6, 1980	5	65	1.64	0.55	July 23, 1983	10	187	<0.01	0.01	<0.001
Pinacles	December 8, 1980	5	282	0.49	0.18	July 22, 1983	10	189	0.01	0.03	<0.001
Tiantupu	December 6, 1980	5	76	2.80	0.84	July 17, 1983	10	213	0.00	0.00	<0.001
Ulaksukan	November 11–13, 1982	10	366	0.05	0.03	July 9–17, 1983	10	29	0.00	0.00	<0.002



**Fig. 5.** *D. antillarum*. Mean and one standard error of population densities over time in Nalunega (12 quadrats, 1 m<sup>2</sup> each), Tiantupu (14 quadrats, 1 m<sup>2</sup> each), and Korbiski (36 quadrats, 1 m<sup>2</sup> each) before mass mortality. Density was determined once a month. Question marks indicate months in which no data were taken. See Fig. 1 for location



**Fig. 6.** *D. antillarum*. Mean and one standard error of population densities over time in Korbiski (3 quadrats 25 m<sup>2</sup> each) and Makerel (11 quadrats, 25 m<sup>2</sup> each). Filled bars represent data collected during the day, shaded bars represent data collected during the night. Asterisks indicate months in which night censuses were not made. See Fig. 1 for locations

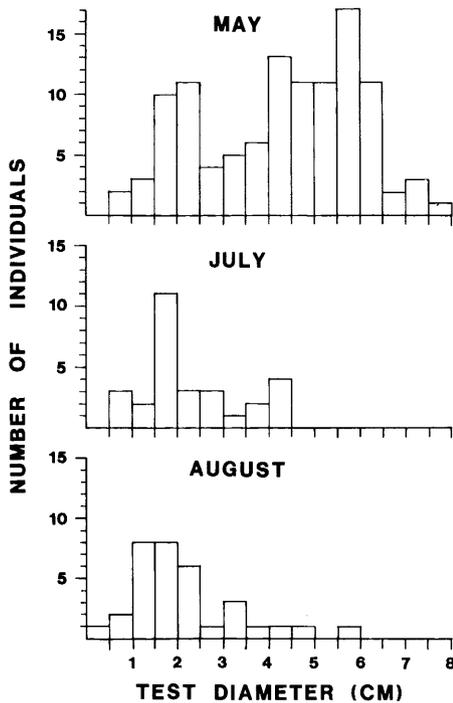


Fig. 7. *D. antillarum*. Numbers over time in each 0.5 cm interval of test diameter in Open Coconut, East End, Panama Flag, and Chichime (four localities combined). See Fig. 1 for locations

m<sup>2</sup>, a 96.9% reduction, and Korbiski 0.08 individuals per m<sup>2</sup>, a 98.6% reduction.

A comparison of sizes of *D. antillarum* found in four quadrats in the Limones before and after the mortality (Fig. 7) shows that population size structure had also been affected. The size distribution in July is significantly different from the size distribution in May (Kolmogorov Smirnov test,  $D=0.509$ ,  $P<0.001$ ). Mean size was reduced from 48.6 mm in May to 25.0 mm in July and

25.3 mm in August. This shift to a smaller mean size could be due to differential survivorship or to recruitment following mass mortality. As Fig. 7 indicates, a few adults were also present after the mass mortality. Unlike the juveniles, which were normal in appearance, the surviving adults exhibited regenerating spines and healing lesions, indicating that they had been affected by the causative agent of the mortality.

Table 4 presents comparisons between population densities of echinoids other than *Diadema* before and after the demise of the latter in the San Blas. Population densities of *Lytechinus variegatus*, *L. williamsi*, *Triploneustes ventricosus*, *Clypeaster rosaceus*, *Echinometra viridis*, *E. lucunter*, and *Eucidaris tribuloides* either did not decrease significantly or increased. It is clear that the cause of mortality which devastated populations of *D. antillarum* did not cause die-offs in other echinoids. Significant population density increases were observed in *Lytechinus variegatus* in the *Thalassia* bed, and in *Echinometra viridis* and *E. lucunter* on the reef flat. We can only speculate as to whether these increases were due to the reduction of *D. antillarum* populations.

#### Bay of Panama

Transects at Isla Taboguilla, on the Pacific coast of Panama, indicate that *Diadema mexicanum*, though closely related to *D. antillarum* (Lessios 1981), suffered no unusually mortality. Mean population density in October 1982 determined in 9 transects, covering an area of 260 m<sup>2</sup>, was 1.04 *D. mexicanum* per m<sup>2</sup>. Mean density in September 1983, determined in 8 transects, covering an area of 366 m<sup>2</sup>, was 0.98 per m<sup>2</sup>. The non-significant (Mann-Whitney U test,  $P>0.1$ ) decrease in *Diadema mexicanum* density at Taboguilla was probably due to our having collected 700 individuals in this area for another

Table 4. *Lytechinus variegatus*, *L. williamsi*, *Echinometra lucunter*, *E. viridis*, *Eucidaris tribuloides*, and *Clypeaster rosaceus*. Population densities in three habitats at House Reef before (July 1982) and after (August 1983) *Diadema antillarum* mass mortality. Probabilities for comparisons between pre- and post-mortality densities refer to Mann-Whitney U test in which density in each transect is considered as a datum point

Species	Before <i>D. antillarum</i> mortality				After <i>D. antillarum</i> mortality				P
	Number of transects	Area covered (m <sup>2</sup> )	Mean density (N/m <sup>2</sup> )	Standard deviation (N/m <sup>2</sup> )	Number of transects	Area covered (m <sup>2</sup> )	Mean density (N/m <sup>2</sup> )	Standard deviation (N/m <sup>2</sup> )	
<i>Thalassia</i> bed.:									
<i>L. variegatus</i>	9	483	0.12	0.07	10	546	0.83	0.52	<0.001
<i>T. ventricosus</i>	9	483	0.12	0.04	10	546	0.16	0.06	>0.05
<i>C. rosaceus</i>	9	483	0.02	0.02	10	546	0.03	0.02	>0.05
Reef flat:									
<i>L. variegatus</i>	9	293	0.01	0.08	10	204	0.33	0.57	>0.05
<i>C. rosaceus</i>	9	293	0.08	0.08	10	204	0.12	0.14	>0.05
<i>E. viridis</i>	9	293	0.58	0.26	10	204	6.22	5.24	<0.002
<i>E. tribuloides</i>	9	293	0.13	0.08	10	204	0.37	0.36	>0.05
<i>E. lucunter</i>	9	293	0.39	0.19	10	204	1.24	1.03	<0.001
Reef slope:									
<i>E. viridis</i>	9	93	48.77	18.16	5	35	47.99	14.91	>0.05
<i>L. williamsi</i>	9	93	5.66	2.35	5	35	10.79	3.67	>0.05

study (Lessios 1984) in the time period between the two density determinations.

### Discussion

Populations of *D. antillarum* in the San Blas Islands were reduced by more than 90%. The reduction at Punta Galeta was so severe, that if we had limited our first post-mortality census to the lagoon edge, where the pre-mortality data were obtained, we would have concluded that *D. antillarum* were extinct in the area. That we are dealing with unusual mass mortality, rather than normal population fluctuations, cannot be doubted by anyone who saw the accumulation of tests and moribund animals while the mortality was in progress. Our comparison of population reduction in May and June 1983 relative to population fluctuations in previous years at the San Blas support this impression. Between 4 and 9 June 1983 we visited reefs in the area between Punta San Blas and the Panama-Colombia border. On each reef we found spines, tests or moribund animals. We found similar situations at the Florida Keys, USA, between 29 and 31 August 1983, and at Saint Thomas, U.S. Virgin Islands, between 12 and 14 January 1984. Bak et al. (1984) and Hughes et al. (in press) describe the same symptoms and a similar decrease of *D. antillarum* population density in Curaçao and Jamaica, respectively. Personal communications with many scientists indicate that *Diadema* mortality spread to the entire Caribbean between January 1983 and January 1984 (Lessios et al. 1984). Descriptions of the symptoms were the same in all cases suggesting that mortality in all places was due to the same cause.

The mass mortality, in addition to reducing the numbers of *D. antillarum*, also changed the size structure of its populations. We cannot say whether the observed decrease in mean size at Cayos Limones was due to post-mortality recruitment, differential survivorship of juveniles or emergence of the juveniles from crevices where they might have been hiding when the adults were abundant. All three factors may have been operating.

The reappearance of recovering adults a month or so after the mortality event was noted on many reefs. It was also evident in Jamaica after mass mortality there (J. Woodley, personal communication). This pattern may be due to the same causes as the abandonment of day-time cryptic habits by affected *Diadema*, namely inability of gravely sick animals to move. Debilitated individuals which happened to be outside crevices must have succumbed to both the effects of the mortality agent and to fish predation, while those hidden in crevices had a slightly better probability of survival if fishes could not reach them. With their spines broken and their tube-feet flaccid, they may have been unable to emerge from hiding until a month later, when they had recovered.

Increases in population densities of some other echinoid species both at Galeta and at San Blas occurred roughly at the same time as mass mortality of *D. antillarum*. It is tempting to postulate that a causal relation-

ship underlies this correlation, but the accumulation of ten years of data on echinoid densities on the Galeta reef flat shows that other factors, such as the seasonal variation in sea level, might be operating. In the San Blas a significant increase was seen in *Lytechinus variegatus* populations in the *Thalassia* bed surrounding House reef, and in *Echinometra lucunter* populations on the reef flat. It is doubtful that these increases are associated with the disappearance of *Diadema*. In the short time between *D. antillarum* mass mortality and our post-mortality density determinations, only changes in distribution could bring about localized changes in population density. Given that the reef flat is the only habitat in which *E. lucunter* is found on House Reef and that *L. variegatus* populations also increased in other habitats, it is hard to see how migration could bring about the observed changes in local abundance of these species. The ten-fold increase of *Echinometra viridis* on the reef flat, however, may well be a consequence of the *Diadema* demise. Williams (1981) has found that removal of *D. antillarum* from coral patches results in immigration of *E. viridis*. Before the mortality *Diadema* was concentrated on the reef flat; the reduction of its density in this habitat may have caused *E. viridis* to move up from the reef slope. It is possible that, because the density of *E. viridis* on the slope is so high, and because the reef slope comprises a larger area than the flat, emigration from the slope resulted only in the non-significant decrease noted.

The wide geographical spread of *D. antillarum* mortality (Lessios et al. 1984) rules out the possibility that it was caused by a pollutant; it is hard to imagine a substance so toxic that it could spread from Panama to Bermuda retaining its lethal effects, yet so specific that no echinoid species except *D. antillarum* was affected. A mass of water with unusual temperature or salinity characteristics might be invoked in view of coral bleaching in the San Blas two months after mass mortality of *Diadema* (Lessios et al. 1983; Glynn 1984). However, the data from Punta Galeta do not show any abnormal fluctuations in physical parameters at the time that *Diadema* was dying. Furthermore, though mass mortality of *Diadema* was severe at Galeta in January 1983, bleaching of cnidarians in this area was confined to a few colonies of *Palythoa caribaeorum* and *Agaricia agaricites* in June 1983 (personal observations). Severe coral mortality occurred in the eastern Pacific and was correlated with elevated water temperatures (Glynn 1983; Glynn 1984). *Diadema mexicanum*, however, though closely related to *D. antillarum* (Lessios 1981), did not suffer any ill effects. The most probable causative agent, which could account for the observed patterns of *D. antillarum* mass mortality, is a host-specific, water-borne pathogen. Such a hypothesis would explain why mortality on the whole seemed to travel with major Caribbean currents over large distances (Lessios et al. 1984), why other species of echinoids were not affected, and why, despite its wide geographical extent, the mortality did not decrease in severity (c.f. Bak et al. 1984; Hughes et al., in press). We are unable to pro-

vide an explanation for why the disease should break out at the particular time that it did. The pathogen responsible for mass mortality of *Strongylocentrotus droebachiensis* at Nova Scotia begins to kill sea urchins when temperatures are at their annual peak (Scheibling and Stephenson 1984). No such temperature dependence is evident in the outbreak of *Diadema* disease. That the epidemic seems to have started next to the mouth of the Panama Canal, where many ships discharge ballast water (Chesher 1968), suggests an accidental introduction of an exotic pathogen, possibly one which coexists without harm to its usual host, but is lethal for *D. antillarum*. The source of this postulated pathogen is unclear, but it is doubtful that it could have originated in the tropical eastern Pacific. We have maintained *D. antillarum* in sea tables on the Pacific coast of Panama since 1976. Though we always sterilize the outflow of these sea tables, we have never sterilized their inflow; yet we never observed animals dying with the characteristic symptoms of the 1983 epidemic. Further speculation on the origin on the pathogen will only be possible after it is identified.

Even though ecologists are becoming aware that disease may play an important role in determining the structure of communities (Sinderman 1970; Kinne 1980; Anderson 1982; Anderson and May 1982; May 1983), the effects of pathogens upon the populations of their host and upon the host's prey, competitors and predators have rarely been documented in marine organisms. Epidemics in sea urchins (Johnson 1971; Pearse et al. 1977; Miller and Colodey 1983; Scheibling and Stephenson 1984), sponges (Smith 1941), starfish (Dungan et al. 1982), fish (Sinderman 1970), and eelgrass (Rasmussen 1977) have been reported in the past. The only documentation of community effects of such an epidemic is by Pearse and Hines (1979); they found that a localized die-off of the sea urchin *Strongylocentrotus franciscanus* in California had important repercussions for the species composition and spatial extent of the kelp forest. Scheibling (in press) has postulated that benthic communities in Nova Scotia may oscillate between two alternate states depending on whether *Strongylocentrotus droebachiensis* is being devastated by disease.

It is too early to tell what effects the diminution of *D. antillarum* population densities will have on coral reef communities; the accumulated evidence for the importance of this species suggests that a number of changes may be observed in the coming years. *D. antillarum* populations have been reduced in a major portion of the species range, so that the pool of larvae available for recolonization has also been diminished. Though *D. antillarum* populations at Punta Galeta increased by at least one order of magnitude in one year, this area could have received an influx of larvae from upstream areas that were still inhabited by large numbers of *Diadema*. It is, therefore, probable that recovery of *Diadema* populations will be slow, and that its absence will be reflected in the distribution and abundance of algae (Carpenter 1981; Sammarco 1982a, b), corals (Sammarco 1980, 1982a),

damsel fish (Williams 1979, 1980, 1981; Sammarco and Williams 1982) and other sea urchins (Williams 1981). The increase of *Echinometra viridis* on the flat of House reef, possibly a result of the reduction of *Diadema* densities, may be a short-term effect of the epidemic. This change in distribution may be followed by a change in overall abundance of this and other echinoid species. Whether algal community patterns will change substantially will depend on the importance of *Diadema* as a grazer relative to other herbivores, and on the ability of other herbivores to compensate through numeric and functional responses. In the lagoon at Punta Galeta lush beds of algae, seagrasses and sabellid polychaetes developed in areas that had been nearly barren when *Diadema* had been abundant there. In the San Blas many areas of *Porites* rubble, previously covered only by coralline algae, now support thick mats of *Dictyota* and filamentous algae. The effects of the reduction of *Diadema* populations on the predators and symbionts of *Diadema* will depend on the extent of their specialization upon this species. *D. antillarum* constitutes an important part of the diet of many fishes (Randall 1967; Hoffman and Robertson 1983). The sudden decline in the availability of *Diadema* probably increased the predation pressure on the few individuals that survived the disease, and on other species of prey. Similar effects have been noted in plant-herbivore communities when the availability of plant forage was reduced (Cubit, in press). A number of symbionts also take refuge beneath *Diadema* or among its spines (Colin 1978). Hughes et al. (in press) noticed heavy infestations of *Diadema* survivors by a palaemonid shrimp that presumably fled from dying sea urchins. We did not see a similar phenomenon in Panama, possibly because these commensals have always been less abundant here than in Jamaica (personal observations). Depending on how long *Diadema* populations take to recover, the presumed disease may also have some long-term effects, such as alteration of the relative frequency of coral species through changing patterns of spat survival (Sammarco 1980, 1982a) and accelerated net rates of calcium carbonate accumulation on reefs (Stearn and Scoffin 1977; Scoffin et al. 1980; Bak et al. 1984). Thus, the *D. antillarum* mass mortality, apart from providing an opportunity to study the dynamics of an epizootic affecting a marine species, may also allow ecologists to evaluate the impact of this species on Caribbean coral reef communities.

*Acknowledgements.* We thank M. A. Coffroth, G. Irvine, K. S. Neva, J. Morin, D. Parker, V. Richey and R. Thompson for help in the field. Observations in Florida were made possible thanks to the help of C. Curtis, R. Causey and J. Halas; R. H. Boulon, Jr. similarly helped in St. Thomas, T. P. Hughes and R. Scheibling commented on the manuscript. J. Wartha-Clark of the U.S. National Weather Service kindly provided sea surface temperature maps. The Kuna Nation and the Government of Panama permitted work in the San Blas. Supported by General Research Funds from the Smithsonian Tropical Research Institute and grants from the Smithsonian Scholarly Studies Program, the Walcott Fund, and the Smithsonian Environmental Sciences Program.

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