Diadema antillarum 10 years after mass mortality: still rare, despite help from a competitor

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SUMMARY

The black sea urchin *Diadema antillarum* was until 1983 an important component of Caribbean coral reef communities, affecting the distribution and abundance of all major guilds of sedentary organisms. Between 1983 and 1984 this species suffered the most extensive and severe mass mortality ever recorded for a marine animal. Continuous monitoring in Panama shows that in the subsequent 10 years *D. antillarum* densities remained at < 3.5 % of their pre-mortality levels. Despite pre-1983 evidence that *D. antillarum* competed with other echinoids, there has been no competitive release by other sea urchin species. Reef-wide inclusions and exclusions of echinoids indicate that: (i) the low rate of *Diadema* recruitment does not result from absence of settlement cues for the larvae or from lack of protection by conspecific adults but from paucity of larvae in the water column; and (ii) *Echinometra viridis* – an echinoid previously shown to compete with adult *Diadema* – actually facilitates the latter's recruitment. The lack of recovery of *D. antillarum* despite its high fecundity, planktonic larvae and the assistance of *E. viridis*, demonstrates that unique disturbance events in the history of a species can have long-lasting effects on its abundance, independently of community-level processes.

1. INTRODUCTION

Unique, large-scale disturbance events have the potential to affect the distribution and abundance of species on local, regional or global scales. However, there is a paucity of evidence regarding their importance because their sudden and unpredictable nature, coupled with their potentially long-lasting consequences, make them difficult to study on the ecological level. Paleontological studies, however, usually lack the necessary resolution to discern changes on the population level. For this reason, it is important that when a large-scale disturbance is observed, it is studied for as long as possible so that the persistence of its effects (and thus its role in structuring ecological communities) can be determined.

An event that perturbed coral reef communities throughout the western tropical Atlantic is the catastrophic death of the black sea urchin *Diadema antillarum* in 1983–1984, the most extensive and most severe mass mortality ever recorded for a marine animal (Bak *et al.* 1984; Lessios *et al.* 1984 *a*, *b*; Hughes *et al.* 1985; Hunte *et al.* 1986; Lessios 1988 *a*). Populations of this important herbivore (Ogden *et al.* 1973; Sammarco 1982; Carpenter 1986), corallivore (Bak & van Eys 1975), competitor (Williams 1981; Hay & Taylor 1985) and bioeroder (Scoffin *et al.* 1980) were reduced everywhere by > 93 % (Lessios 1988 *a*). The cause of mortality was presumed to be an unidentified pathogen (Lessios *et al.* 1984 *a*). The near-extinction of this important member of Caribbean coral reef communities had both immediate (Carpenter 1985, 1988; Liddel & Ohlhorst 1986; de Ruyter van Steveninck & Bak 1986; Morrison 1988) and long-term (Hughes *et al.* 1987; Levitan 1988 *a*; Carpenter 1990; Robertson 1991; Hughes 1994) effects on the distribution and abundance of other species. This report presents the results of continuous monitoring of echinoid populations in Panama over the 10 years following the mass mortality, intended to determine whether *D. antillarum* has recovered, and of reef-wide manipulations of echinoid densities over 8 years, designed to assess factors that affect rate of recruitment and population recovery.

2. MATERIALS AND METHODS

Permanent 25 m² quadrats were established at depths of 1–3 m on six reefs in the San Blas Archipelago in May 1983, before the demise of *Diadema* populations (Lessios *et al.* 1984 *b*; Lessios 1988 *b*). Five quadrats were located in the Cayos Limones (see Lessios *et al.* (1984 *b*) for map); they were established before the mass mortality reached this area. The sixth quadrat (Vieja) was located close to Punta San Blas; it was established when dead tests were already present on the reef. Size and number of *Diadema* and number of all echinoid species encountered in the quadrats were monitored through the advance of mass mortality and in bimonthly intervals over the next ten years. Size of *D. antillarum* was determined by measuring the horizontal test diameter at the ambitus with vernier calipers. *Diadema* population density was also measured in 11 additional reefs, for which there were pre-mortality data, with transects extending from shallow to deep water and performed once a year. For each reef, ten 1.8 m

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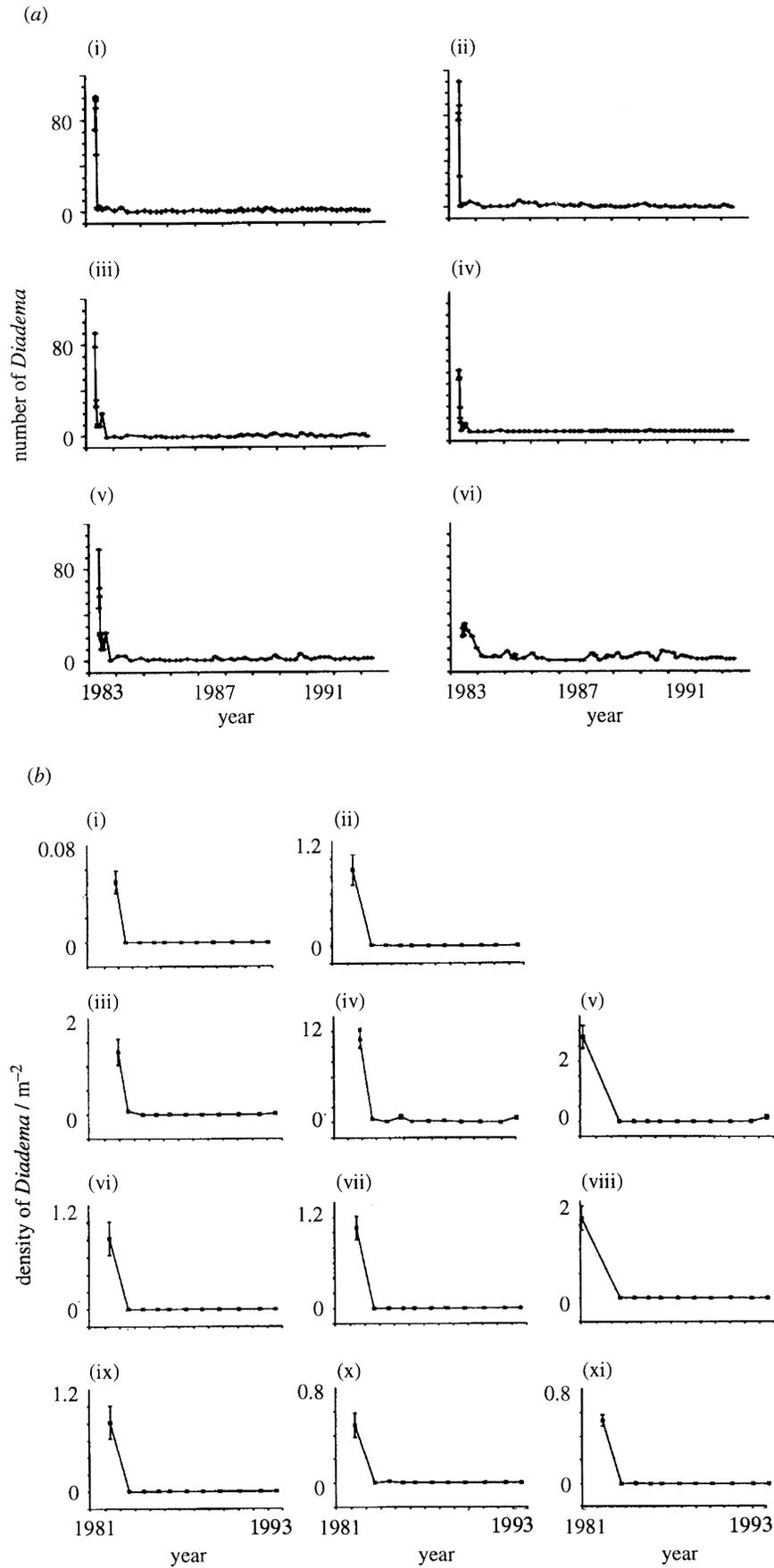
Proc. R. Soc. Lond. B (1995) **259**, 331–337
Printed in Great Britain

331

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Figure 1. For 17 reefs in the San Blas Archipelago, (*a*) number of *Diadema antillarum* in 25 m² permanent quadrats in (i) Cayo Gallo, (ii) Open Coconut, (iii) Panama Flag, (iv) Chichime, (v) East End, and (vi) Vieja, and (*b*) mean density±s.e. in transects in (i) Ulaksukan, (ii) Mamitupu, (iii) Aguadargana, (iv) House Reef, (v) Tiantupu, (vi) Pinnacles, (vii) Korbiski East, (viii) Korbiski West, (ix) Mosquito, (x) Makerel East, and (xi) Makerel West.

wide transects were extended from the shallowest point at which *Diadema* were present before the mass mortality, to a depth of 17 m, or to the base of the reef if shallower, and *D. antillarum* located in each transect were counted.

A large-scale field experiment was established to answer two questions regarding the factors which might affect rate of *Diadema* recovery: (i) is settlement by *Diadema* larvae hindered by the absence of adults?; and (ii) does competition by *Echinometra viridis* and other echinoids affect recruitment of *D. antillarum*? Four reef-wide treatments were set up on patch reefs located at depths of 4–6 m at the San Blas Archipelago in September 1983. In one reef, named Omyra and measuring 408 m², all echinoids were removed. In another reef, named Greek and measuring 128 m², *E. viridis* was removed, but Diadema was added from surrounding reefs to produce a density of approximately one individual per m². This value is close to the average density on all reefs that were censused in the San Blas before the mass mortality had reached them (Lessios *et al.* 1984*b*). A third, larger reef was divided in two by a hardware cloth fence. All surviving *Diadema* were removed from one part of the reef (D26N, measuring 440 m²), but other echinoids (primarily *E. viridis*) were permitted to stay. The natural complement of echinoids was present in the other part (D26S, measuring 1800 m²), and *Diadema* densities were augmented to a density of one per m². Thus, the four treatments consisted of: (i) no echinoids; (ii) *Diadema* present but *Echinometra* absent; (iii) *Echinometra* present but *Diadema* absent; and (iv) all echinoids present. The sea urchin species *Eucidaris tribuloides*, *Lytechinus williamsi* and *Tripneustes ventricosus* were manipulated along with *E. viridis*, but their density was very low at all times.

Recruitment of *D. antillarum* at these reefs was monitored until 1992. Five evenly spaced permanent transects, each 1 m wide and 4–18 m long, were established on all but one reef (only four transects in D26N). Number and sizes of echinoids were determined at each transect every 2 weeks from September 1983 to June 1984, every month from July 1984 to August 1986, and at irregular intervals until August 1987. In May 1988 the assignment of treatments was changed between reefs to assess the degree to which the results were affected by uncontrolled inter-reef variability. Sea urchins were moved from one reef to the other, and *Diadema* recruitment was again monitored once a month until July 1992. Densities of echinoids were adjusted intermittently throughout the experiment to maintain each treatment as an inclusion or exclusion of the appropriate species. The density of individuals with horizontal diameter less than 1.5 cm taken in each transect, averaged over the number of times that the transect was monitored during the entire period that each treatment was applied to a reef, was considered as the recruitment rate. Comparisons between treatments of mean rate of recruitment were performed by ANOVA, with recruitment rates of the two reefs that received the same treatment nested within the treatment. Data were log[1000(X+1)] transformed. Fisher's Protected Least Significant difference was used for post-hoc comparisons.

3. RESULTS

Data from the permanent quadrats established before the mass mortality and continuously monitored thereafter indicate clearly that there has been little recruitment and no population recovery (see figure 1*a*). Average number of *D. antillarum* in these quadrats in May 1993 remained at a level 99.96 % lower than peak values in May 1983. Yearly censuses of the additional 11 reefs in the San Blas area confirm the generality of the finding. Average densities in these
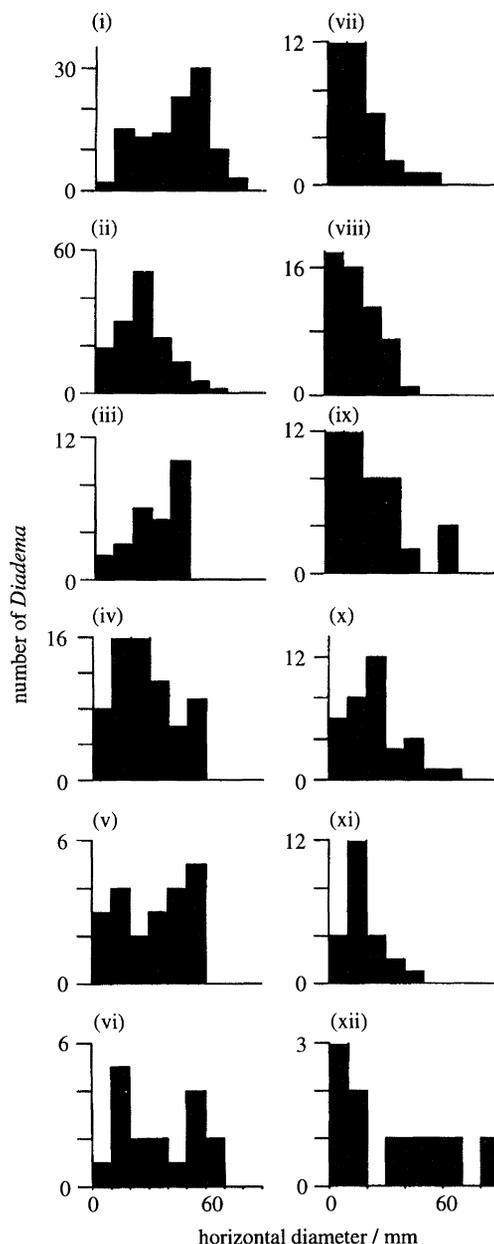

Figure 2. Number of *Diadema antillarum* over time in each size class in the six quadrats depicted in figure 1 for (i) May 1983, (ii) June–December 1993, (iii) 1984, (iv) 1985, (v) 1986 (vi) 1987, (vii) 1988, (viiii) 1989, (ix) 1990, (x) 1991, (xi) 1992, (xii) 1993. May 1993 data represent the pre-mortality size distribution.

transects in July 1993 were 96.57 % lower than pre-mortality ones (see figure 1*b*). Thus *D. antillarum* remains absent not only in its preferred habitat in shallow water, but also in all depths it previously inhabited in 17 reefs that encompass an area of 10⁴ hectares.

Mean horizontal diameter of *D. antillarum* in the six quadrats was 42.2 mm before the mass mortality. Yearly average in the next ten years fluctuated between 17.3 and 35.2 mm (see figure 2). Thus, size as well as numerical abundance of *Diadema* has been reduced, so biomass has remained low. Despite the concomitant reduced grazing pressure by this dominant herbivore, however, other echinoids – all unaffected by mass mortality (Lessios 1988*b*) – showed no clear numerical
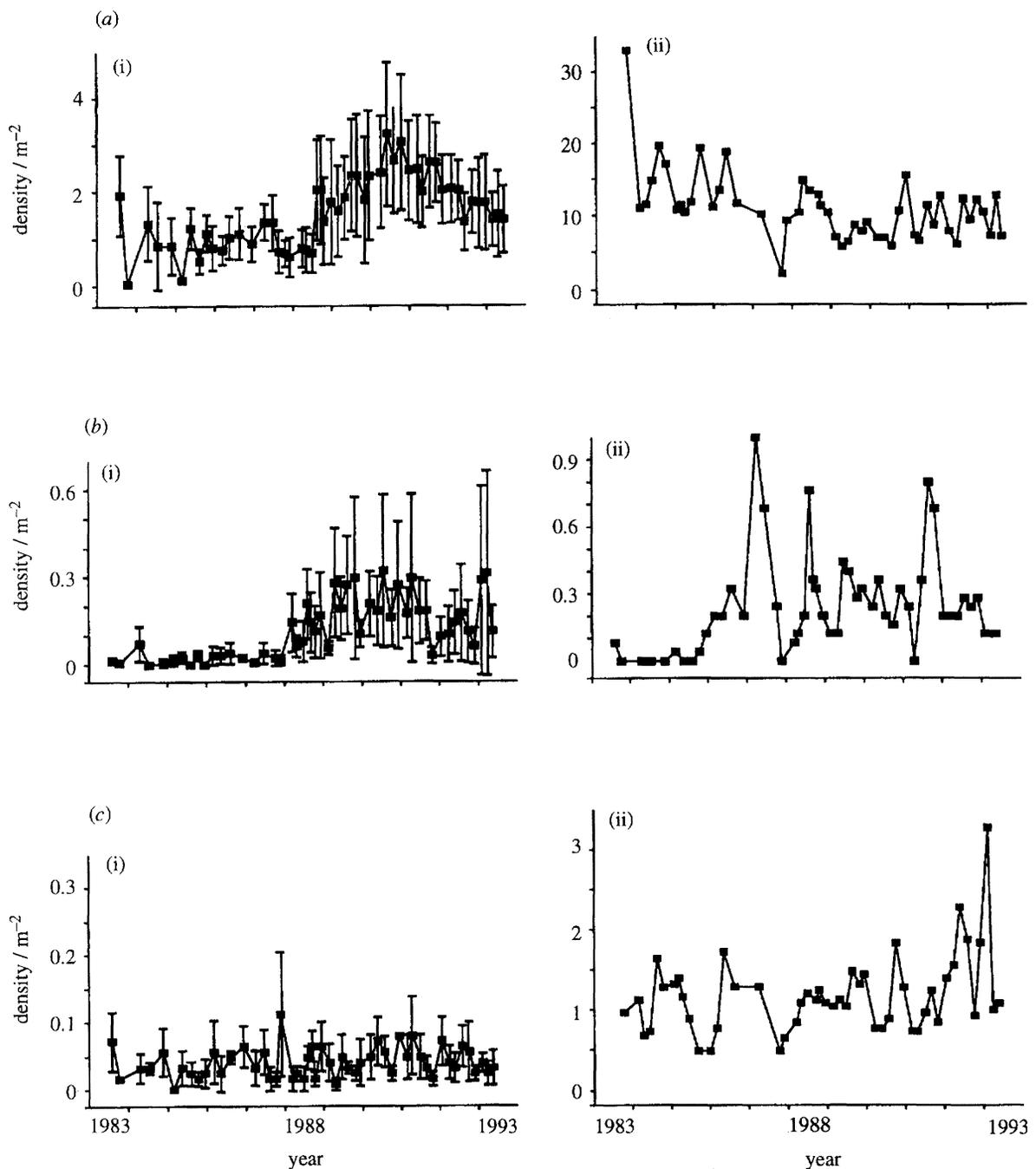
Figure 3. Density of (a) *Echinometra viridis*, (b) *E. lucunter*, and (c) *Eucidaris tribuloides* at the same permanent 25 m² quadrats shown in figure 1, from (i) Cayos, Limones and (ii) Vieja. Other echinoid species (*Tripneustes ventricous*, *Lytechinus williamsi*, *Clypeaster rosaceus*) were only occasionally encountered. Data from the five quadrats in Cayos Limones have been averaged; bars indicate one standard error.

increase (see figure 3). Non-significant (SNK test $p >$ 0.05) elevations in the population densities of two species of *Echinometra* starting in 1988, 5 years after the *Diadema* mass mortality, did not persist.

In the reef-wide exclusion–inclusion experiments designed to assess the importance of the presence of conspecific and heterospecific adults on *Diadema* recruitment, there was wide variation both between reefs and between sampling time-periods. However, the nested ANOVA analysis showed that after this variability in space and time was taken into account, mean recruitment rate was significantly different between treatments ($F = 3.042$, $p = 0.044$). Contrary to what might have been expected from consideration of the

possible effects of conspecific and heterospecific adults, recruitment rates on reefs in which adult *Diadema* had been added or removed were not different from each other, whereas recruitment on reefs in which *E. viridis* was present by itself was significantly higher than on reefs on which it was absent (see figure 4). The multiple comparison test indicated that presence or absence of *Diadema* on reefs containing *Echinometra* caused no statistical differences. Thus the presence of adult *Diadema* in densities encountered in Panama before the mass mortality seems to have had no effect on recruitment by its juveniles. *E. viridis*, however, appears to facilitate either larval settlement or juvenile survival of *D. antillarum*.
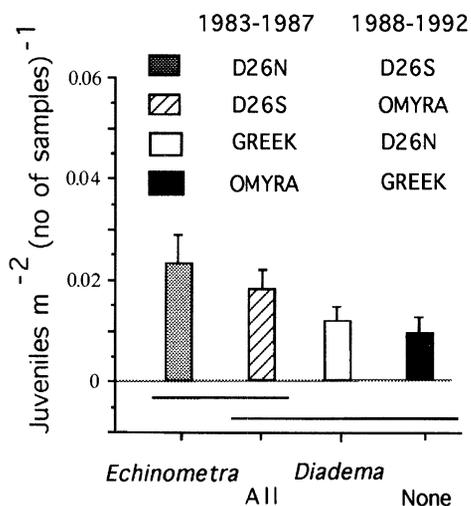
Figure 4. Mean recruitment rate of *Diadema antillarum* (across transects) + s.e. for each treatment of echinoid inclusion or exclusion. Individuals with horizontal test diameters smaller than 1.5 cm were considered as juveniles. Treatments, shown below the X-axis: *Echinometra*: *E. viridis* included (mean adult density: 6.41–8.62 per m²), *D. antillarum* excluded (0.01–0.04 per m²). *All*: *E. viridis* included (mean density: 8.05–8.61 per m²), *D. antillarum* included (0.42–1.94 per m²) *Diadema*: *D. antillarum* included (0.69–1.21 per m²), *E. viridis* excluded (0.16–0.87 per m²). *None*: *D. antillarum* excluded (0.00–0.01 per m²), *E. viridis* excluded (0.31–0.38 per m²). Legend indicates reefs that received each treatment during each sampling period. Lines below the histogram join treatments in which mean recruitment rates are not significantly different from each other.

4. DISCUSSION

The lack of recovery by *Diadema antillarum* is not limited to the coast of Panama. At Jamaica, population densities in 1993 were at one tenth of what they used to be before 1983 (Hughes 1994). However, in contrast to Jamaica (Hughes 1994) and the U.S. Virgin Islands (Levitan 1988 *a*), mean size of individuals present at the San Blas after the catastrophic mortality has not increased, probably because in this area of low fishing pressure herbivorous fish have kept extensive algal blooms from occurring. Levitan (1988 *a*) has pointed out that in the Virgin Islands the decrease in *Diadema* density has been in part compensated by an increase in individual size, caused by higher food availability, so that grazing pressure by this species of sea urchin has been reduced only partially. This is clearly not the case in Panama, because biomass has been reduced even more precipitously than numerical abundance. It is, therefore, unlikely that the continuing paucity of *Diadema* or the lack of competitive release by other species could be explained by resource limitations due to elevated per capita grazing pressure.

Competition between *D. antillarum* and *Echinometra viridis* had been postulated before the mass mortality on the basis of numerical responses by each species to additions and removals of individuals of the other to small coral patches (Williams 1981). The lack of any noticeable competitive release by *E. viridis* after *D. antillarum* mass mortality may mean that populations of the former were never regulated by competition with the latter, or that the void left by the *Diadema* demise

was quickly filled by other herbivores, such as acanthurid fish (Robertson 1991). The former alternative seems more likely because, in Jamaica, where fishing pressure is so high that in the absence of *Diadema* the reefs are being destroyed by algae (Hughes 1994), there was still no numerical increase of *E. viridis*, or of any other echinoid species (Hughes *et al.* 1987; Hughes 1994).

One possible explanation for the low rates of recruitment and population recovery of *Diadema antillarum* might have been that settlement and juvenile survivorship are adversely affected by the absence of adults. It has been demonstrated that adults of some echinoids provide settlement cues to the larvae (Highsmith 1982; Pearce & Scheibling 1990), or protection to the juveniles (Cameron & Schroeter 1980; Tegner & Dayton 1981), phenomena that can cause the interruption of self-reinforcing loops when adult populations are severely reduced (Tegner & Dayton 1977). Another possibility might have been that juveniles are competitively excluded by *Echinometra viridis*. This species is aggressive towards other echinoids and tends to win fights against smaller individuals (Shulman 1990). It could, therefore, exclude *Diadema* recruits from shelter, and thus cause juvenile mortality. The echinoid exclusion and inclusion experiments, however, showed that, contrary to expectations, the presence of potential competitors is more beneficial for *Diadema* recruitment than the presence of conspecific adults. This counterintuitive result may be due to the propensity of *Diadema* larvae to settle in areas cleared of filamentous algae (Bak 1985). Areas with high densities of the small-bodied *Echinometra* may be grazed more heavily than areas with fairly low (in comparison with other areas in the Caribbean (Bauer 1980)) densities of the larger *D. antillarum*. Whatever the mechanism responsible for this pattern might be, the data from the manipulated reefs indicate that future *Diadema* population recovery may be aided by *E. viridis*, a result that could not have been predicted from small-scale, short-term experiments which did not consider recruitment (Williams 1981).

Diadema antillarum populations failed to recover in 10 years despite high fecundity (10^6 eggs per female (Levitan 1988 *b*), produced each month (Lessios 1984), throughout the year (Lessios 1981)), which was unaffected by the mass mortality (Lessios 1988 *b*; Levitan 1988 *b*), despite facilitation of larval settlement by the ubiquitous (Lessios *et al.* 1984 *b*). *E. viridis*, despite lack of elevated competition from other echinoids, and despite the absence (except for isolated, mild events (Lessios 1988 *a, b*)) of the pathogen presumed to have caused the 1983 mass mortality. The lack of any increased recruitment on reefs with simulated pre-mortality densities rules out the possibility that larvae do not settle solely because they are not induced to do so by the presence of adults, or that they settle but die in the absence of protection by adult spine canopies. Why then do population densities remain so low?

The most likely explanation for the continuing rarity of *Diadema* is that populations in Panama and in upstream areas are unable to produce enough larvae to

overcome mortality in the planktonic stage. Inadequate larval production may, in turn, be the result of poor fertilization success arising from low adult densities of free-spawning adults (Levitan 1991). If so, they will remain at low levels until episodic recruitment, resulting from chance convergence of factors favourable for larval survivorship, establishes enough individuals on some reefs to help reseed the rest of the region (Karlson & Levitan 1990). Given the ecological importance of the species, especially in overfished areas (Hay 1984), its continuing absence is likely to have drastic affects on the future of Caribbean coral reefs (Hughes 1994).

Diadema antillarum is the first marine species affected by mass mortality to have been monitored continuously for 10 years. The data, both from Panama and Jamaica (Hughes 1989, 1994), indicate that a one-time historical event can not only reduce the density of a previously abundant species through a whole region, but also maintain it at constant low levels for a long time, even when the affected species is characterized by high fecundity and planktonic larvae – traits thought to confer resilience to catastrophic mortality and extinction (Jackson 1974; Vermeij 1987) – and even when community-level processes are conducive towards recovery. Because we lack historical information on the composition of most communities (Hubbell & Foster 1986; Hughes 1989), we cannot be sure that rare species may not be rare, not because of any continuous process, such as competition or predation, but because of some similar catastrophe in their past. Indeed, ecologists have only recently begun to consider the role of historical events on species diversity (Ricklefs 1987; Hughes 1989; Dayton *et al.* 1992; Ricklefs & Schluter 1993). The only way to evaluate the potential importance of such events is through long-term studies of their consequences, so that their persistence can be assessed.

REFERENCES

Bak, R. P. M. 1985 Recruitment patterns and mass mortalities in the sea urchin *Diadema antillarum*. *Proc. 5th Int. Coral Reef Congr.* **5**, 267–272.

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

Bak, R. P. M., Carpay, M. J. E. & de Ruyter van Steveninck, E. D. 1984 Densities of the sea urchin *Diadema antillarum* before and after mass mortalities on the coral reefs of Curaçao. *Mar. Ecol. Prog. Ser.* **17**, 105–108.

Bauer, J. C. 1980 Observations on geographical variations in population density of the echinoid *Diadema antillarum* within the Western North Atlantic. *Bull. mar. Sci.* **30**, 509–515.

Cameron, R. A. & Schroeter, S. C. 1980 Sea urchin recruitment: effect of substrate selection on juvenile distribution. *Mar. Ecol. Prog. Ser.* **2**, 243–247.

Carpenter, R. C. 1985 Sea urchin mass mortality: effects on reef algal abundance, species composition, and metabolism and other coral reef herbivores. *Proc. 5th Coral Reef Congr.* **4**, 53–60.

Carpenter, R. C. 1986 Partitioning herbivory and its effects on coral-reef algal communities. *Ecol. Monogr.* **56**, 345–363.

Carpenter, R. C. 1988 Mass-mortality of a Caribbean sea-urchin: immediate effects on community metabolism and other herbivores. *Proc. natn. Acad. Sci. U.S.A.* **85**, 511–514.

Carpenter, R. C. 1990 Mass mortality of *Diadema antillarum* I. Long-term effects on sea urchin population-dynamics and coral reef algal communities. *Mar. Biol.* **104**, 67–77.

Dayton, P. K., Tegner, M. J., Parnell, P. E. & Edwards, P. B. 1992 Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecol. Monogr.* **62**, 421–445.

de Ruyter van Steveninck, E. D. & Bak, R. P. M. 1986 Changes in abundance of coral reef bottom components related to mass mortality of the sea urchin *Diadema antillarum*. *Mar. Ecol. Prog. Ser.* **34**, 87–94.

Hay, M. E. 1984 Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? *Ecology* **65**, 446–454.

Hay, M. E. & Taylor, P. R. 1985 Competition between herbivorous fishes and urchins on Caribbean reefs. *Oecologia, Berl.* **65**, 591–598.

Highsmith, R. C. 1982 Induced settlement and metamorphosis of sand dollar (*Dendraster excentricus*) larvae in predator-free sites: adult sand dollar beds. *Ecology* **63**, 329–337.

Hubbell, S. P. & Foster, R. B. 1986 Biology, chance, and history and the structure of tropical rain forest tree communities. In *Community ecology* (ed. J. Diamond & T. J. Case), pp. 314–329. New York: Harper and Row.

Hughes, T. P. 1989 Community structure and diversity of coral reefs: the role of history. *Ecology* **70**, 275–279.

Hughes, T. P. 1994 Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science, Wash.*, **265**, 1547–1551.

Hughes, T. P., Keller, B. D., Jackson, J. B. C. & Boyle, M. J. 1985 Mass mortality of the echinoid *Diadema antillarum* Philippi in Jamaica. *Bull. mar. Sci.* **36**, 377–384.

Hughes, T. P., Reed, D. C. & Boyle, M. J. 1987 Herbivory on coral reefs: community structure following mass mortalities of sea urchins. *J. exp. mar. Biol. Ecol.* **113**, 39–59.

Hunte, W., Cote, I. & Tomascik, T. 1986 On the dynamics of the mass mortality of *Diadema antillarum* in Barbardos. *Coral Reefs* **4**, 135–139.

Jackson, J. B. C. 1974 Biogeographic consequences of eurytopy and stenotopy among marine bivalves and their evolutionary significance. *Am. Nat.* **108**, 541–560.

Karlson, R. H. & Levitan, D. R. 1990 Recruitment-limitation in open populations of *Diadema antillarum*: an evaluation. *Oecologia, Berl.* **82**, 40–44.

Lessios, H. A. 1981 Reproductive periodicity of the echinoids. *Diadema* and *Echinometra* on the two coasts of Panama. *J. exp. mar. Biol. Ecol.* **50**, 47–61.

Lessios, H. A. 1984 Possible prezygotic reproductive isolation in sea urchins separated by the Isthmus of Panama. *Evolution* **38**, 114–1148.

Lessios, H. A. 1988a Mass mortality of *Diadema antillarum* in the Caribbean: what have we learned? *A. Rev. Ecol. Syst.* **19**, 371–393.

Lessios, H. A. 1988b Population dynamics of *Diadema antillarum* (Echinodermata: Echinoidea) following mass mortality in Panamá. *Mar. Biol.* **99**, 515–526.

Lessios, H. A., Robertson, D. R. & Cubit, J. D. 1984*a* Spread of *Diadema* mass mortality through the Caribbean. *Science, Wash.* **226**, 335–337.

Lessios, H. A., Cubit, J. D., Robertson, D. R., Shulman, M. J., Parker, M. R., Garrity, S. D. & Levings, S. C. 1984*b* Mass mortality of *Diadema antillarum* on the Caribbean coast of Panama. *Coral Reefs* **3**, 173–182.

Levitan, D. R. 1988*a* Algal-urchin biomass responses following mass mortality of *Diadema antillarum* Philippi at Saint John, U.S. Virgin Islands. *J. exp. mar. Biol. Ecol.* **119**, 167–178.

Levitan, D. R. 1988*b*. Asynchronous spawning and aggregative behavior in the sea urchin *Diadema antillarum* (Philippi) [sic]. In *Echinoderm biology* (ed. R. D. Burke, P. V. Mladenov, P. Lambert & R. L. Parsley), pp. 181–186. Rotterdam: A. A. Balkema.

Levitan, D. R. 1991 Influence of body size and population density on fertilization success and reproductive output in a free-spawning invertebrate. *Biol. Bull. mar. biol. Lab., Woods Hole* **181**, 261–268.

Liddel, W. D. & Ohlhorst, S. L. 1986 Changes in benthic community composition following the mass mortality of *Diadema* at Jamaica. *J. exp. mar. Biol. Ecol.* **95**, 271–278.

Morrison, D. 1988 Comparing fish and urchin grazing in shallow and deeper coral reef algal communities. *Ecology* **69**, 1367–1382.

Ogden, J. C., Brown, R. A. & Salesky, N. 1973 Grazing by the echinoid *Diadema antillarum*. Formation of halos around West-Indian patch reefs. *Science, Wash.* **182**, 715–717.

Pearce, C. M. & Scheibling, R. L. 1990 Induction of settlement and metamorphosis in the sand dollar *Echinarachnius parma*: evidence for an adult-associated factor. *Mar. Biol.* **107**, 363–369.

Ricklefs, R. E. 1987 Community diversity: relative roles of local and regional processes. *Science, Wash.* **235**, 167–171.

Ricklefs, R. E. & Schluter, D. 1993 Species diversity: regional and historical influences. In *Species diversity in ecological communities: historical and geographical perspectives* (ed. R. E. Ricklefs & D. Schluter), pp. 350–363. The University of Chicago Press.

Robertson, D. R. 1991 Increases in surgeon fish populations after mass mortality of the sea urchin *Diadema antillarum* in Panama indicate food limitation. *Mar. Biol.* **111**, 437–444.

Sammarco, P. W. 1982 Effects of grazing by *Diadema antillarum* Philippi (Echinodermata: Echinoidea) on algal diversity and community structure. *J. exp. mar. Biol. Ecol.* **65**, 83–105.

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. Part II. Erosion, sediments and internal structure. *Bull. mar. Sci.* **30**, 475–508.

Shulman, M. J. 1990 Aggression among sea urchins on Caribbean coral reefs. *J. exp. mar. Biol. Ecol.* **140**, 197–207.

Tegner, M. J. & Dayton, P. K. 1977 Sea urchin recruitment patterns and implications of commercial fishing. *Science, Wash.* **196**, 324–326.

Tegner, M. J. & Dayton, P. K. 1981 Population structure, recruitment and mortality of two sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) in a kelp forest. *Mar. Ecol. Prog. Ser.* **5**, 255–268.

Vermeij, G. J. 1987 *Evolution and escalation.* Princeton University Press.

Williams, A. H. 1981 An analysis of competitive interactions in a patchy back-reef environment. *Ecology* **62**, 1107–1120.