externally visible signs of the sensitization training were apparent 24 hours after training.

8. Statistical significance was assessed by a t test for paired values. One-tailed analysis was used in statistical tests based on pilot studies on five animals.
9. Each of the first 11 animals studied behaviorally were tested electrophysiologically; no selection procedures were used. After the last posttest, each animal was anesthetized by injection of isotonic $MgCl_2$ in an amount equal to approximately one-half the animal's volume, and the ganglia were removed.
10. E. T. Walters, J. H. Byrne, T. J. Carew, E. R. Kandel, *J. Neurophysiol.* **50**, 1522 (1983).
11. *I-V* relations were determined by delivering 300-msec pulses to potentials between −80 mV and +25 mV in increments of 15 mV. Pulses were separated by 40 seconds.
12. No fewer than two and no more than six cells were successfully clamped in any single cluster. A total of 46 cells from the control sides and 51 cells from sensitized sides were successfully clamped.
13. E. T. Walters, *Soc. Neurosci. Abstr.* **11**, 795 (1985); ———, J. H. Byrne, T. J. Carew, E. R. Kandel, *J. Neurophysiol.* **50**, 1543 (1983); N. Dale, E. R. Kandel, S. Schacher, *Soc. Neurosci. Abstr.* **12**, 1339 (1986); N. Dale, E. R. Kandel, S. Schacher, in preparation; E. T. Walters, *J. Neurosci.*, in press; M. Klein, B. Hochner, E. R. Kandel, *Proc. Natl. Acad. Sci. U.S.A.* **83**, 7994 (1986).
14. P. G. Montarolo *et al.*, *Science* **234**, 1249 (1986).
15. L. J. Cleary and J. H. Byrne, *Soc. Neurosci. Abstr.* **11**, 642 (1985); *ibid.* **12**, 397 (1986); J. H. Byrne, *J. Neurophysiol.* **45**, 98 (1981); R. D. Hawkins, V. F. Castellucci, E. R. Kandel, *ibid.* p. 304; J. H. Byrne, *ibid.* **49**, 491 (1983); W. N. Frost and E. R. Kandel, *Soc. Neurosci. Abstr.* **10**, 510 (1984).
16. C. H. Bailey and M. Chen, *Science* **220**, 91 (1983).
17. We thank L. Cleary and A. Susswein for their comments on an earlier draft of this report and J. Abikhaled and J. Mustacchia for assistance in training animals. This work was supported by NIH grant NS 19895 (to J.H.B.).

11 September 1986; accepted 16 December 1986

Diadema antillarum Was Not a Keystone Predator in Cryptic Reef Environments

JEREMY B. C. JACKSON AND KARL W. KAUFMANN

The ecological impact of the disappearance of a major predator depends on the responsiveness of the prey. Mass mortality of the most abundant grazer in Caribbean cryptic reef environments, the sea urchin *Diadema antillarum*, selectively decreased rates of mortality of encrusting organisms by half, yet community composition hardly changed because alternative species failed to become established.

KEYSTONE PREDATORS CAN RADICALLY alter the composition of ecological communities by consuming potentially dominant competitors (*1*). Before 1983, the sea urchin *Diadema antillarum* was the most abundant large grazing invertebrate on most Caribbean coral reefs (*2, 3*). Because of its enormous densities (*4*) and voracious appetite (*5*), *Diadema* has been considered a keystone predator (*3, 4, 6*), a view supported by severalfold increases in algal abundance on many reefs after mass mortality of *Diadema* in 1983 (*7, 8*). *Diadema* was also an important grazer on encrusting organisms in cryptic reef environments such as crevices in the reef framework and under corals (*9*). Thus one would predict that *Diadema*'s disappearance would result in large changes in the composition of the encrusting community, but it did not.

Population dynamics of encrusting organisms and *Diadema* were studied for 27 months at Rio Bueno, Jamaica. Undersurfaces of 38 foliaceous corals situated along 200 m of reef between 8 to 14 m in depth were photographed at approximately weekly intervals (*10*). We determined abundances by projecting photographs onto a digitizer tablet overlain by randomly placed points and then by recording what organisms coincided with the points at each census (*11*). Causes of changes in abundance were determined by observing the fates of organisms at randomly chosen points during five different 6-week periods (*12*). Overgrowth was readily observed in sequences of photographs as one organism advanced over another, and predation by large grazers was noted by their characteristic feeding scars. Together these two processes caused 82% of all changes observed.

More than 98% of the *Diadema* died between 26 July and 4 August 1983, and the population did not recover for the duration of the study (*7, 13*). Before the sea urchins died, predators (*14*) cleared 6.9% of the total surface in 6 weeks, whereas afterward this amount dropped as low as 1.1% and was still only 3.3% after 27 months (Fig. 1A; $\chi^2 = 372$, $P < 0.0001$, 4 df). In contrast, space overgrown by encrusting organisms stayed around 5% ($\chi^2 = 4.89$, $P > 0.10$, 4 df), so that the relative importance of mortality due to predation and competition was reversed.

Surprisingly, mean abundances of major encrusting taxa changed little during the 27 months after the disappearance of *Diadema* (Fig. 1B). However, abundances under individual corals varied considerably during the same period (Fig. 2), demonstrating that the overall stability of the encrusting community is not due to slow growth or lack of disturbance by other organisms. In contrast, animals with erect growth increased more than threefold but were never abundant.

Why was the composition of the cryptic community so stable in view of such a marked ecological change? One possibility is that larval recruitment of species able to dominate space under corals was extremely slow (*15*), so that new or previously uncommon species under a given coral may have simply failed to appear. To test this, we searched the photographs for larval recruits of sponges, which are the best overgrowth competitors under corals (*9, 16*), during two different 6-week intervals after the *Diadema* died (*17*). None appeared. Moreover, only seven bryozoan colonies settled, and there was no obvious increase in recruitment of any other groups under corals, including erect animals, which appear to have increased entirely by clonal propagation. Throughout this period, however, substrata suitable for larval settlement, such as crustose algae, were abundant. In contrast, erect animals recruited heavily after removal of another diadematoid sea urchin from a California rock reef (*18*).

Another possible explanation for the stability of the cryptic community may be associated with the diet of *Diadema* under corals. Before the urchins died, 57% of the predation was upon crustose algae and another 38% upon the bryozoan *Steginoporella* sp. Crustose algae are among the poorest overgrowth competitors under corals (*9*), so that their reprieve from grazing would not be expected to result in much community change. In contrast, *Steginoporella* sp. is among the best overgrowth competitors (*15*), but this ability is restricted to the growing margins of colonies, whereas older regions of the same colonies become senescent and are easily overgrown (*19*). For this reason we examined the condition of grazed versus ungrazed *Steginoporella*. Zooids were classified as young, middle-aged, and old, and their fates were determined after 6 weeks in June and July 1983 (*20*). The oldest zooids constituted 20% of the colonies, yet they sustained 75% of the predation. Thus *Diadema* fed almost exclusively and preferentially (*21*) on organisms or parts of organisms that were not actively affecting the abundance of other organisms.

Keystone predators, by definition (*1*), feed on potentially dominant competitors for space. *Diadema* behaves this way on upper reef surfaces by feeding preferentially on algae that might otherwise overgrow and

J. B. C. Jackson, Smithsonian Tropical Research Institute, Box 2072, Balboa, Republic of Panama.
K. W. Kaufmann, Department of Invertebrates, American Museum of Natural History, New York, NY 10024.

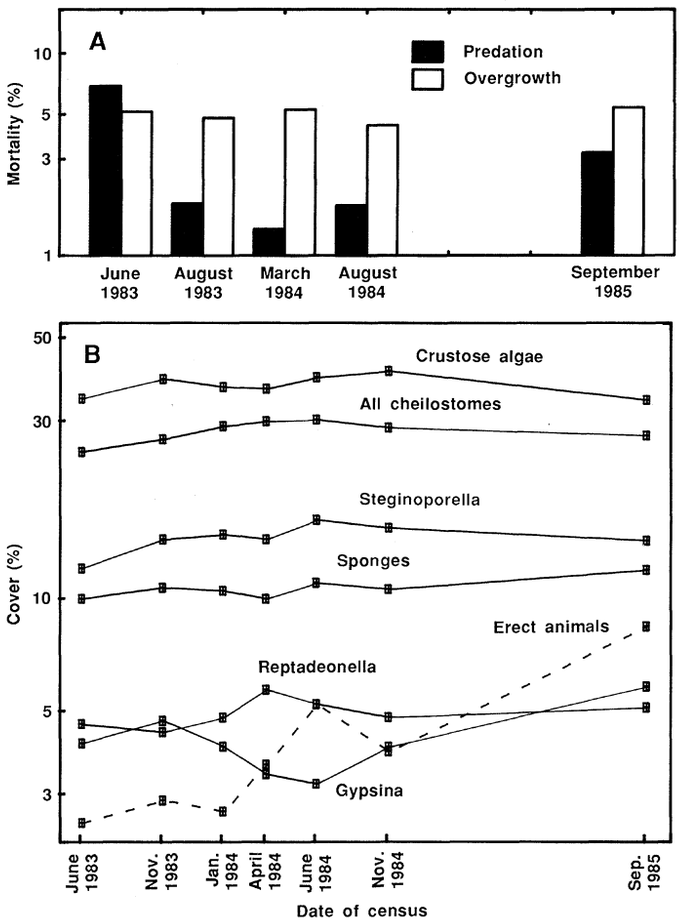

Fig. 1 (**left**). Abundance and turnover of sessile organisms under corals between June 1983 and September 1985 on a vertical reef face just west of Rio Bueno, Jamaica. Data are plotted on a logarithmic scale for clarity of presentation. (**A**) Proportion of mortality due to grazing compared to mortality due to overgrowth under corals (*12*). Mortality is expressed as the percentage of points examined whose inhabitants changed during each 6-week interval. (**B**) Mean percent cover of major taxa. *Steginoporella* spp. and *Reptadeonella* spp. are the most abundant cheilostome bryozoans (*9*); the category "all cheilostomes" includes these species. *Gypsina* sp. is an encrusting foraminiferan. Erect animals include arborescent or vinelike hydroids, stylasterine hydrocorals, scleractinian corals, and bryozoans.

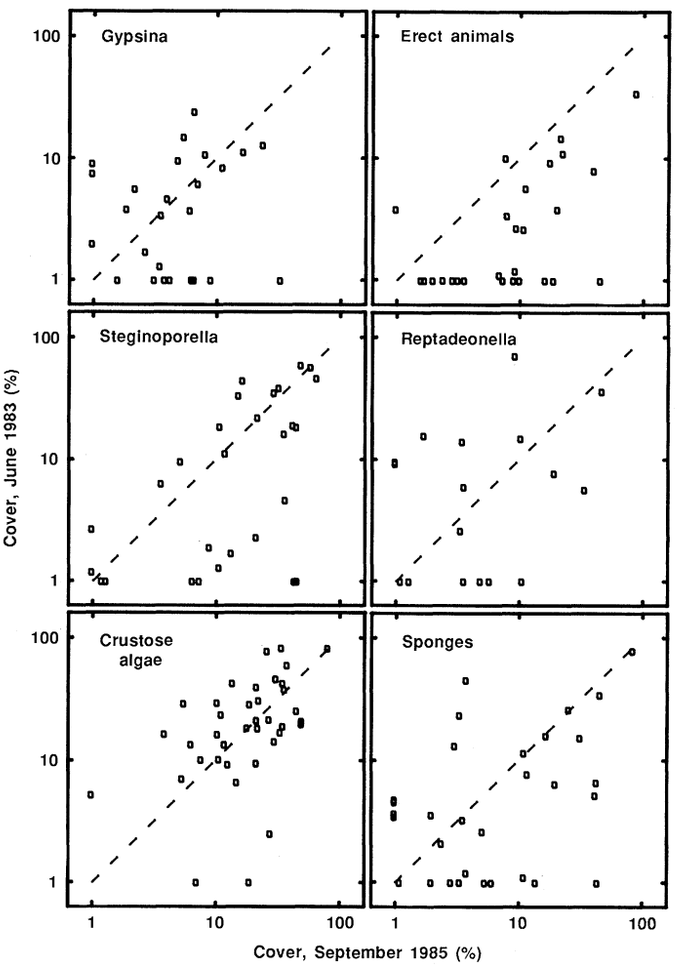

Fig. 2 (**right**). Percent cover of taxa under individual corals at the beginning and end of 27 months of observation. Each point represents the cover of a taxon under the same coral in June 1983 and September 1985. The number of points for each taxon varies with the number of corals inhabited. If no changes had occurred under individual corals, the points would lie on the diagonal lines.

kill corals (*3, 4, 6, 8*), but it acts the opposite in cryptic reef environments by feeding preferentially on inferior competitors. This is not the first instance of such behavior by an abundant predator; the starfish *Acanthaster planci* in the eastern Pacific feeds preferentially on competitively inferior corals (*22*).

After 27 months, the most striking natural disappearance of a major predator ever recorded in the sea had little effect on the community structure of a habitat where it was previously the principal predator. Erect animals potentially capable of excluding encrusting organisms have increased slowly, but *Diadema* populations are already increasing as well (*13*), so that further increase of erect animals is unlikely. Thus by established criteria (*1, 3*), *Diadema* was not a keystone predator in cryptic reef environments, despite its extensive grazing that scraped the equivalent of approximately 38% of the entire undersurface of corals each year (*23*).

We do not believe, however, that *Diadema* was ecologically unimportant under corals. Many of the most abundant cryptic species show structural and physiological adaptations to resist durophagous grazers such as *Diadema* (*15, 24*), and it seems unlikely that these defenses would have evolved and persisted if the most abundant such predator (*25*) had not had some influence. Mass recruitment of potentially dominant competitors might occur occasionally, after which intensive or selective grazing of these recruits by *Diadema* could alter the direction of community development. The ecological and evolutionary impact of a species may be great, even if it cannot be observed on a short time scale.

REFERENCES AND NOTES

1. R. T. Paine, *Am. Nat.* **100**, 65 (1966); *ibid.* **103**, 91 (1969); *Ecology* **50**, 950 (1969); *Oecologia* **15**, 93 (1974).
2. J. E. Randall, R. E. Schroeder, W. A. Starck II, *Caribb. J. Sci.* **4**, 421 (1964); J. C. Ogden, R. A. Brown, N. Salesky, *Science* **182**, 715 (1973).
3. P. W. Sammarco, J. S. Levinton, J. C. Ogden, *J. Mar. Res.* **15**, 471 (1974).
4. P. W. Sammarco, *J. Exp. Mar. Biol. Ecol.* **45**, 245 (1980); *ibid.* **61**, 31 (1982).
5. C. W. Stearn and T. P. Scoffin, *Proc. 3rd Int. Coral Reef Symp.* **2**, 471 (1977).
6. R. C. Carpenter, *J. Mar. Res.* **39**, 749 (1981).
7. H. A. Lessios, D. R. Robertson, J. D. Cubit, *Science* **226**, 335 (1984); H. A. Lessios *et al.*, *Coral Reefs* **3**, 173 (1985); T. P. Hughes, B. D. Keller, J. B. C. Jackson, M. J. Boyle, *Bull. Mar. Sci.* **36**, 377 (1985).
8. R. C. Carpenter, *Proc. 5th Int. Coral Reef Symp.* **2**, 66 (1985).
9. J. B. C. Jackson and J. E. Winston, *J. Exp. Mar. Biol. Ecol.* **57**, 135 (1982); J. B. C. Jackson, unpublished data.
10. Clips were attached to the edges of corals to provide reference points. We photographed undersurfaces by using a Nikonos IV camera, 28-mm Nikor lens with Nikon closeup lens and framer (image ratio,

1:6; field of view, 21 by 14 cm), Oceanic 2001 strobe, and Kodachrome 25 film. Resolution was usually sufficient to count individual zooids of bryozoans (<1 mm). Number of photographs per coral varied with coral size from one to four. Intervals between censuses were 4 days during the first year, and weekly thereafter. Most cryptic species require 1 week to heal lesions >1 to 2 mm [S. R. Palumbi and J. B. C. Jackson, *J. Exp. Mar. Biol. Ecol.* **64**, 103 (1982)]. Some sponges regenerate more rapidly [J. B. C. Jackson and S. R. Palumbi, in *Biologie des Spongaires*, C. Levi and N. Boury-Esnault, Eds. (Colloquium International, Centre National de la Recherche Scientifique, no. 291, Paris, 1979), p. 303], so that small injuries to these species would have been missed in our photographs.

11. Abundances were determined for the distinctive community found between 0 and 8 cm from coral edges [J. B. C. Jackson, *J. Exp. Mar. Biol. Ecol.* **75**, 37 (1984)]. Altogether 40,916 points were examined in seven repeated censuses of a 0.16-m^2 area.
12. Different sets of random points were followed for 6-week periods beginning in June 1983, August 1983, March 1984, August 1984, and September 1985; a minimum of 4028 points were followed per census. Only the most abundant groups were examined, including the five commonest species of cheilostomes, all pink and purple crustose algae, and all sponges; together these taxa cover almost 60% of the undersurface studied.
13. On the basis of counts within a 2-m^2 quadrat placed around each coral at 4- to 8-day intervals, densities dropped from 3.3 (SD, 0.48; $n = 45$) to 0.05 (SD, 0.02; $n = 45$) per square meter. By September 1985, densities had increased to 0.30 (SD, 0.60; $n = 45$) per square meter.
14. Principally *Diadema*, as evidenced by characteristic feeding scars [J. B. C. Jackson, in *Biotic Interactions in Recent and Fossil Benthic Communities*, M. J. S. Tevesz and P. L. McCall, Eds. (Plenum, New York, 1983), pp. 39–120, figure 21B].
15. J. E. Winston and J. B. C. Jackson, *J. Exp. Mar. Biol. Ecol.* **76**, 1 (1984); J. B. C. Jackson and T. P. Hughes, *Am. Sci.* **73**, 265 (1985).
16. J. B. C. Jackson and L. Buss, *Proc. Natl. Acad. Sci. U.S.A.* **72**, 5160 (1975); L. W. Buss and J. B. C. Jackson, *Am. Nat.* **113**, 223 (1979).
17. Care was taken to exclude colonies newly formed by asexual reproduction [J. B. C. Jackson and J. E. Winston, in *Recent and Fossil Bryozoa*, G. P. Larwood and C. Nielsen, Eds. (Olsen & Olsen, Fredensborg, Denmark, 1981), p. 121].
18. R. R. Vance, *Ecology* **60**, 537 (1979).
19. S. R. Palumbi and J. B. C. Jackson, *Biol. Bull.* **164**, 267 (1983).
20. Young zooids are bright red and unfouled by epibionts, middle-aged zooids are reddish brown and lightly fouled, and old zooids are dark brown and heavily fouled (*16, 23*). Numbers of points overlying grazed and ungrazed zooids (G/U): young, 12/622; middle-aged, 23/474; old, 107/181; total, 1419; $\chi^2 = 298$, $P < 0.0001$, 2 df.
21. Feeding on both crustose algae (G/U: 214/1658 = 0.13) and old *Steginoporella* (G/U: 107/181 = 0.59) was higher than feeding on all other encrusting organisms combined (G/U: 53/3193 = 0.02). These differences are highly significant for each group ($\chi^2 = 231$ for crustose algae and 772 for old *Steginoporella*: $P < 0.0001$ with 1 df in both cases).
22. P. W. Glynn, *Environ. Conserv.* **1**, 295 (1974); *Ecol. Monogr.* **46**, 431 (1976); in *Coevolution*, M. H. Nitecki, Ed. (Univ. of Chicago Press, Chicago, 1983), p. 111.
23. Total predation before the die-off was 6.9% of cover in 6 weeks, and the average for the three following censuses (before *Diadema* started to increase) was 1.6%. This result suggests that *Diadema* had grazed 5.3% of the total cover every 6 weeks. To estimate annual rates, we assumed that the urchins grazed independently of previous grazing (that is, they could feed again at the same spot, which was observed). The amount of space remaining ungrazed by *Diadema* after 1 year (that is, 8.66 measurement periods or 52 weeks divided by 6 weeks per census) was $(1 - 0.053)^{8.66} = 0.62$. Thus the amount grazed by *Diadema* was $1 - 0.62 = 38\%$ of the total space available.
24. R. S. Steneck, *Paleobiology* **9**, 44 (1983); B. A. Best and J. E. Winston, *Biol. Bull.* **167**, 390 (1984).
25. Abundance of *Diadema* may have increased historically as a result of extreme overfishing [M. E. Hay, *Ecology* **65**, 446 (1984)], but the sea urchin was also an important grazer in areas where large grazing fishes are still abundant, as at Morocoy and Los Roques, Venezuela [E. Weil, F. Losada, D. Bone, *Bijdr. Dierkde* **54**, 73 (1985).
26. This study was made possible by the field assistance of M. J. Boyle, G. Bruno, M. Gleason, and T. P. Hughes. Comments by M. Buzas, H. Caffey, N. Knowlton, H. Lessios, K. McGuinness, E. Weil, and two reviewers improved the manuscript. Supported by NSF grants OCE-82-15469 and OCE-84-15712. Contribution of the Discovery Bay Marine Laboratory, Jamaica.

7 July 1986; accepted 25 November 1986

Can Microscale Chemical Patches Persist in the Sea? Microelectrode Study of Marine Snow, Fecal Pellets

ALICE L. ALLDREDGE AND YEHUDA COHEN

Microelectrode studies demonstrate the existence of persistent oxygen and *p*H gradients around flocculent, macroscopic marine particles known as marine snow. Oxygen is partially, but continuously, depleted within and around marine snow in the dark and can be completely depleted within large fecal pellets. Boundary layers hundreds of micrometers thick are maintained despite advection of fluid past the particles. The existence of chemical microhabitats on the scale of millimeters around macroscopic particles in the pelagic zone may significantly influence the distribution and activity of marine microorganisms and permit processes requiring low oxygen, including denitrification.

THE EXISTENCE OF PELAGIC MICROzones enriched in nutrients, oxygen, or dissolved organic matter has been hypothesized to explain high growth rates of phytoplankton and bacteria in seemingly impoverished oceanic waters (*1–4*). Microzones of nutrient enrichment would attract microorganisms and support high metabolic activity, whereas microzones of oxygen-depleted water might support denitrification or even permit sulfate reduction or methanogenesis. Although microscale nutrient patches lasting a few tens of seconds are produced by zooplankton excretion and potentially affect the course of competition and coexistence among phytoplankton (*5*), it has been argued that chemical gradients on the scale of millimeters cannot persist in the planktonic environment because they could not be maintained against processes of molecular or turbulent diffusion (*6, 7*).

However, the pelagic zone contains abundant macroscopic particles, both flocculent aggregates known as marine snow and the fecal pellets of zooplankton, whose large size and high microbial activity (*8, 9*) could produce and maintain microscale chemical gradients. Using microelectrodes to measure oxygen and *p*H, we have demonstrated that oxygen is partially depleted within marine snow particles in the dark and may become fully depleted in large fecal pellets. The boundary layer surrounding the particles further increases the volume of the microzone. We present experimental evidence (i) that microscale chemical gradients can persist in the ocean against processes of advection and diffusion on a scale significant to microorganisms and (ii) that these patches may have important implications for nutrient recycling in the sea.

Particles of marine snow (flocculent, macroscopic particles consisting of phytoplankton, detritus, bacteria, and fecal pellets embedded in a mucous matrix) ranging from 1 to 4 mm in diameter were collected by hand in small cylinders by scuba divers in surface waters of the Santa Barbara Channel, California (*10*). All particles were maintained at 18°C and tested within 1 to 24 hours after being collected. Freshly defecated fecal pellets were also obtained from planktonic macrocrustaceans collected by net and aged for up to 3 days in sterile seawater in the laboratory at 25°C. Each individual particle was placed in a small cone, 7 mm high and 3.5 mm in radius, made from 120-μm mesh-size plankton net, which sat in a 30-ml vessel filled with filtered seawater maintained at 18° to 20°C. A stream of fine bubbles emitted from a pipette tip placed near the bottom of the vessel outside the cone was used to mix water throughout the vessel. This bubble stream produced a suction effect, advecting water toward it from the cone and the rest of the vessel. Measurements of the time required for a fine suspension of carmine particles placed within 500 μm of the marine snow to leave the cone indicated that current velocities around the particles were on the order of 0.04 cm sec^{-1}.

A. L. Alldredge, Department of Biological Sciences and Marine Science Institute, University of California, Santa Barbara, CA 93106.
Y. Cohen, Marine Biology Laboratory, Hebrew University of Jerusalem, Post Office Box 469, Eliat, 88103 Israel.