

Mass mortality of a Caribbean sea urchin: Immediate effects on community metabolism and other herbivores

(*Diadema antillarum*/algae/coral reef ecosystem/primary productivity)

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Communicated by Eugene P. Odum, September 2, 1987

ABSTRACT The echinoid *Diadema antillarum* Philippi was an important herbivore in many areas of the Caribbean prior to the mass mortality that eliminated 95–99% of the individuals throughout the Caribbean in 1983–84. Five days after the mass mortality in St. Croix, U.S. Virgin Islands, algal biomass increased by 20% and algal community primary productivity dropped on both a per unit area basis (37% decrease) and per unit algal biomass basis (61% decrease). This accompanied a 50% decrease in the amount of algal biomass removed by herbivores. Concurrent with the changes in the algal community were increases in the rates of grazing by herbivorous fishes, suggesting that exploitative competition for food was occurring between *D. antillarum* and some herbivorous fish species. These results suggest that *D. antillarum* has an important role in structuring both the producer and consumer components of Caribbean coral reef ecosystems.

Grazing by the Caribbean echinoid *Diadema antillarum* Philippi has a dramatic influence in coral reef habitats, including effects on the settlement and survival of juvenile corals (1–3), the control of plant abundance (4–7) and species composition (6, 7), and the metabolism of the algal community (6, 8). Previous results suggest that exploitative interspecific competition for food occurs between some herbivorous fishes and *D. antillarum* (9, 10). Since January 1983, Caribbean-wide mass mortality has resulted in the natural removal of 95–99% of the individuals of this ecologically important echinoid species (11, 12). No other organisms were affected by the unknown causative agent (12). The immediate effects of this removal (5 days after mortality) were a decrease in algal community primary productivity, both per unit area and per unit algal biomass, and an increase in the grazing intensity by herbivorous fishes. The natural removal of *D. antillarum* provides a test of competition as one of the structuring forces on reef herbivore populations (13, 14) and the opportunity to study the differential effects of these herbivores on algal community structure and function.

Caribbean coral reef algal communities are grazed by a number of herbivores. In St. Croix, U.S. Virgin Islands, the most notable of these are herbivorous fishes in the families Acanthuridae, Pomacentridae, and Scaridae; and echinoids, mainly *D. antillarum*, but also *Echinometra viridis* Agassiz and *Eucidaris tribuloides* (Lamarck). Algal communities studied were those that cover up to 80% of open reef surfaces, commonly referred to as algal turfs. Algal turfs consist of a variety (up to 50 species per square meter) of algal filaments and crusts from five algal divisions (Cyanophyta, Chlorophyta, Chrysophyta, Phaeophyta, and Rhodophyta). These species are generally small (10- to 500- μ m diameter for

filaments, 1- to 20-mm diameter for crusts) and have canopy heights rarely exceeding 1–2 mm under regimes of intense herbivory. If released from such intense grazing pressure, canopy heights can increase to 20–30 mm, as in damselfish territories (15). Algal turf communities are responsible for the majority of primary production of coral reefs (16–20) and are maintained in a high turnover state by the repeated grazing of herbivores (6, 7, 21). Natural settling plates (*Acropora palmata* skeleton) of uniform size (8 \times 8 \times 1 cm) and texture were submerged 3 years prior to the collection of data presented here. There were no differences between algal communities on these substrata and those on surrounding dead coral after 180 days, in terms of biomass, species composition, or rate of primary productivity (Table 1). Data from previous studies show a positive relationship between algal biomass and primary productivity per unit area (23) and an inverse relationship between algal biomass and biomass-specific productivity rates [μ g of O₂ per μ g of chlorophyll *a* (Chl *a*) per hr] (24).

METHODS

Primary productivity was estimated by changes in dissolved oxygen in clear acrylic chambers (2.9 liters) over short incubation times (15 min) at the study site. All replicate incubations were conducted at saturation photon flux densities (1000–1400 μ E·m⁻²·s⁻¹; 1 einstein, E, is 1 mol of photons) determined from productivity versus photon flux density experiments. Dissolved oxygen was measured by using Yellow Springs Instrument polarographic oxygen probes and water was circulated in the chambers by using air-driven magnetic stirrers and a surge-driven paddle. Productivity rates measured by this method compare favorably with rates estimated by other techniques (20, 25).

Algal biomass was estimated by two methods. Plates were returned to the lab and random subsamples were scraped from the plates to a depth of 1 mm. For one set, samples were decalcified in <5% hydrochloric acid, filtered and rinsed, and dried to constant mass at 60°C. The other samples were ground with a mortar and pestle in 90% acetone and MgCO₃ and Chl *a* concentration was estimated by using standard methods (26) and the spectrophotometric equations of Jeffrey and Humphrey (27).

Algal biomass removed was estimated in the following way. Algal production rates per unit area were converted to carbon equivalents assuming a photosynthetic quotient of 1.0. Assuming a 50% carbon content, these rates were then converted to dry weight production estimates. Rates of

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Abbreviation: Chl *a*, chlorophyll *a*.

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Table 1. Characteristics of algal communities growing on experimental settling plates and the surrounding natural substratum 180 days after plates were submerged

Community	Biomass, g (dry wt)·m ⁻²	<i>n</i>	Net productivity, g O ₂ ·m ⁻² ·hr ⁻¹	<i>n</i>	Species composition, index of similarity	<i>n</i>
Settling plates	25 ± 3	18	0.55 ± 0.10	6	0.88	6
Surrounding substratum	27 ± 2	18	0.61 ± 0.15	6		

Results are presented as mean ± SD with number of observations. There were no significant differences between substratum types ($P > 0.05$, *t* test). Species compositions are compared by Czekanowski's index of similarity (22).

removal before the die-off were estimated from plates in a series of open-topped inclusion and exclusion cages (including appropriate cage controls) that allowed access by selected

herbivores. After the die-off, rates were estimated from plates accessible to all herbivores [mostly fishes, since other herbivores have been shown to be of limited importance for

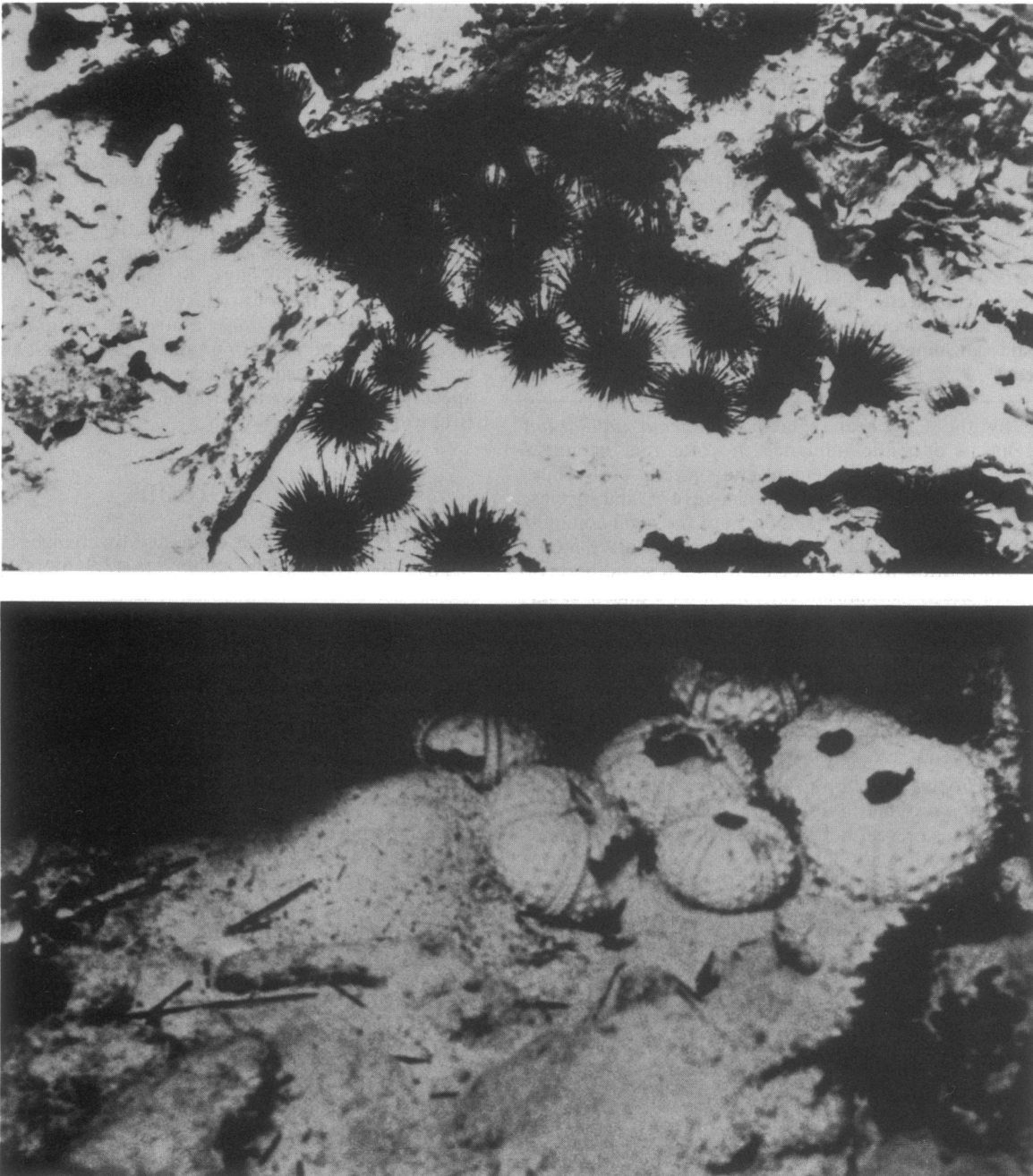


FIG. 1. Photographs of aggregations of *D. antillarum*. (Upper) Before the mass mortality event. Densities of individuals were 4–21 per m², with higher densities, as pictured here, occurring in shallow (3- to 5-m depth) forereef zones. (Lower) After the mass mortality. Densities of individuals were reduced by 95–99% within a 5-day period (J. Ogden, personal communication) across reef zones, including patch reefs. Maximum test diameters of sea urchin tests pictured here were 55–72 mm.

these algal communities (24)]. Algal biomass removed [ABR, g (dry wt) \cdot m $^{-2}$ \cdot day $^{-1}$] was then calculated from the equation

$$ABR = \frac{[DWP \times (t_2 - t_1)] - [B_1 - B_2]}{(t_2 - t_1)}, \quad [1]$$

where DWP is daily dry weight production per m 2 , B $_1$ is algal biomass [g (dry wt) \cdot m $^{-2}$] at sampling time t_1 , and B $_2$ is algal biomass at sampling time t_2 .

RESULTS AND DISCUSSION

On February 5, 1984, the first evidence of *D. antillarum* mortality appeared near study locations in 1–2 m of water on the backreef/reefcrest of Tague Bay reef, on the northeastern coast of St. Croix (17 $^{\circ}$ 45' N, 64 $^{\circ}$ 42' W). By February 10, 99% of *D. antillarum* individuals at these sites had died (Fig. 1, Table 2). Since 100% or more of daily algal production is frequently removed by herbivores, particularly *D. antillarum* (24), the response of the algal community to this disturbance was expected to be rapid. Algal primary productivity estimates obtained 5 days after this mortality event (February 15) revealed striking differences from those obtained in December 1983 (Fig. 2 Upper), 2 months before the sea urchin mortality. Maximum net primary productivity, expressed on an areal basis, was reduced by 37%, while biomass-specific productivity rates dropped by 61% (Table 2). The decrease in biomass-specific primary productivity could be explained by an increase in self-shading due to algal biomass accumulation. However, an increase in areal-based productivity would have been predicted from existing data on the relationship between reef algal standing crop and algal metabolism (18, 23), since more algal biomass was present per unit area.

These data demonstrate a positive effect on algal community primary productivity associated with grazing by *D. antillarum* and are consistent with data obtained previously by using sea urchin inclusion–exclusion cages, where algal communities grazed by *D. antillarum* were 5–8 times more productive per unit biomass than algal communities not grazed by this sea urchin (24). Nutrient regeneration from *D. antillarum* may have a stimulatory effect on algal turf production. Soluble excretions and decomposition of *D. antillarum* fecal pellets could result in the higher production rates of these algal communities. *D. antillarum* is ammonotelic and excretes approximately 99 μ g of ammonium nitrogen per hr (28), most of which is released from the respiratory surfaces, such as the tube feet and gills. Ammonium excreted from these structures on the oral side of the sea urchin enters a restricted volume of water with reduced water exchange and in close proximity to the algae-covered substratum. Ammonium is the preferred form of nitrogen for algae and may be taken up very efficiently by algae adapted to such nutrient pulses (high V_{max}) (29, 30). Preliminary scanning electron microscopy of *D. antillarum* fecal pellets shows a large number of bacteria on the surface membrane.

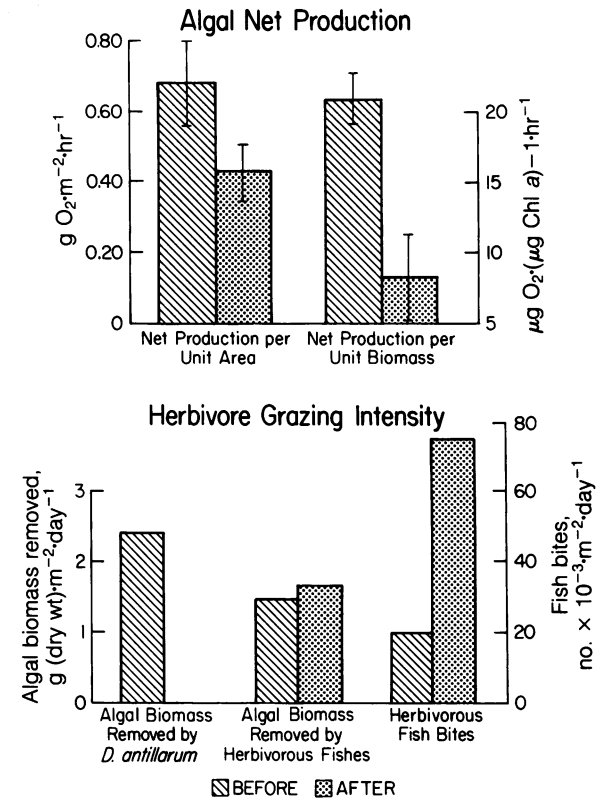


FIG. 2. Effects of mortality event on reef community. (Upper) Mean net algal community primary productivity rates (± 1 standard deviation) per unit area and per unit algal biomass (Chl *a*) before (December 1983) and after (February 1984) the mass mortality of *D. antillarum*. Primary productivity rates (area- and biomass-specific), estimated by changes in dissolved oxygen as described in *Methods*, were significantly lower after the removal of *D. antillarum* (Table 2). (Lower) Herbivore grazing intensity as expressed by algal biomass removed for both *D. antillarum* and herbivorous fishes, before and after the removal of *D. antillarum*, and by the number of bites per m 2 per day for herbivorous fishes for the same time periods. Algal biomass removed was calculated from Eq. 1, with DWP, B $_1$, and B $_2$ as means with $n = 12, 18,$ and $18,$ respectively. Numbers of fish bites were determined from frame-by-frame analysis of time-lapse movies taken of the natural settling plates. Bites were defined as mouthparts in contact with the substratum and rates were normalized for day length and area photographed.

As pellets disintegrate, increasing the surface area, these bacteria may decompose the remaining organic matter, slowly releasing nitrogen for algal uptake. The importance of such nutrient pulses would be great for tropical algal communities due to the extremely low ambient nutrient concentrations in the oceanic water surrounding most coral reefs. Such a mechanism has been suggested to be responsible for increased growth rates of corals underlying resting schools of

Table 2. Characteristics of algal communities and herbivory before (December 1983) and after (February 1984) mass mortality of *D. antillarum*

Characteristic	Value before	<i>n</i>	Value after	<i>n</i>	Statistical test	<i>P</i>
<i>D. antillarum</i> density, no. \cdot m $^{-2}$	6.4 \pm 3.6	16	0.1 \pm 0.2	20	One-way	<0.01
Algal biomass, g (dry wt) \cdot m $^{-2}$	30 \pm 4	18	38 \pm 3	12	One-way	<0.05
Algal canopy height, mm	1.0 \pm 0.3	12	2.9 \pm 1.6	39	One-way	<0.05
Algal productivity per unit area (net), g O $_2$ \cdot m $^{-2}$ \cdot hr $^{-1}$	0.68 \pm 0.12	8	0.43 \pm 0.09	12	Two-level	<0.001
Algal productivity per unit biomass (net), μ g O $_2$ (μ g Chl <i>a</i>) $^{-1}$ \cdot hr $^{-1}$	20.91 \pm 4.55	8	8.15 \pm 4.20	12	Two-level	<0.001
Total algal biomass removed by herbivores, g (dry wt) \cdot m $^{-2}$ \cdot day $^{-1}$	3.74		1.58			
% daily algal net production removed by herbivores*	93		45			

Results are presented as mean \pm SD for n determinations. Statistical tests were one-way analysis of variance and two-level nested analysis of variance.

*Calculated from Eq. 1 and percent daily production removed = (ABR/DWP) \times 100.

reef fishes (31). The role of nitrogen in limiting algal production and growth on coral reefs is currently ambiguous (32). High rates of water flow (allowing algal contact with a large volume of water) and the abundance of nitrogen-fixing cyanobacteria within algal turfs have been advanced as arguments against nitrogen limitation of algal growth (32).

One alternative to the nutrient regeneration hypothesis is that grazing by *D. antillarum* results in algal communities dominated by species with high productivity-to-biomass (P/B) ratios. Removal of urchin grazing could lead to domination by other algal species with lower P/B ratios, thereby lowering overall productivity. Plates were subsampled (six 1-cm² subsamples) for algal species composition by scraping to a depth (into the plate) of 1 mm, decalcifying, and mounting on microscope slides. The entire slide was scanned to determine the number of algal taxa present. Relative abundances were estimated from the number of intersections of a 10 × 10 ocular grid that fell on each species. All counts were made at ×100, and 84 microscope fields were quantified. Although species composition differed slightly between December 1983 and February 1984, Czekanowski's index of similarity (22) was high (0.88). This does not support the alternative hypothesis that the decreased productivity per unit area is the result of a shift in algal species composition.

Estimates of the amount of algal biomass removed by herbivory also reveal large differences between December 1983 and February 1984 (Fig. 2 Lower). Total algal biomass removed dropped from 3.74 to 1.58 g (dry wt)·m⁻²·day⁻¹. This corresponds to a drop from 93% to 45% of daily algal production. However, there was a slight increase in the amount of algal biomass removed by herbivorous fishes and a marked increase in the frequency of bites by these fishes (Fig. 2 Lower). The majority (91–95%) of the herbivorous fishes were juvenile scarids with small mouthparts. As a result, a large increase in the number of bites led to only a small increase in the amount of algal biomass removed. Such increases would be predicted if exploitative competition were occurring between fishes and *D. antillarum* (9, 10).

Based on the previous relationships between *D. antillarum* abundance and algal community characteristics (5, 6), long-term predictions would include further increases in algal biomass, an eventual increase in algal productivity per unit area, and a continued decrease in productivity per unit of algal biomass as algal species composition changes. Patterns of herbivory by fishes are predicted to depend on the rate of recolonization and recovery of *D. antillarum* populations. If competition is occurring, then an immediate response of fishes to increased food resources will be a continued increase in grazing rate (functional response); if urchin recovery is slow, an eventual increase in herbivorous fish population sizes (numerical response) would be expected if food resources are a factor limiting population size. Other factors, such as recruitment, may also play an important role in determining local population sizes of herbivorous fishes. A reversal of the above changes in algal community characteristics and other herbivore populations should occur if *D. antillarum* populations become reestablished.

Positive-feedback processes have been demonstrated to occur in terrestrial plant-herbivore interactions (33–35) and have been reported in some aquatic environments (6, 36, 37). Although marine herbivores are known to increase algal species diversity under specific conditions (6, 38, 39), the data presented here provide confirmation that this benthic marine herbivore has a positive effect on the rate of algal primary productivity. *D. antillarum* has been recognized as an important species affecting certain aspects of the organization of benthic reef communities (1–8); however, the

magnitude of its role in controlling the structure and function of coral reefs may be determined only as a result of its absence.

I am grateful to J. Porter, G. Helfman, and J. Meyer for criticizing an early draft of the manuscript and to J. Ogden for supporting the fieldwork. I am especially grateful to H. Carpenter for unselfish assistance throughout. This study was supported in part by a National Science Foundation Doctoral Dissertation Improvement Award (OCE-8300209), a grant from the Sea Grant Program of Puerto Rico (UPR PD-21), and the West Indies Laboratory. This is a contribution from the Institute of Ecology, University of Georgia, contribution no. 137 from the West Indies Laboratory, and contribution no. NURP-FDU-J-461 from the National Undersea Research Program at Fairleigh Dickinson University.

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