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Grazing and Control of Coral Reef Community Structure by *Diadema antillarum Philippi* (Echinodermata: Echinoidea): A Preliminary Study

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Grazing and Control of Coral Reef Community Structure by Diadema Antillarum Philippi (Echinodermata: Echinoidea): A Preliminary Study[1]

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ABSTRACT

The grazing activities of the tropical echinoid *Diadema antillarum* Philippi can markedly influence the structure of the shallow-water epibenthic coral reef community. The elimination of an entire *Diadema* population from a patch reef in St. Croix, U.S. Virgin Islands resulted in a great increase in macro-algal biomass, alterations in species composition, shifts in dominance, an increase in species numbers, and a decrease in equitability. The increase noted in number of species may be indicative of either initial pre-competitive phases of succession or the creation of a new habitat—the micro-canopy. Experiments involving the caging of *Diadema* have shown that the organism's browsing habits may be extensively disruptive to virgin coral substrate. This evidence introduces the possibility that epifaunal community structure may be controlled through the disturbance of newly settled larvae of sessile epibenthic macro-invertebrates.

1. *Introduction.* The echinoid *Diadema* is one of the most common and conspicuous members of tropical coral reef communities on a global basis. Although a number of investigations have alluded to its ecological function in the community (Lewis, 1964; Randall, Schroeder, and Stark, 1964; Yonge, 1963), the importance of its role remains to be conclusively established.

A keystone species has been defined as the single terminal species on a high trophic level, exerting predatory control on the structure of the levels beneath it (Paine, 1966, 1969). But a wide spectrum of evidence from terrestrial, freshwater, and marine ecosystems has shown that the concept may be expanded to include even the primary-producer/primary-consumer level (see Harper, 1969; Paine and Vadas, 1969; Vadas, 1968). Predation affects prey species diversity in terms of both equitability and number of species (Tansley and

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Adamson, 1925; Vadas, 1968), species composition (Brooks and Dodson, 1965; Dodson, 1970; Maguire, Belk, and Wells, 1968; Vadas, 1968), longevity and reproductive success (Hope-Simpson, 1940) and succession (Paine and Vadas, 1969; Vadas, 1968). The purpose of this investigation was to preliminarily determine whether *Diadema* was acting in such a manner to maintain control of shallow-water reef community structure.

2. *Methods and Materials.* During the summer of 1972, a preliminary investigation of the effects of grazing by *Diadema antillarum* was conducted at the West Indies Laboratory of Fairleigh Dickinson University on the northern coast of St. Croix, U.S. Virgin Islands (see Sammarco, 1972). During mid-April, 1972 the *Diadema* population (> 8,000 individuals) was completely removed from one of five generally homogeneous patch reefs in Tague Bay (see Ogden *et al*, 1973); this particular patch (PR-2) was determined to be approximately 800 sq. m. in size. Between August 12 and August 28, the macro-algae[2] of each of the five patches were sampled by six 0.25 sq. m. quadrats laid systematically at uniform intervals along east-west transects. Biomass estimates for each species were determined by placing samples in a Fisher Isotemp Oven usually for 18–24 hours (but sometimes up to 60 hours, depending on the time required for complete dehydration) and then obtaining dry weights on a Mettler H-10T or P-11 balance.

Another experiment was designed to help determine the degree to which *Diadema*'s grazing activities impose actual physical disturbance on the benthic substrate. Four open-bottom urchin inclusion cages measuring $1.0 \times 1.0 \times 0.5$ m. and containing densities of 0, 2, 4, and 6 *Diadema* individuals/m^2 were implanted on PR-3. Large pieces of *Acropora palmata* (Coelenterata: Scleractinia) were then collected from the barrier reef, killed by immersing in freshwater for several hours, cleaned with fresh-water forced through a pipette under high pressure, and exposed to the sun to bleach-dry. The coral branches were then subdivided so that two small pieces measuring approximately 25×25 cm. could be introduced into each cage. Two weeks after implantation, small subsamples were taken from one of each of the coral pieces and examined for comparative qualitative differences in physical structure with the aid of a binocular dissecting microscope.

3. *Results.* The results of the macro-algae analysis are summarized in Table I. Total algal biomass of all samples for each patch in grams dry weight per square meter is presented with the number of species and Pielou's measure of equitability, J′ (Pielou, 1969). A mean and standard deviation are given as a summary of the values for the control patches.

Pieces of coral substrate were examined and found to exhibit varying degrees

2. The term 'macro-algae' used in this paper is defined as those algae readily noticed with the naked eye while sampling.

of physical disturbance. The subsample from the $0/m^2$ density cage showed, as expected, no abrasion of the calices. At a density of $2/m^2$ evidence of grazing was apparent on various parts of the exposed surface. But at densities of 4 and $6/m^2$ the upper portions of the calices had been abraided greatly altering the substrate's physical shape and appearance at a microscopic level.

4. *Discussion.* Although only the initial phases of succession following the perturbation caused by grazing were monitored, the ungrazed patch (PR-2) was found to differ from the controls in the following ways: First, shifts in dominance were noted. *Halimeda opuntia*, the most dominant species by dry weight (the most heavily calcified alga), was replaced by several other species on the ungrazed patch. Although the general order of magnitude of dry-weight for *Halimeda* was not altered, the vast increase in biomass of other algae caused a decline in its relative position in the dominance hierarchy. Most notably, the calcareous phaeophyte *Padina sanctae-crucis* increased in biomass by over two orders of magnitude and became the conspicuous dominant in the absence of grazing. Also found in massive abundances were *Turbinaria turbinata*, *Dictyota* sp., and *Jania adherens*. It is not yet understood whether these dominance shifts and increases in biomass were caused by a high degree of colonization, more rapid vegetative growth, or a combination of these factors (see Table I).

Changes in species diversity as measured by number of species and Pielou's measure of equitability were also striking. Table I shows that the number of species on the ungrazed patch increased by a factor of five. This increment is due to five new species: *Halimeda tuna*, *Liagora* sp., *Dictyopterus delicatula*, and two cyanophytes. None of these was located on any of the four grazed controls. The overdominance of several species, but particularly *Padina sanctae-crucis*, caused the sharp decrease in equitability.

Table I. Macro-algal biomass, species diversity, and equitability in the presence and absence of *Diadema antillarum* Philippi.

Condition	Patch Reef No.	Algal Biomass in gms. dry wt. per sq. m.	Number of Species	$J'(=H'/H'_{max})$
Controls (Grazed)	PR-1	18.5567	17	0.6596
	PR-3	11.3915	16	0.5695
	PR-4	8.6797	14	0.6293
	PR-5	8.9165	19	0.6821
Mean		11.8861	16.5	0.6351
Standard Deviation		4.6131	2.1	0.0488
Experimental (Ungrazed)	PR-2	159.0183	23	0.4447

It is possible that the absence of *Diadema*'s extensively disruptive grazing activities resulted in the sudden availability of newly opened space and an initial colonization of new species. However, as new opportunistic dominants increase in biomass and cover they occupied the available space. Interspecific competition for space and light may eventually result in a decrease of species numbers to a point lower than that observed on the naturally grazed patches. This has been observed under similar experimental conditions in the *Agarum* kelp-bed communities of Washington (Paine and Vadas, 1969; Vadas, 1968). Increase in species numbers also may be caused by development of a micro-canopy by the leafy fronds of *Padina*, with the concurrent appearance of new understory species. These new species, necessarily sciaphilic (or 'shade-loving'; Boudouresque and Luck, 1972) would be afforded protection from predation by the *Padina* cover. *Padina* is supposedly a low preference food of the locally abundant grazing fish—the Scaridae and Acanthuridae (I. Clavijo, personal communication). In this case, it cannot be predicted that species numbers will decline, as new types of ecological space may have been created.

The results of the caging experiment have shown that *Diadema antillarum*, even at the moderate densities of 4 and 6/m^2, is able to alter the micro-structure of the hard substratum upon which it grazes. This introduces the possibility that *Diadema* may secondarily control epifaunal species composition, diversity, equitability, dominance, and biomass in a manner similar to its control of algae. The types of fauna most likely to be sensitive to a grazing perturbation might include many of the sessile epibenthic macro-invertebrates which compete for space: hermatypic (Lang, 1971) and ahermatypic corals, zoanthids, actinarians, gorgonians, corallimorphariids, sponges, sedentary polychaetes, etc.

Newman (1960) and Bakus (1964, 1966) suggest that marine grazers may have a strong influence on epifaunal community evolution. Dayton (1971) has experimentally demonstrated that intertidal limpets can affect the success of cirripede settlement. These grazing activities tend to disturb newly settled larvae (Connell, 1961; Hatton, 1938; Lewis, 1954; Southward, 1956; Stimson, 1970) and have been found in some cases to be differential with respect to species (Dayton, 1971). This influence on community structure may be compounded by the fact that certain invertebrate larvae are extremely sensitive to variations in the micro-structure of the benthic substrate and respond to such by altering settling behaviour (Crisp and Barnes, 1954).

Vadas (1968) has found that areas possessing different densities of *Strongylocentrotus* spp. in Washington may be associated with different levels of algal species diversity—that is, maximum diversity at intermediate urchin densities. Observations of fore-reef and back-reef lagoon areas made during April, 1973 in Discovery Bay, Jamaica, West Indies by two of us (P.W.S. and J.S.L.) tend to support Vadas's findings, but further suggest that a similar relationship may exist between *Diadema* densities and the sessile macro-invertebrate epifauna.

5. *Conclusions.* After conducting urchin exclusion experiments in Tague Bay, St. Croix, we conclude that *Diadema antillarum* Philippi may markedly influence the macro-algal community structure of coral reefs by its grazing activities which biomass, species composition, dominance, species numbers, and equitability. It is also concluded that even at moderate densities, *Diadema* can impart an ecologically significant disturbance to the substrate upon which it feeds. On this basis, it has been hypothesized that the urchin may exercise similar control over the community structure of sessile epibenthic macro-invertebrates in the shallower zones of coral reefs.

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