Sea Urchin Mass-Mortality: Effects on Reef Algal Abundance, Species Composition, and Metabolism and Other Coral Reef Herbivores

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MORTALITE MASSIVE DES OURSINS : EFFETS SUR L'ABONDANCE, LA COMPOSITION SPECIFIQUE, ET LE METABOLISME DES ALGUES RECIFALES ET DES AUTRES HERBIVORES DU RECIF

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ABSTRACT

Grazing by *Diadema antillarum* has been demonstrated to control the biomass, species composition, and most recently, the metabolism of many coral reef algal turf communities. The majority of these data have been obtained using inclusion-exclusion cage experiments. The recent mass-mortality of this sea urchin in the Caribbean provided a natural test of many of the experimentally-generated hypotheses. In St. Croix, two-years of pre-mortality data showed that algal turfs grazed by *D. antillarum* had higher biomass-specific production (production/algal biomass/time), and production/area/time not less than, higher biomass turfs not grazed by urchins. The natural removal of 957. of the *D. antillarum* individuals produced similar patterns in the turf biomass and production. Five days after the mortality event, algal bianass had increased by 277. while biinass-specific production decreased by 607.. In addition, algal species composition began changing within five days of the die-off. Larger macroalgal species such as *Laurencia obtusa* and *Acanthophora spicifera* increased in abundance while smaller algal filamentous species, although increasing in size, decreased in overall abundance. These patterns have persisted for ten months and are most pronounced in shallow reef zones.

Recent studies have suggested that exploitative competition for algal resources may be occurring between herbivorous fishes and sea urchins. Preliminary data suggest that such competition was occurring prior to the *Diadema* die-off. The near removal of this species resulted in an immediate functional response by herbivorous fishes, mainly scarids. Fish grazing intensity, as measured by time-lapse photography, increased 3807. one week after the sea urchin mass-mortality. The possibility of a long-term numerical response by herbivorous fish populations is being investigated.

The resulting shifts in algal abundance, species composition, and metabolism as a result of the removal of *D. antillarum,* strongly support previous experimental results and reaffirm the concept that this sea urchin species is instrumental in structuring many Caribbean coral reef algal communities.

RESUME

I1 a etc demontre que le broutage par *Diadema antillarum* controlait la biomasse, Is composition specifique et plus rec enment le metabolisms de ninbreuses c ammo mutes de gazons recifaux. La majorite de ces donnees ont etc obtenues en utilisant des cages experimentaley d'inclusion-exclusion. Les mortalites massives recentes de cet oursin clans les Caraibes ont fourni un test naturel a beaucoup de ces hypotheses emises a partir d'experiences. A Sainte-Croix, deux ate de donnees obtenues avant is mortalite massive ont montre que lea gazons broutes par *D. antillarum* avaient une production de biomasse specifique plus elevee (production par algue et biimasse en fonction du temps). La disparition naturelle de 957. des *Diadema* a entrains des modeles similaires lane la production et la biomasse des gazons. Cinq jours apres la mortalite, la bianasse algale avait augments de 27% alors que is production de biomasse specifique decroissait de 607. De plus, un changement clans la c imposition specifique algale avait debuts moans de 5 jours de la mort des oursins. Les plus grandes especes d'algues comme *Laurencia obtusa* et *Acanthophora spicifera* augmentaient en abondance alors que lee plus petites especes d'algues filamenteuses bien qu'augmentant en taille, decroiesaient en abondance dana touter lee zones. Ces phenomenes ont persists 10 mois, et furent plus prononces dens les zones recifales peu profondes. Des etudes recentes ont euggere que la competition pour 1'exploitation des ressources algales dolt exister entre lee poissons herbivores et lee oursins. Des resultats preliminaires suggerent qu'une telle competition existait avant la disparition des *Diadema.* La disparition proche de cette espece a entrains une reponse immediate des poissons herbivores et principalement des Scaridae. L'intensite du broutage des poissons, mesuree par photographic, a augments de 3807 une semaine apres la mort des *Diadema.* La possibilite d'une reponse numerique a long terme par lee populations de poissons herbivores eat actuellement examinee. Les changements dens 1'abondance des algues, clans leur composition specifique, et clans le metabolisme, resultant de is disparition de *D. antillarum* corroborent les resultats experimentaux anterieurs et reaffirment le concept que cette espece d'oursin intervient daps la structuration de beaucoup de c anmunautes algales des recife des Caralbes.

INTRODUCTION

Herbivorous organisms are important in many marine habitats particularly in coral reef environments (Stephenson and Searles, 1960; Wanders, 1977; Ogden and Lobel, 1978). Herbivores are very abundant on most Caribbean reefs and consist of species in several families of fishes (Acanthuridae, Blenniidae, Kyphosidae, Pomacentridae, and Scaridae) and numerous species of invertebrates in several phyla. Although the relative importance of these herbivores in structuring the algal community is likely to vary between reef sites, on many of the reefs investigated to date, the echinoid *Diadema antillarum* Philippi has been demonstrated to have a major effect on the plant community. Grazing by this species has been shown to have a dramatic effect on algal abundance and species composition (Ogden et al., 1973; Sammarco et al., 1974; Ogden, 1976; Carpenter, 1981, 1983, 1984a; Sammarco, 1982a), and on algal community metabolism (Carpenter, 1983, 1984a). Grazing by this sea urchin also affects the survival of settling coral spat (Sammarco, 1980, 1982a). All of the above effects have been demonstrated by the employment of some kind of field experiment, including whole reef manipulations (usually patch reefs, Ogden et al., 1973; Sammarco et al., 1974; Sammarco, 1982b) or structures designed to include/exclude *Diadema* individuals (Carpenter, 1981, 1984a; Sammarco, 1982a). Several of these studies have employed appropriate experimental designs that have included treatment replication and controls, however many have not been either spatially or temporally replicated making generalized interpretation of the results inappropriate. The pitfalls of field experimental design and the resulting data interpretation in benthic marine ecology and particularly the use of caging structures, have been examined by Dayton and Oliver (1980), Underwood (1981, 1983), Kennelly (1983), and Hurlbert (1983).

With these caveats in mind, the results from previous experiments with *Diadema* suggest that this sea urchin species keeps the algal community in a low biomass, high turnover state. This generalized grazing can enhance (Carpenter, 1981; Sammarco, 1982a) or lower (Sammarco, 1982a) algal species diversity, depending on sea urchin population density and algal settlement patterns (Sammarco, 1982a). Algal community productivity (per unit algal biomass) was demonstrated to be higher for algal communities grazed by *Diadema* than those not grazed by sea urchins (Carpenter, 1984a). The increase in productivity was suggested to be the result of nitrogen input from *Diadema* excretions. The reef algal species present under urchin-grazed conditions are typically small filaments, unicells, and crusts (Marsh, 1976; Wanders, 1976; de Ruyter van Stevenick and Breeman, 1981; Carpenter, in press b). Sizes range from 10-1000 um for the filaments and unicells and 1-20 mm for crustose forms. The canopy heights attained by these multispecific turfs under normal grazing regimes rarely exceed 2-3 mm (Carpenter, 1984a). When *Diadema* are removed, larger, macroalgal species gradually dominate suggesting that they are superior competitors for space. The absence of macroalgae (or presence only as juveniles) under urchin-grazed conditions indicates that either the spores of these species do not settle in grazed areas or that they settle but do not survive. The following hypotheses are based on the previous experimental results and predict the effects of removing *Diadema* on coral reef algal turfs.

HYPOTHESIS 1: Following the removal of *Diadema,* algal turf biomass will increase.

HYPOTHESIS 2: Algal community productivity (per unit area and per unit algal biomass) will decrease following *Diadema* removal. Productivity unit area will gradually increase again as algal biomass accumulates the point where increased biomass per unit area compensates for the reduction in biomass-specific rates.

HYPOTHESIS 3: *Diadema* removal will lead to shifts in algal species compositon with algal filaments decreasing in abundance while macroalgal species become more abundant.

Mass-mortality of *Diadema* occurred throughout the Caribbean beginning in Panama in January 1983 and reached St. Croix, U.S. Virgin Islands in February 1984 (Bak et al., 1984; Hughes et al., in press; Lessios et al., 1984; Carpenter, in press a). Where previous data on population density existed it is estimated that between 95-99% of *Diadema* individuals died. This represents a natural removal experiment that eliminates many of the experimental artifacts associated with manipulations in the previously described studies. However, although this experiment is replicated spatially (i.e. sites throughout the Caribbean), it is not replicated temporally and has no true control (i.e. changes observed after the die-off may be unrelated to the absence of *Diadema* and instead are the result of temporal flucuations; since the die-off occurred over all sites, no suitable control for the detection of such temporal variabilty exists). This limitation should be recognized when using data from this experiment to test the above experimentally-generated hypotheses. If data obtained from the natural experiment do not support the predictions made by these hypotheses, this may be grounds for rejecting what have become generalizations about the effects of this important herbivore on reef algal communities.

STUDY SITE, METHODS, AND MATERIALS

Natural algal turf communities were allowed to develop on uniform experimental settling plates (cross-sections of *Acropora Ealmata)* in St. Croix, U.S. Virgin Islands (17 45 N., 64° 42' W.). The plates were initially sub-merged in December 1981 at a backreef/reefcrest site on Tague Bay Reef in 1.5-2 m of water. Plates were allocated to one of several grazing treatments that permitted algal communities to be grazed by selected herbivore groups. *Diadema* inclusion cages, exclusion cages, and cage controls were placed in the same locality as treatments available to all herbivores. Additional details of the experimental design are given in Carpenter (1984a, in press a,b). Monthly estimates of algal turf biomass (decalcified dry weight) mere obtained by scraping randomly located 1-cm samples from the plates to a depth of ca. 1 mm into the plate. Biomass samples were decalcified in <5% HC1 and 5% formalin, filtered, rinsed, and dried to constant mass (>24 h) at 60 °C. Subsamples were also taken in the same manner for chlorophyll a determinations. Such samples were ground with a mortar and pestle in 90% acetone and 1 ml of a saturated MgCO solution and allowed to extract in the dark it 4 °C for 20-24 h. Chlorophyll a was determined spectrophotometrically and calculated using the equations of Jeffrey and Humphrey (1975).

Algal community productivity was estimated from changes in dissolved oxygen during 15 min in *situ* incubations of the algal plates in Plexiglas chambers (volume 2.9 L). All incubations were conducted at saturating irradiances determined from production-irradiance experiments. Water motion was created inside the chambers by air-driven magnetic stirrers and by a surge-driven paddle that created an oscillatory flow over the plate surface. Conditions were maintained that result in maximum rates of apparent photosynthesis. For additional details of production methods see Carpenter (in press b).

Random subsamples were also scraped from the plates to assess relative abundance of algal species. Samples were decalcified in <5% HC1 and 5% formalin, rinsed, filtered, and spread evenly on microscope slides. The data on algal species abundance that is presented here was obtained by scanning each slide and recording whether each species encountered was rare, common, or abundant.

The first signs of *Diadema* mortality appeared near the established study site in St. Croix on February 5 (J. Ogden, pers. comm.). By February 10, 99% of the individuals had died (Carpenter, in press a and Table 1). The first post-mortality sampling of the algal community was conducted on February 15. Additional sampling took place in April, June, September, and December 1984. Two cages containing two *Diadema* individuals each (mean maximum test diameter 61 mm) were placed over plates previously uncaged (i.e. available to all herbivores) in April. These cages were maintained as a separate treatment until October, when a storm liberated the sea urchins. Cage controls were not established since results from the previous year had shown no significant effects of the caging structures on the algal communities (Carpenter, 1984a).

Reference to *Diadema* throughout this paper will refer specifically to *D. antillarum.*

RESULTS

Although microherbivores were present to some extent in all treatments, previous experiments at this locality suggest that they do not exert an important influence on algal communities in areas exposed to other herbivores (Carpenter, 1984a). Grazing treatments will be referred to as: fish-grazed, for those algal communities inside sea urchin exclusion cages (prior to the urchin die-off) but available to herbivorous fishes, and algal communities outside cages after the die-off; Diadema-grazed, for treatments inside sea urchin inclusion cages both before and after the die-off; and *Diadems* and fish-grazed for treatments outside cages before the die-off.

Table 1- Mean number (± S.D.) of *Diadema* individuals per m^2 at the backreef/reef crest study site before and after the mass-mortality event.

	n	No. ind./m^2
Aug. 1983	18	6.1 ± 1.8
Oct. 1983	16	5.2 + 1.6
Dec. 1983	20	6.4 + 3.6
mass-mortality		
Feb. 1984	20	0.1 + 0.2
April 1984	20	0.4 + 0.8
June 1984	20	0.2 + 0.4
Sept. 1984	20	0.1 ± 0.3
Dec. 1984	20	0.1 + 0.2

Algal Biomass

Algal turf biomass for the *Diadems* and fish-grazed treatment ranged from 1.2-4.5 mg/cm before the mortality event (Fig. 1). Biomass of turfs grazed by *Diadems* only were not significantly different from the *Diadems* and fish-grazed treatment. Algal biomass for the fish-grazed algal communities however was significantly higher ($p< 0.01$, 2-way ANOVA) than biomass in the other grazing treatments (Carpenter, 1984a).

The mean biomass for the Diadema and fish-grazed treatment in December 198 was 3.0 ± 0.4 mg/cm^2 S.D., n=18). Five days after the mass-mortality of *Diadema,* algal biomass on these plates increased to 3.8 ± 0.3 (n-12, $p< 0.05$, ANOVA, Carpenter, in press a). Biomass continued to increase in this treatment until September 1984 when it leveled off at a mean value of 12.4 ± 3.8 mg/cm .

The Diadems-grazed treatment that was re-established in April showed decreases in algal biomass ($p< 0.001$, 2-way ANOVA) between April (5.1 ± 1.0) and June (2.6 ± 0.8), and again between June and September (1.7 ± 0.8). December values were not obtained due to the destruction of the inclusion cages in October.

Algal Community Productivity

Algal community productivity per unit area was not significantly different between pre-mortality grazing treatments, although the *Diadema-grazed* treatments were often higher than turfs not grazed by sea urchins (Carpenter, 1984a). In December 1983 the mean productivity per unit area for turfs grazed by *Diadema* and fiches was 0.68 ± 0.12 g 0 m h (Carpenter, 1984a and Fig. 2R). Five days after the mortality event productivity per unit arga dripped by 37% to 0.43 ± 0.09 g 0_2 m h (Carpenter, in press a). Areal

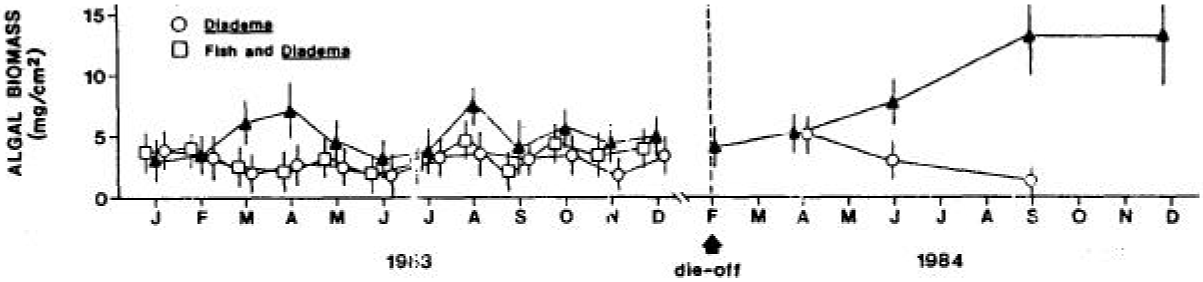

Figure 1 : Mean algal biomass (decalcified dry wt.) ± S.D. for grazing treatments before and after the Diadema mass-mortality. Pre-mortality data are from Carpenter (1984a). N=12 for all points.

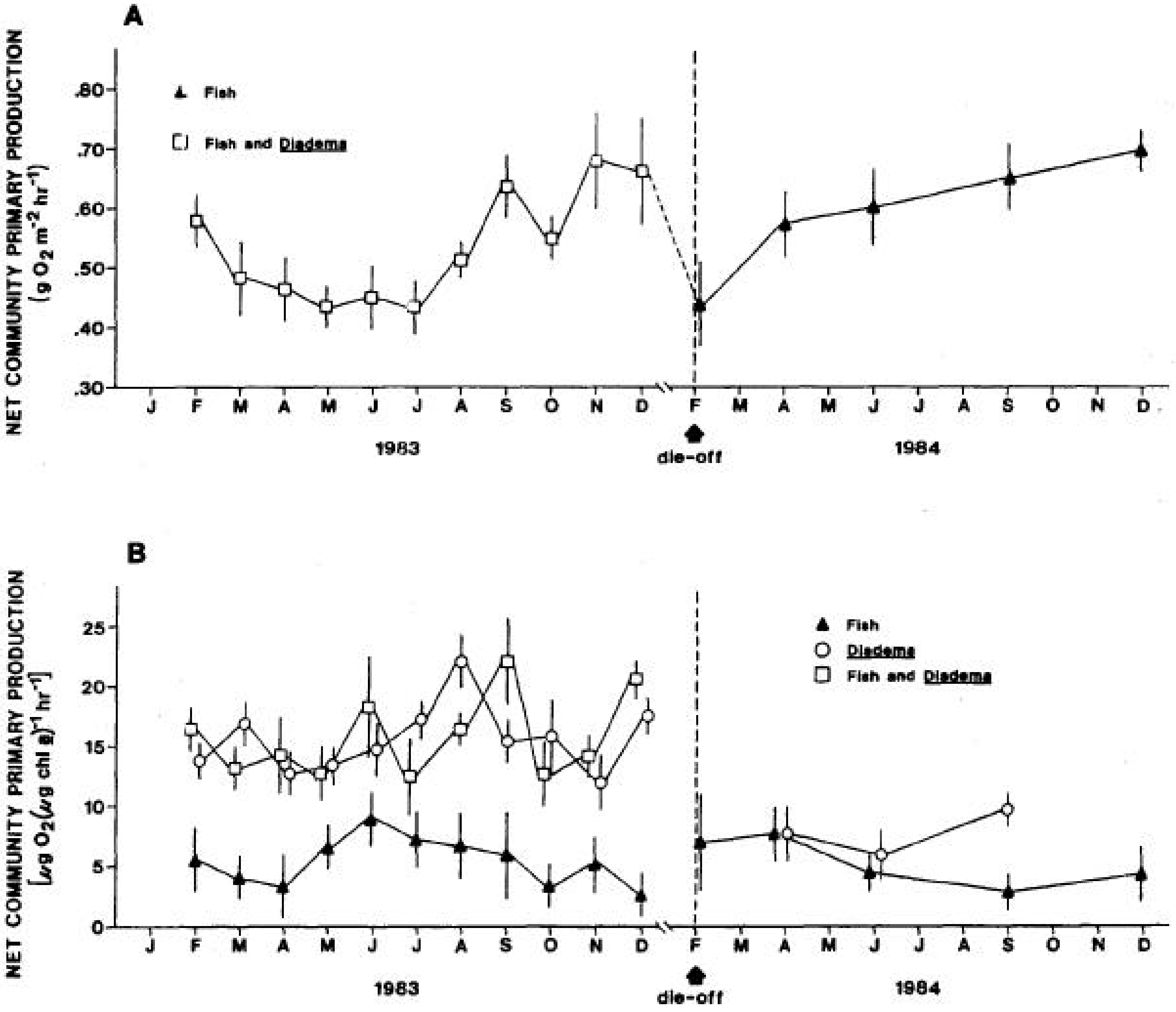

Figure 2 : Mean community primary production (± S.D.) per area (A) and per unit biomass (B) before and after Diadema mass-mortality. Post-mortality Diadema-grazed treatments are inclusion cages. Pre-mortality data from Carpenter (1984a).

Table 2- Relative algal abundances before (Dec. 1983) and after (Feb. and Sept. 1984) mass-mortality of *Diadems.* Abundance categories are; rare (R), common (C), or abundant (A). Macroalgal species are preceeded by an asterisk.

Taxa	Dec. 1983			Feb. 1984			Sept. 1984		
	R	C	A	R	C	A	R	C	A
Cyanophyta									
Calothrix cruetacea		x			x		x		
Mastigocoleus testarum			x		x			x	
Oscillatoria sp.	x			x					
0. *submembranacea*		x			x			x	
Chrysophyta									
pennate diatoms		x			x		x		
Chlorophyta									
**Acetabularia pusilla*	x			x				x	
Cladophora delicatula	x			x					
Cladophoropsis membranacea				x					
coccoid green	x			x				x	
**Dictyosphaeria cavernosa*							x		
Protoderma marinum			x		x				
Phaeophyta									
**Dictyota* sp.								x	
Giffordia rallsiae			x			x			
Sphacelaria tribuloides	x				x			x	
Rhodopyta									
**Amphiroa fragilissima*					x				x
Aspara opsis taxiformis (Falkenbergia stage)	x			x					
Asterocytis ramosa	x								
Ceramium byssoideum	x				x				
Centroceras clavulatum					x				
crustose corallines		x			x				
Gelidiella trinitatensis	x				x				x
Herposiphonia secunda			x			x			
**Jania capillacea*					x			x	
**Laurencia obtusa*					x			x	
Polysiphonia subtilissima		x		x					
Polysiphonia sp.	x			x					
Taenioma macrourum		x				x			
Wurdemannia miniata	x				x			x	

activity increased after February as algal activities increased and returned to pre-mortality rates (fig. 2a). Before the urchin die-off, biomass specific activity was significantly higher for fish grazed turfs than for those not inhabited by sea urchins (Fig. 2b). The immediate mortality biomass-specific rates decreased (Carpenter, in press a) and have remained at levels that closely correspond to rates by pre-mortality rates by pre-mortality rates in fish-grazed treatments. In contrast, biomass-specific productivity in the re-established *Diadem* inclusion treatments increased and was significantly higher than rates in the fish-grazed treatments by September ($p< 0.01$, t-teat).

Algal Species Composition

Algal turfs prior to the *Diadema* mortality were dominated by several species of filementous algae and blue-greens (Table 2). The presence of macroalgal species was rare and only represented by juvenile plants. Five days after the die-off macroalgal species were present in the changing turf communities and many were moderately abundant by June. These species have become persistent members of what was previously an algal turf community. As a result of changes in species composition, algal canopy heights, which were ca. 1 mm before the die-off, increased to a mean value of 7 mm by September. Some areas colonized by species such as *Sargassum* sp. and *Turbinaria turbinata* have canopy heights exceeding 30 cm. Patterns in the number of algal species that have coexisted within the algal community before and after the die-off will be examfined after a more complete analysis of the relative abundances of algal species is conducted.

DISCUSSION

Although manipulative field experiments may be affected by artifacts and variability beyond the control of the experimenter, such experiments remain the most powerful tool for ecologists to discern the processes that produce patterns in the distribution and abundance of biota. Interpretation of data from natural experiments resulting from episodic disturbances is usually limited by a lack of a suitable control. Spatial replication is often adequate but temporal replication is improbable (Dayton and Oliver, 1980). However, if combined with accurate natural historical observations (documentation of patterns) and field experiments that produce testable hypotheses, natural experiments can provide limited tests of the proposed hypotheses and insights into the functioning of ecological systems.

Ten years of field experiments with *Diadems* has produced several hypotheses concerning how this species affects reef algal communities in the Caribbean. Three hypotheses were singled out and tested by data obtained following the near elimination of *Diadema,* presumably by a natural agent (Lessios et al., 1984), at pre-established study sites.

Data on post-mortality algal biomass support Hypothesis 1 that predicted an increase in biomass following *Diadems* removal. In St. Croix, *Diadems* is the major herbivore in terms of grazing intensity (Carpenter, 1984a). Herbivorous fishes can remove as much biomass per unit time but maintain the algal community at a higher biomass than do urchins. At other localities, herbivorous fishes may be more abundant and graze more intensely (M. Hay, pers. comm.), which may result in low biomass turfs similar to those maintained by *Diadema.* However, inherent differences in the foraging behaviors between *Diadema* and herbivorous fishes (Carpenter, 1984a,b) may lead to the maintenance of very different types of algal communities. The frequency with which fishes regraze a particular area is lower than the regrazing frequency of *Diadema* (Carpenter, 1984a) resulting in a less systematic mode of grazing (Steneck and Watling, 1982) which allows patches of algal turf to attain a higher biomass than urchin-grazed turfs. Patchiness in turf biomass is evident in reef areas that are differentially available to fishes and urchins. Qualitative differences in herbivory (i.e. which herbivore groups graze an aran) result In qualitative differences in fish abundance.

(hypothesis 2 predicted that algal primary productivity would decrease immediately following the removal of Diadema. This is supported by the observed decreases in both productivity and in unit area and biomass-specific productivity urchin mortality and suggests shat grazing has a positive effects on turf productivity. This has been hypothesized to result from nitrogen regeneration and input by this urchin species (Carpenter, in press a), productivity per unit area has gradually increased again as algal biomass has more than doubled. The lack of correspondence between production tries per unit area in February 1983 and February 1984 suggests that seasonal changes in production are probably not responsible for the observed short term decrease in production. Production data from subsequent years are needed to substantiate this.

Biomass-specific productivity has remained low and corresponds closely with levels demonstrated in the previous experimental treatments that excluded grazing by *Diadema.* Alternative hypotheses exist that can partially explain the demonstrated productivity effects and are not mutually exclusive of the nitrogen regeneration hypothesis. An increase in self-shading resulting from the increased canopy height could lower biomass-specific productivity as could the presence of algal species with lower productivity/ biomass ratios (Littler et al., 1983). Experimental tests of these hypotheses are being conducted.

The reversal of the above patterns in algal biomass and productivity for algal communities in the re-established Diadema-grazed treatment, strongly supports the contention that *Diadema* is extremely important in controlling algal turf biomass and productivity.

Although quantitative data are not yet available, the algal presence/ absence data presented in Table 2 are supportive of Hypothesis 3. Macroalgal species that were absent or rare in Diadems-grazed turfs have increased in abundance since the mortality event. Many of these species are usually found in reef areas not accessible to herbivores (at least initially). Macroalgae likely settle in all areas, but only in crevices or on reef tops do they obtain a refuge from generalized grazing. Spatial escapes may be required for macroalgae to acquire structural or chemical deterrents to herbivory (Norris and Fenical, 1982; Littler et al., 1983) or to achieve an escape in size which makes them unavailable (sensu Steneck and Watling, 1982) to many grazers such as *Diadema.* Data presented here suggest that generalized grazing by *Diadema* in St. Croix prevents the survival of macroalgae in areas that are repeatedly grazed. Persistence of any algal species under a grazing regime is dependent on either escapes from herbivory, as outlined above (see Lubchenco and Gaines, 1981), or on the ability to maintain a biomass production rate that at least equals the rate of removal by herbivores. Many macroalgal species have lower ratios of photosynthetic to structural tissue which results in lowered biomass-specific growth rates (Littler et al., 1983) and probably limits their ability to survive under most intense grazing regimes.

The changes in algal turfs described for back-reef/reefcrest habitats have also occurred to varying degrees over all reef zones (Carpenter, pers. obs.). Changes are most pronounced in areas where *Diadems* was previously most abundant. Shallow forereef habitats (where urchins were abundant) have undergone changes similar to those shown here for backreef/ reefcrest communities. Deeper (5 m and 10 m) forereef habitats have changed to some degree but differences are less dramatic than those exhibited in shallow reef areas.

The response of herbivorous fishes to the increased availablity of algae have been consistent with the hypothesis that exploitative competition was occurring between these species and *Diadema* prior to the die-off (Williams, 1981; Hay, 1984). An immediate functional response (increased grazing intensity) was demonstrated five days after the mortality event (Carpenter, in press a). Although the variance is high for this data, this functional response has continued (Carpenter, unpubl.). An eventual numerical response of herbivorous fishes (increased population sizes) to increased algal resources will likely depend on recruitment patterns and mortality rates of individual species of herbivorous fishes and on the recolonization rates of *Diadems.*

The lack of a suitable control for this natural experiment may not seriously limit the generality of the results given their close correspondence with previous experimental results. The probability of natural temporal variability producing the observed changes in algal biomass and productivity are unlikely. This interpretation is supported by the reversal of algal biomass and productivity trends observed in the treatment where grazing by *Diadema* was re-established.

The mass-mortality of *Diadema* has resulted in patterns of algal community change (at least in the short term) that support experimentally-generated hypotheses on the effects of this urchin species on Caribbean algal communities. The eventual recolonization and recovery of *Diadema* populations will allow tests of the converse predictions of the same hypotheses. The degree of concordance between the results of previous field experiments and this natural experiment demonstrates the utility of well-designed field experiments in elucidating the processes that control complex ecological systems.

Acknowledgements

Portions of this research were supported by the Sea Grant Program of Puerto Rico (UPR PD-21), the University of Georgia Sea Grant Program, the West Indies Laboratory, and the Marine Systems Laboratory. Special thanks are extended to J. Ogden for providing laboratory facilities and to H. Carpenter and S. Williams for their unflagging help with the fieldwork. This is Contribution No. 150 from the West Indies Laboratory, St. Croix, U.S. Virgin Islands.

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