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Herbivory and algal dynamics on the coral reef at Discovery Bay, Jamaica

Abstract—The cover of noncoralline macroalgae increased dramatically on Caribbean reefs during the 1980s and 1990s. A top-down hypothesis, based largely on observations at Discovery Bay, Jamaica, is that this change was caused by reduced herbivory. Herbivory was reduced by the regional mass mortality of the echinoid *Diadema antillarum* in 1983–1984 and by human exploitation of herbivorous fishes. An alternative, bottom-up explanation is that nutrient concentrations increased past threshold levels for algal blooms. Surveys at Discovery Bay showed that *Diadema* reappeared on the shallow fore reef after 1996, accompanied by drastically reduced macroalgal cover. There is no evidence to suggest that nutrient levels declined at the same time. These observations corroborate predictions of the top-down hypothesis, and they confirm the key role of herbivory in structuring shallow reef communities of the Caribbean.

Coral cover has declined and the cover of fleshy and filamentous macroalgae has increased substantially on coral reefs of the western Atlantic and Caribbean region over the past two decades (Jackson 1994; Steneck 1994; Aronson and Precht in press). A large body of literature suggests that coral mortality and reduced herbivory were the factors primarily responsible for the coral-to-macroalgal transition on Caribbean reefs. Hurricanes, diseases, and other disturbances killed coral colonies, opening space for colonization (e.g., Rogers 1985; 1993; Aronson and Precht 1997, in press). Herbivory was reduced by the regional mass mortality of the echinoid *D. antillarum* in 1983–1984 and by overfishing of parrotfish (Scaridae) and surgeonfish (Acanthuridae), permitting luxuriant algal growth (Lessios 1988; Knowlton 1992; Steneck 1994). This top-down scenario was based to a large extent on observations of reef dynamics at Discovery Bay and elsewhere along the north coast of Jamaica (Woodley et al. 1981; Liddell and Ohlhorst 1986; Knowlton et al. 1990; Hughes 1994). Experimental work at Discovery Bay and other Caribbean localities demonstrated the importance of herbivory (Sammarco 1982; Carpenter 1986; Lewis 1986), and the effects seemed particularly obvious in Jamaica. Studies in the Indo-Pacific also suggested that herbivory controls algal biomass and distribution (McClanahan and Muthiga 1988; McCook 1996).

Lapointe (1997; Lapointe et al. 1997) presented an alternative, bottom-up explanation for the increase in macroalgal cover and biomass. Using Discovery Bay and southeastern Florida as study sites, he argued that nutrient concentrations on those reefs have increased past threshold levels for algal blooms. The nutrients are supplied in inputs of freshwater from terrestrial sources, and that water has been enriched and increased in volume by human activities. According to Lapointe, eutrophication was primarily responsible for increased macroalgal abundance in both places. Hughes et al. (1999) presented counterarguments to Lapointe's (1997) assertions, based on equivocal evidence for nutrient enrichment and the conjunction of the *Diadema* mass mortality with the increase in macroalgal cover (see also Szmant and Forrester 1996).

If nutrient concentrations determine macroalgal abundance, and if those concentrations have increased beyond threshold levels in recent years, then an increase in herbivory now should not affect macroalgal cover. No effect of increasing herbivory under these circumstances would falsify the hypothesis that herbivory is the sole control on macroalgal abundance. On the other hand, if the cover of fleshy macroalgae now declines in the face of increased herbivory, as predicted by Hughes et al. (1999), that would falsify the hypothesis that nutrient concentrations exert exclusive control.

A third alternative is the relative dominance model of Littler and Littler (1985; Littler et al. 1991), in which nutrient concentrations and grazing pressure from herbivores together determine which functional group(s) of primary producers will occupy most of the reef substratum. According to this model, corals predominate at low nutrient and high grazing levels, coralline algae predominate at high nutrient and high grazing levels, algal turfs predominate at low nutrient and low grazing levels, and macroalgae predominate at high nutrient and low grazing levels. If this model is correct, and if the macroalgal-dominated reefs in Florida and Jamaica are indeed subject to high levels of nutrient input, then increased herbivory now should lead to reduced cover of macroalgae and increased cover of coralline algae but not to the reappearance of corals. Recent changes at Discovery Bay constitute an ongoing natural experiment that allow us partially to distinguish the top-down, bottom-up, and relative dominance alternatives.

We surveyed a 40 × 30 m area of the Long-Term Study (LTS) site at 4–6 m depth on the fore reef at Discovery Bay, near the Discovery Bay Marine Laboratory (DBML). Surveys were conducted in February of each year during the period 1993–1999, with the exception of 1997. During each survey year, six 25-m surveyor's tapes were laid haphazardly in the study area. A diver swam along each transect, counting scarids and acanthurids within 1 m on either side of the line. The diver then swam back along the transect, recording the sessile organism or substratum type beneath each 10 cm mark on the tape. This linear point intercept (LPI) sampling strategy yielded six estimates of each category of substratum cover (one from each transect), with each estimate based on 250 point counts. The LPI method is sufficiently accurate for comparative purposes, particularly on low-diversity reefs or where only a few functional categories are compared (Ohlhorst et al. 1988). Finally, the diver swam the transect a third time, recording regular echinoids (*D. antillarum, Tripneustes ventricosus, Echinometra viridis*, and any other species) within 1 m on either side.

Since the positions of the transects were different in each sampling year, among-year variations in the counts of scar-

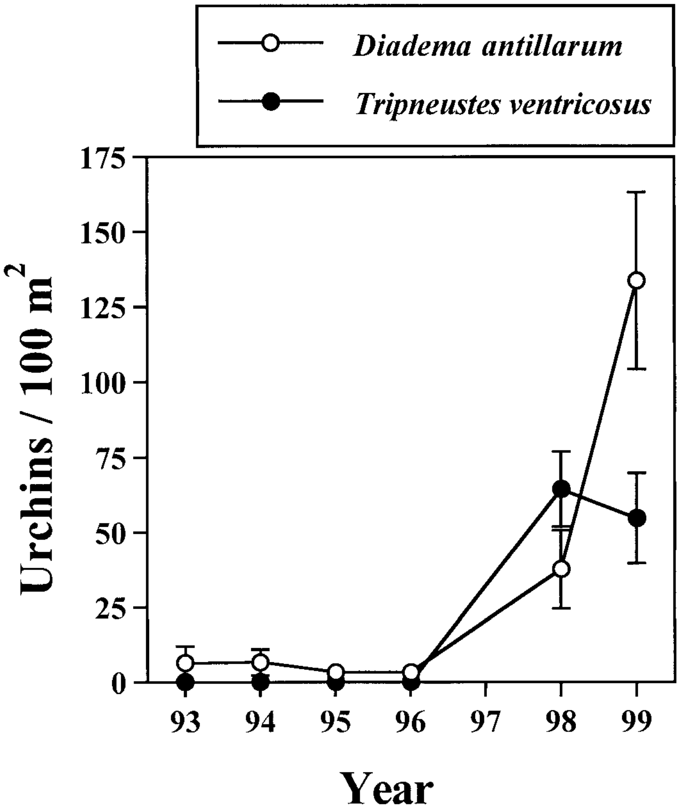

Fig 1. Mean population densities through time of two species of regular echinoids in the study area. Error bars represent standard deviations. Although the censuses were conducted along replicate 50-m² belt transects, the densities are scaled to 100 m² for ease of interpretation.

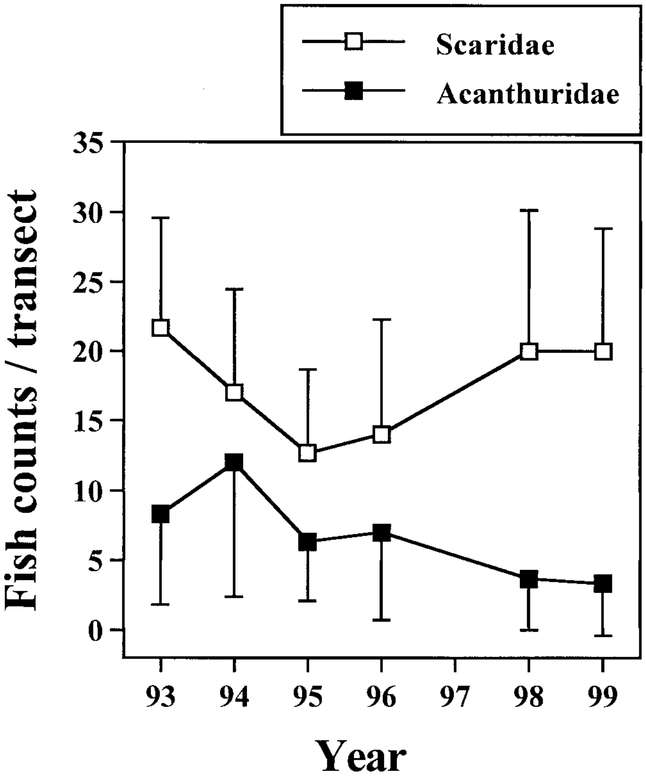

Fig. 2. Mean numbers of parrotfish (Scaridae) and surgeonfish (Acanthuridae) in the 50-m² belt transects. Error bars represent standard deviations. Only positive or negative error bars are shown.

ids, acanthurids, and *D. antillarum* were evaluated using a one-way factorial analysis of variance (ANOVA) design, with time as the factor. *T. ventricosus* could not be analyzed by ANOVA, as discussed below. The abundances of *E. viridis* and other echinoids were negligible in all surveys, and counts of these species were not analyzed.

Point counts for each transect were tallied for the following functional categories of substratum occupants: fleshy and filamentous macroalgae; hard corals (Scleractinia plus Milleporina); *Halimeda* spp., which are calcareous green algae; and a category combining crustose coralline algae, algal microturfs (algal filaments <2 cm tall and so sparse that the substratum was visible), and bare space. The latter combined category is henceforth abbreviated CTB. Among-year variations in these benthic categories were again analyzed by one-way ANOVAs.

The data sets were tested prior to ANOVA for conformity to the assumptions of parametric statistics. The F_{max} test was used to assess homogeneity of variances and the Lilliefors test was used to assess normality. Data that violated either assumption were transformed if possible. The counts of scarids and acanthurids did not require transformation (F_{max} and Lilliefors tests, $P > 0.05$). The counts of *D. antillarum* violated the assumptions of both homogeneity of variances and normality (F_{max} and Lilliefors tests, $P < 0.05$), and these data were brought into conformity using the square root transformation, $(Y+1)^{0.5}$. The counts of *T. ventricosus* were problematic because the means and variances were zero until 1998, when *Tripneustes* abundance (and hence the variance) increased sharply. Although zero variances during the period 1993–1996 prevented us from performing an ANOVA, the temporal pattern was so distinct that the statistical test was unnecessary. The point count data for macroalgae, hard corals, *Halimeda* spp., and CTB conformed to the assumptions ($P > 0.05$ in F_{max} and Lilliefors tests) and were analyzed without transformation.

D. antillarum were rare from 1993–1996 (Fig. 1), as they had been since the mass mortality a decade before. After 1996, the population density of *Diadema* at the study site increased by more than an order of magnitude. ANOVA of the root-transformed data showed this increase to be highly significant ($P < 0.0005$). Tukey HSD a posteriori comparisons revealed that the counts for 1998 and 1999 were significantly different from each other and significantly different from the counts for the years 1993–1996, which were themselves not significantly different ($93 = 94 = 95 = 96 < 98 < 99$). *T. ventricosus* showed a similar pattern (Fig. 1), although the data were not analyzed by ANOVA.

Neither the scarid counts nor the acanthurid counts showed significant among-year variation ($P > 0.30$ and $P > 0.15$, respectively; Fig. 2). Nearly all of these fish were of a small size (<20 cm total length). The rarity of large scarids and the absence of large schools of acanthurids at Discovery Bay have been noted by other investigators and

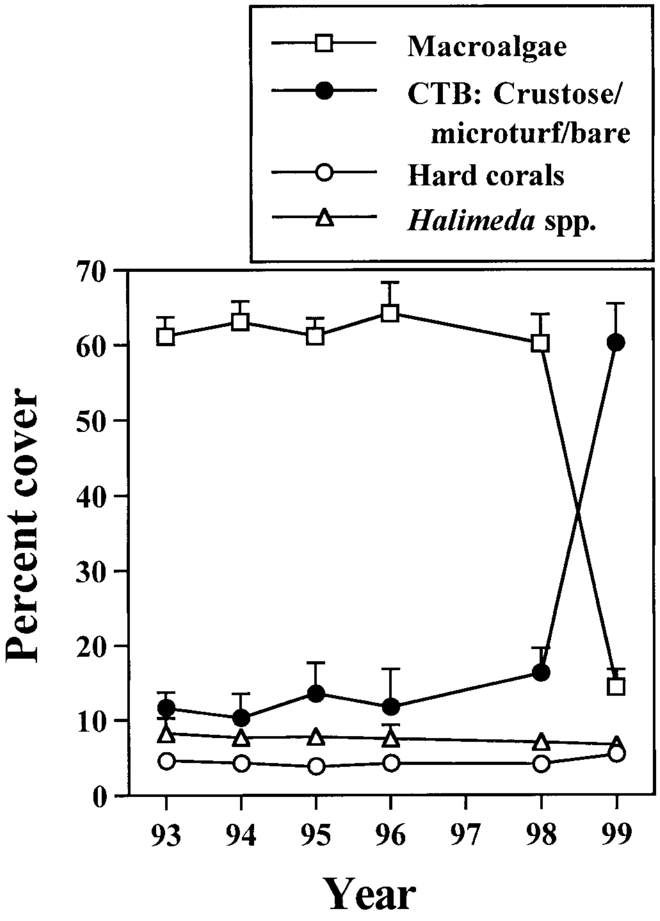

Fig. 3. Mean percent covers of substratum components, based on point counts along the 25-m transects. Error bars represent standard deviations, and only positive error bars are shown. Errors associated with mean coral cover and mean *Halimeda* cover in most years are too small to appear on the graph.

are the result of decades of heavy fishing pressure (Munro 1983; Hughes 1994).

Point counts of macroalgae exhibited significant among-year variation (ANOVA, $P < 0.0005$). Macroalgal cover was high through the 1998 survey and then dropped sharply in 1999 (Tukey comparisons, 1999 significantly different from all the other years; Fig. 3). Point counts of the CTB category showed the opposite pattern, with low cover through 1998 and then a sharp rise (ANOVA, $P < 0.0005$; Tukey comparisons, 1999 significantly different from all other years). Hard coral counts also showed a significant effect of year (ANOVA, $P < 0.035$); coral cover was low throughout the study, but cover in 1999 was significantly greater than in 1995 (Tukey comparison, $P < 0.025$). Point counts of *Halimeda* showed a non-significant declining trend (ANOVA, $P > 0.50$), barely perceptible in Fig. 3. Adjustment of the significance levels (α) to control experimentwise error did not alter the conclusions drawn from this set of ANOVAs.

In summary, benthic cover changed as the abundance of two species of herbivorous sea urchins increased. Macroalgal cover declined, CTB cover increased, and coral cover may have increased. The abundance of herbivorous fishes, especially the larger size classes, remained low throughout the study due to continued heavy fishing pressure in Discovery Bay and elsewhere along the north coast of Jamaica.

The composition of reef biotas varies at a spatial scale of kilometers to tens of kilometers along the north coast of Jamaica, but ecological patterns and processes tend to be relatively uniform at a scale of hundreds of meters to kilometers within individual reefs (Edmunds and Bruno 1996). Thus, while the statistical conclusions derived from this study are restricted to the area surveyed and to the winter season, videotaped transects and direct observations elsewhere and in other seasons suggest that the patterns apply over a larger area of the fore reef at Discovery Bay in the 4–6-m depth range. Below 6 m, however, population densities of sea urchins remain extremely low and macroalgal cover remains high.

The recent increase in the population density of *D. antillarum* down to 6 m depth at Discovery Bay after more than a decade of virtual absence has been noted by other investigators (Woodley 1999). Woodley et al. (1999) pointed out that the current high abundance of *T. ventricosus* on the shallow fore reef is unprecedented in at least that last several decades. *Tripneustes* is commonly found in back-reef and seagrass habitats (Keller 1983). Its appearance on the shallow fore reef in large numbers at Discovery Bay and elsewhere along the coast of Jamaica (Lapointe 1999) was unexpected, although Ogden (1976) reported increased abundance of *Tripneustes* on patch reefs in St. Croix from which *Diadema* had been experimentally removed.

If nutrients exert exclusive control over algal dynamics, the decline in macroalgal cover in 1998–1999 should have resulted from a sudden decline in nutrient input to Discovery Bay. Although we do not have direct measurements of nutrient flux to our study area, rainfall provides a proxy measure of nutrient input from terrestrial sources. Lower rainfall in 1998–1999 would have reduced surface and groundwater input to Discovery Bay. Since human population density has not declined recently at Discovery Bay, and since there have been no reductions in agriculture, bauxite mining and processing, or sewage disposal, a decline in rainfall in 1998–1999 would have been essentially the only way in which terrestrial nutrient input could have been reduced. Rainfall did not in fact decline at Discovery Bay during 1998–1999 compared with previous years (DBML, unpubl. rain gauge data). There is, therefore, no indication that nutrient input from terrestrial sources suddenly abated. Thus, there is no reason to believe that a decline in nutrient input caused the macroalgae to disappear.

While correlative studies are no substitute for multifactorial experiments (Hatcher and Larkum 1983; McCook 1996; Larkum and Koop 1997), direct observation is the only way to ascertain whether hypothetical explanations have any real-world validity. The changes that we and others have observed on the shallow fore reef at Discovery Bay corroborate predictions of the top-down/herbivory hypothesis. Increased echinoid abundance was accompanied by decreased cover of fleshy and filamentous macroalgae and increased cover of CTB. These results are also predictions of the relative dominance model. We conclude that in this area nutrients do not exert exclusive control over the abundance of different functional groups of primary producers. The difference between the top-down and relative dominance explanations is that the top-down hypothesis predicts an increase in coral abundance with increasing herbivory, whereas the relative dominance model predicts that coral cover should remain low despite increased herbivory, because nutrient levels should remain high. Distinguishing these models will thus be a matter of additional monitoring to determine whether coral cover continues to increase, presuming that the population density of *Diadema* remains at its present level or continues to increase. If coral cover does increase, it will most likely do so on a time scale of years to decades, considering the slow growth and recruitment rates of corals in the Caribbean (reviewed in Aronson and Precht in press).

Today's Caribbean reefs probably exist along a continuum of relative importance of top-down and bottom-up control of macroalgal abundance. At Discovery Bay, low herbivory, in combination with high coral mortality, explained the dramatic increase in macroalgal cover after 1983 (Hughes et al. 1999). The simultaneous reversal of trends in herbivory and macroalgal cover in 1998–1999 confirms the importance of herbivory, but we cannot at present rule out a role for nutrients.

Richard B. Aronson

Dauphin Island Sea Lab
101 Bienville Boulevard
Dauphin Island, Alabama 36528
and
Department of Marine Sciences
University of South Alabama
Mobile, Alabama 36688

William F. Precht

PBS&J
2400 East Commercial Boulevard, Suite 400
Fort Lauderdale, Florida 33308

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