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DIFFERENTIAL EFFECTS OF CORAL REEF HERBIVORES ON ALGAL COMMUNITY STRUCTURE AND FUNCTION

Robert C. Carpenter
Institute of Ecology
University of Georgia
Athens, Georgia 30602

ABSTRACT

Functional herbivore groups were categorized according to the intensity and frequency of disturbance resulting from feeding. Biomass removal, species composition and primary productivity of experimental algal communities subjected to herbivory by each functional group revealed differences among groups. Combined removal of biomass by all herbivores ranged from 32 to 84% of daily algal production. Algal species composition varied according to grazing regime, with crustose forms dominating the most intensely grazed treatments. Specific rates of primary production of urchin grazed treatments were 2 to 4 times those in non-urchin grazed treatments. Species composition of reef algal communities is affected differentially by herbivores, which leads to subsequent changes in community metabolism.

INTRODUCTION

Coral reef communities are characterized by a high level of primary production that supports an abundant and diverse assemblage of organisms. The majority of this production is accomplished by the free-living algal component (Marsh, 1976); however, this component is notably inconspicuous when compared to other highly productive marine algal communities such as kelp forests. Intense grazing pressure by herbivores has been repeatedly shown to limit the standing crop of reef algae (Stephenson and Searles, 1960; Sammarco, et al., 1974; Carpenter, 1981). The predominance of such herbivores in reef communities invites speculation on how such biomass can be achieved and supported by the apparently sparse algal community. In addition, such intense disturbance (herbivory) may have significant effects on the structure of the algal community. Because herbivores differ in their magnitude and mode of biomass removal and the frequency with which such removal takes place, the effects may not be the same for different groups of herbivores.

This paper reports some preliminary results of a study to quantify the effects of different functional groups of herbivores on shallow reef algal community structure and function. A more detailed description of methods and results will be presented elsewhere.

MATERIALS AND METHODS

Functional herbivore groups were categorized using two criteria: the size of patch (disturbance) created per feeding bout, and the probability (frequency) of regrazing the same patch on a subsequent feeding bout. The former is mainly dependent on the size of the feeding apparatus and foraging behaviors such as the number of bites in a particular feeding bout. The second criterion depends on the mobility of the organism as well as on behaviors which determine the size of the foraging range (i.e., homing). These groups cross

phylogenetic boundaries (Figure 1) and are depicted as non-overlapping only for illustration. The organisms listed are potential Caribbean members of each group; the actual composition at a given locality, even on a micro-habitat level, will depend on patterns of species distribution and abundance. For the present study site, Group 1 consists of several fish species in the families Scaridae and Acanthuridae and hereafter will be referred to as the herbivorous fish category. The most important herbivore in Group 2 at this locality is the echinoid *Diadema antillarum*. Members of Group 3 include several amphipods, tanaids, syllid polychaetes and small gastropods.

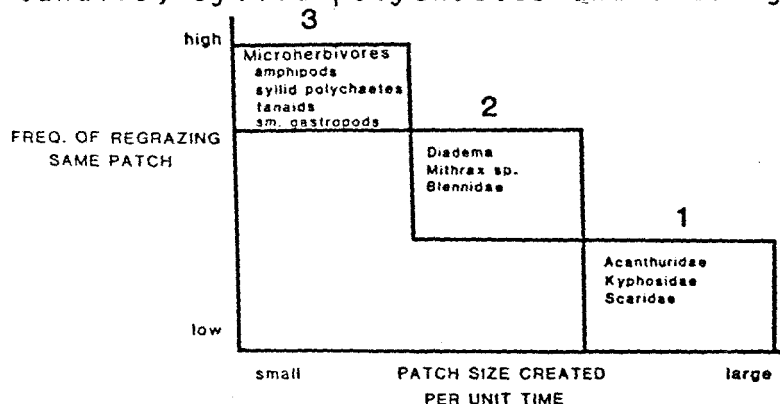


Figure 1. Diagrammatic representation of herbivore functional groups. Group members are potential Caribbean herbivores.

Algal communities were allowed to develop under ambient backreef conditions (depth, 2 m) in St. Croix, U.S. Virgin Islands on experimental substrata consisting of 8 cm x 8 cm x 1 cm cross-sections of the coral *Acropora palmata*. These experimental plates were randomly placed in one of the following treatments: grazing by groups 1 and 3, grazing by groups 2 and 3, grazing by group 3 only, no grazing and control. The accessibility of plates to functional groups was controlled using a combination of cages and suspended platforms at the same depth. Each treatment was replicated once. A detailed description of the experimental design and methods is forthcoming (Carpenter, ms. in prep.). Algal community primary productivity was estimated monthly from changes in dissolved oxygen in well-stirred light and dark plexiglass chambers on randomly chosen plates from each treatment. From the same plates samples were taken to estimate algal biomass (decalcified dry wt.), species composition and chlorophyll *a* content.

The amount of algal biomass removed by each functional group was estimated in two ways. The difference in algal standing crop between plates not grazed and those grazed by a given group gave one estimate. The second, more accurate method converted the areal production rate (corrected for a constant percent of dissolved organic matter excretion (Fogg, 1976)) for a treatment to carbon equivalents, and assuming a constant carbon content, this was translated into the expected dry, decalcified biomass accumulation over a time period. The difference between this expected amount and the actual algal standing crop was assumed to be removed by herbivores.

All data reported here were obtained at least one year after the initiation of the described treatments.

RESULTS

Removal of Algal Biomass

Herbivores removed between 0.88 and 2.10 g dry wt. $m^{-2} day^{-1}$, which represents between 32 and 84% of the daily production of algal biomass (Table 1). The temporal variation in the total biomass removed was mainly the result of variation in the amount removed by the herbivorous fish component. The percent of the total biomass removed by all herbivores that was taken by fishes varied between 3 and 39%. The percent removed by Diadema only varied from 41 to 68%, and micro-herbivores removed from 11 to 28% of the biomass.

Table 1. Mean decalcified dry wt. removed ($g m^{-2} d^{-1}$) $\pm$ S.D. by each functional herbivore group; the % of daily algal production that this represents; and, in parentheses, the % of the total amount removed (N=4). Note that the biomass removed by all herbivore groups is an independent estimate, not the sum of the removals by the three separate groups.

GROUP	JUNE		JULY		AUGUST	
	wt.	%	wt.	%	wt.	%
1	0.45 $\pm$ 0.12	19(38)	0.78 $\pm$ 0.18	33(39)	0.03 $\pm$ 0.05	1(3)
2	0.65 $\pm$ 0.05	26(51)	0.85 $\pm$ 0.14	35(41)	0.59 $\pm$ 0.11	22(68)
3	0.09 $\pm$ 0.07	6(11)	0.31 $\pm$ 0.20	16(20)	0.25 $\pm$ 0.17	9(28)
ALL	1.27 $\pm$ 0.28	51	2.10 $\pm$ 0.61	84	0.88 $\pm$ 0.26	32

Based on herbivore densities in the study area, Diadema is responsible for approximately 50% of the herbivory, fishes 20-30%, and micro-herbivores the remaining 20-30% of the biomass removed.

Algal Species Composition

Algal species composition differed both in terms of what species were present, and their relative abundance. Analyses are not yet complete, so percent relative abundance can not be given; however, presence/absence and dominance data show a pattern related to grazing regime. Plates grazed by all herbivore groups and those grazed by Diadema show similar patterns of algal community structure. Each is dominated by crustose forms (Ulvelia lens and crustose corallines) with minute (10-50 μm diameter) filamentous representatives of the Chlorophyta, Phaeophyta and Rhodophyta. Cyano-bacteria were also well represented. No large corticated algal species were found on any of these plates. Plates from the fish grazing treatment were dominated by a single species of filamentous brown algae (Sphacelaria tribuloides) that formed patches of varying size. Observations suggest that this species is actively avoided by herbivorous fishes. Crusts and other filaments were also of primary importance on these plates.

In contrast, plates grazed only by micro-herbivores fluctuated from a community dominated by larger algae (Coelothrix irregularis, species of the family Gelidiaceae, the upright corallines Jania adherens and Amphiroa fragilissima) to one comprised primarily of crusts and benthic foraminifera. This shift in community structure coincided with

the recruitment of the gastropod Cerithium litteratum onto the plates. This was also accompanied by an increase in the amount of algal biomass removed by micro-herbivores (Table 1). Small filaments also occurred on these plates.

The filamentous species Herposiphonia secunda, Giffordia rallsiae and several blue-greens dominated plates where herbivory was absent or minimal. Pennate diatoms were also abundant. Several larger algal species (Champia parvula, Ceramium nitens and Laurencia obtusa) were present only on these plates.

At this time there appears to be no clear pattern in the number of algal species occurring under each type of grazing regime.

Algal Primary Production

Production per unit area was not significantly different between treatments (Figure 2). When expressed per unit algal weight or per chlorophyll a weight, productivity rates varied widely between grazing regimes. A consistent pattern of higher specific

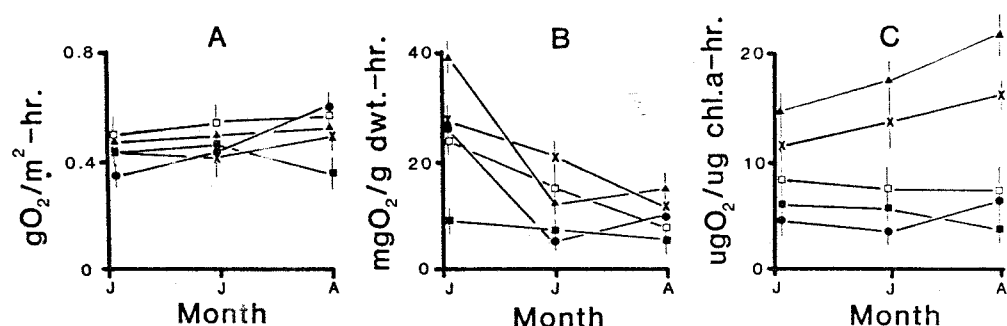


Figure 2. Mean net community primary production $\pm$ 95% confidence limits; A) per area, B) per unit algal weight, and C) per unit chl. a weight. (X)- all herbivore treatment. (□)- group 1 and 3 treatment. (▲)- group 2 and 3 treatment. (■)- group 3 only treatment. (●)- no grazing treatment. J, J, and A on the x axis indicate June, July, and August. Plates were submerged initially in December, 1981, and these data were collected during the summer of 1983.

production rates in urchin grazed treatments (all herbivore treatment and urchin only treatment) than in fish grazed, micro-herbivore grazed and non-grazed treatments, was maintained. Net specific community primary production rates ($ug\ O_2\ ug\ chl.\ a^{-1}\ hr^{-1}$) differed by a factor of two to four among the treatments. The micro-herbivore grazed and ungrazed treatments had the lowest specific rates of algal production. Specific rates were inversely related to algal standing crop.

DISCUSSION

These data provide evidence that different herbivores have variable effects on the benthic algal community. Data on algal species composition and specific primary productivity between treatments demonstrate that functionally different herbivores have qualitatively and quantitatively different effects on these parameters. Algal communities grazed by Diadema apparently consist of algal species with much higher specific rates of production. Such low biomass communities are main-

tained in a high turnover state by intense herbivory. Without urchin grazing, specific production rates decrease by a factor of approximately two, and it appears that different algal species become dominant. This difference may be the result of the visual nature of fish grazing, allowing discrimination and preferences for certain algal species (Ogden and Lobel, 1978). Differential effects on algal specific productivity are in part due to differences in grazing intensity between treatments (amount of biomass removed). In this locality, the abundance of Diadema (and grazing intensity) is sufficiently great to maintain a very productive, low biomass algal community. In other localities, the abundance of herbivorous fishes may be high enough to maintain a similar algal community. However, if fishes avoid some algal species, biomass would be higher (and specific production lower) than if truly generalized grazing occurs.

The rates of algal biomass removal reported here are very close to those found for herbivores on the Great Barrier Reef (Hatcher, 1981) and, though temporally variable, represent between 50 and 60% of net daily algal production. Variations in the percent of daily production removed can result from changes in the absolute amount of biomass taken by herbivores, variations in rates of production, or a combination of both these factors. For the data presented here, variations in the percent biomass removed did not consistently correlate with variations in algal production and represent changes in the absolute amount of biomass removed. This estimate of the percent production taken by herbivores may be an underestimation due to the assumption that all the net primary production (less excretion) is going into biomass accumulation that is available for consumption by herbivores. However, a larger proportion of material goes to herbivores in this than in most ecosystems (Wiegert and Owen, 1971). An interesting contrast between these results and those obtained in Australian reefs is that Hatcher (1981) found that herbivorous fishes were responsible for all of the algal consumption. In this study, the amount removed by fishes was less than 50%, with urchins consuming 40-70%. This probably reflects the relative abundances of these herbivores at each site.

For algal communities accessible to all herbivore groups, the differential effects of various herbivores may be masked. Spatially complex reefs, however, preclude access by all groups, at least in some areas, which may lead to mosaics of algal communities with different structure and function. Patterns of herbivore distribution and abundance between and within reef zones would introduce additional variability in these parameters. This suggests that shallow reef algal communities are not only structured by a complex of environmental factors (water movement, nutrient availability, substrate type, etc.), but also by biologically, possibly species-specific, mediated processes which in turn affect functional aspects of the community.

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