herbivore responsible for most of the herbivory switched from parrot fish to urchins at ~ 50 m (Fig. 1). Parrot fish herbivory was significantly higher 0 - 50 m from the reef crest than from 50 - 75 m (X^2 = 11.19, P < 0.001; Table 1). Urchin herbivory was significantly higher farther from the reef (50 - 75 m) than it was near the reef (0 - 50 m)(X^2 = 13.86, P < 0.001; Table 1).

DISCUSSION

We did not observe the predicted halo effect, as overall herbivory did not change with distance from the reef. However, we evidenced very little parrot fish herbivory past 50m from the reef, suggesting that the fish are taking refuge from predators in the reef and thus preferentially grazing on the grass closest to the reef (Randall 1965). In Discovery Bay this behavior is particularly interesting given the scarcity of larger predatory fish in the area. Perhaps the fish derive other benefits from living in the reef or the behavior is strongly genetically fixed and not responsive to changes in the surrounding environment.

Discovery Bay has only very small populations of *Diadema*, the urchin widely held responsible for causing the halo effect (Ogden 1973). The urchin herbivory in this study was likely caused by the common *Tripneustes ventricosus* and *Lytechinus variegatus* which appeared prevalent in the study area. Almost all urchin herbivory was observed further than 50m from the reef. While herbivory near the reef was caused allmost exclusivly by parrot fish. This suggests a niche separation between the parrot fish and urchins, although the mechanism for this separation is not clear. Further studies examining potential mechanisms of this niche differentiation would help determine the nature of the herbivory patterns and the changing role of *Tripneustes*. in the backreef of Discovery Bay.

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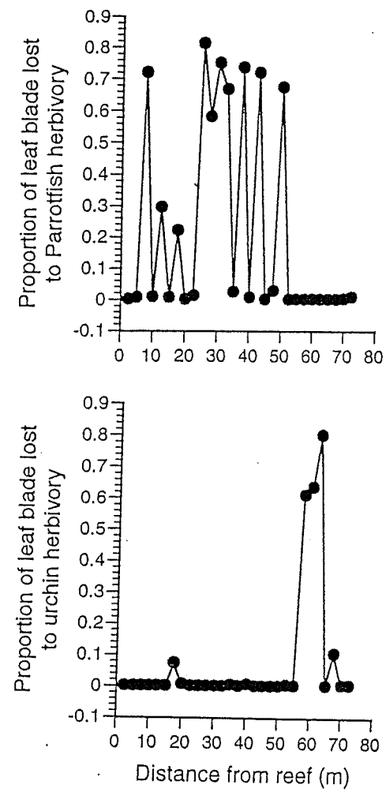

FIG. 1. Proportion herbivory on turtle grass blades by parrot fish and urchins.

Table 1. Proportion of herbivory on *Thallasia testudinum* at different differences from the reef. Proportion of herbivory represents the mean porportions of leaves eaten by a herbivore.

Distance from reef (m)	Herbivore Type	Proportion of Herbivory	SE
Near (0-50)	Parrot fish	0.3128	0.0764
Far (50-75)	Parrot fish	0.0011	0.0009
Near (0-50)	Urchin	0.0042	0.0036
Far (50-75)	Urchin	0.2413	0.1128

EFFECTS OF PREVIOUS LEVELS OF HERBIVORY ON SUBSEQUENT HERBIVORY OF THALASSIA TESTUDINUM

ANA I. BAPTISTA, MATTHEW J. UNGERER, AND KYTJA E. WEIR

Abstract.Thalassia testudinum, a common seagrass in the West Indies, is consumed by parrotfish (family Scaridae) for the nutritious epiphytes growing on the leaf, rather than the blade itself (J.J. Gilbert, pers. comm.). Previous studies, which indicate that tropical marine plants may have stronger chemical defenses than their temperate counterparts (Bolser and Hay 1996), and the observation that *T. testudinium* has few predators, led us to question whether inducible secondary metabolites were deterring herbivory on *T. testudinium*. We investigated this indirectly by comparing the herbivory on *T. testudinium* blades with varying levels of simulated prior herbivory to control blades with no prior herbivory. Because simulated herbivory reduces the amount of edible blade area, fish also may avoid blades with simulated herbivory because this is a less-optimal foraging strategy. On the other hand, the presence of bites may signal blades with epiphytes. We hypothesized that previous herbivory on *T. testudinum* blades would reduce subsequent levels of herbivory, because induced secondary metabolites or lower blade area would deter fish from eating leaves with herbivory damage. Our results indicate that previous blade herbivory has no effect on blade preference. Blades were grazed regardless of preexisting herbivory level.

Key Words: herbivory, inducible plant defense, optimal foraging theory, parrotfish (family Scaridae), secondary metabolites, turtle grass

INTRODUCTION

Thalassia testudinum is a common seagrass in the tropical Western Atlantic which few herbivores feed on directly. Parrotfish (family Scaridae) and sea urchins graze on *T. testudinium* blades to obtain nutrients from epiphytes growing on the distal portions of the blades (J. J. Gilbert, pers. comm.). Only the green sea turtle is thought to obtain nutrition directly from *T. testudinium* blades. This led us to question why such an abundant resource has few natural grazers. Bolser and Hay (1996) found that tropical marine plants may have stronger chemical defenses than their temperate counterparts. It is possible that inducible secondary metabolites exist in *T. testudinium* and deter herbivory.

We hypothesized that previous herbivory on *T. testudinum* blades would reduce subsequent herbivory because it would act as a visual cue warning fish about the presence ofs econdary metaboites. Besides However, previous herbivory may also reduce foraging efficiency in herbivorous fish by decreasing the amount of ingested material per unit time spent foraging as outlined in optimal foraging theory. Therefore, we predicted that (1) if secondary metabolites exist, grazers would avoid blades with preexisting herbivory damage, regardless of herbivory level, or (2) if previous herbivory reduces foraging efficiency, fish would avoid eating leaves with simulated parrotfish herbivory in proportion to the amount of leaf area missing. Alternatively, grazers may preferentially feed on blades with prior herbivory because previously bitten leaves may be a visual cue to high blade palatability (i. e. high epiphyte load).

METHODS

On February 25-26, 1998, we assessed the effect of varying levels of simulated herbivory of *T. testudinum* on foraging preference by parrotfish in the west back reef of Discovery Bay, Jamaica.

We collected 180 intact blades of *T. testudinum* with similar epiphyte loads. For each replicate, we attached ten 14 cm blades (measured from the tip) with a clothespin which was weighted with a metal bolt and buoyed by a plastic vial marked with flagging tape. To simulate 10 % and 20 % previous parrotfish herbivory, we used a hole punch to remove three or six semi-circles, respectively, from each blade. Intact leaves served as a control. Six replicates of each treatment were haphazardly arranged > 5m

from each other in the mangrove cove on the edges of *T. testudinum* beds.

After 24 hours in the water, we removed the blades and measured final blade area by placing the leaves on a grid of 3mm squares and counting the number of missing squares. We calculated original area of blade by multiplying blade width by 14 cm and subtracting simulated herbivory. Percent removed by herbivorous fish was then calculated by subtracting the final blade area from the original blade area and dividing the result by the original blade area. Of the original 180 blades, a total of 20 leaves were lost (0-2 per replicate) from clothespin enclosures. The leaves of two sets of treatments were pooled within replicates because these treatments were mixed up (probably winds or currents scattered them) between the different sites. In addition, one replicate of control leaves was not included because waves carried it ≈ 5m away from original placement. We used a one-way ANOVA to analyze the effect of simulated herbivory on subsequent parrotfish herbivory. Proportion of blade area removed was arcsin-transformed prior to analysis. Figure 1 exhibits non-transformed data.

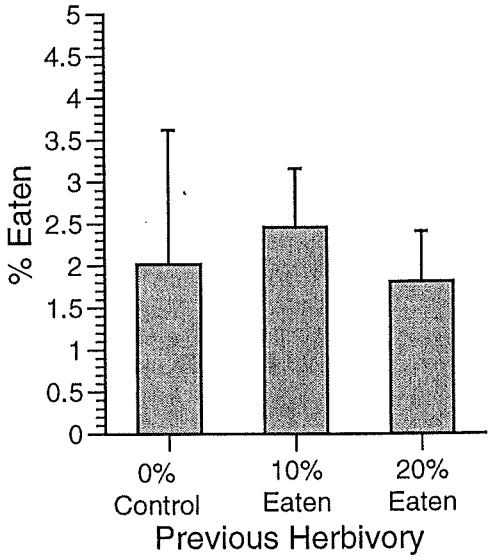

FIG. 1. Herbivory on *Thalassia testudinum* blades with preexisting simulated herbivory levels. Mean ± 1 SE.

RESULTS

We found that simulated previous herbivory on *T. testudinum* blades had no effect on fish foraging preference. Percentage of leaf blade removed was similar between the control and 10 % and 20 % levels of simulated prior herbivory treatments ($F_{2, 12} = 0.45$, $P = 0.65$; Fig. 1).

DISCUSSION

Herbivorous fish are not affected by prior herbivory on turtle grass blades. They feed on both damaged and undamaged blades indiscriminately. Therefore, it appears that any possible secondary metabolites induced by herbivory do not deter subsequent feeding on blades; nor are previous bites a visual cue to blade palatability.

Initally, our results suggest that the predictions of the optimal foraging theory would not apply to *T. testudinum* blades. However, observational data taken at the time of the study suggest that herbivorous fish feed in short bouts within a patch, spending little feeding time per blade. This suggests that it is more efficient for fish to feed continuously within a patch than to waste handling time assessing the available leaf area per blade. Thus, herbivorous fish may choose which turtle grass beds to feed in, perhaps by visual cues of patch density or epiphyte load instead of previous herbivory. It would be interesting for future studies to examine the effect of *T. testudinum* patch density on herbivorous fish foraging patterns.

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