territories (F = 27.3, df = 17, P < 0.0001; Fig. 1). There was no significant difference in the amount of herbivory between threespot and dusky damselfish territories.

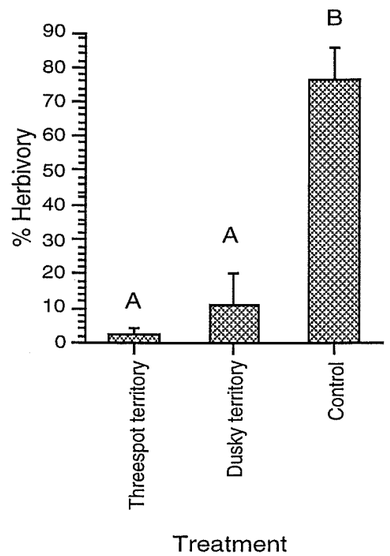

Figure 1. Percent area removed by herbivory (mean ± 1 SE) on *Thalassia* leaves within threespot and dusky damselfish territories and outside territories in the west back reef, Discovery Bay, Jamaica (n = 6). Treatments with the same letter are not statistically different (alpha = 0.05).

Discussion

Herbivory was less in threespot and dusky damselfish territories than in undefended control treatments. This suggests that, although damselfish do not feed on turtle grass, they aggressively defend plants and algae within their territories against herbivores. Because of this territorial defense, damselfish territories serve as effective refuges for *Thalassia*.

There was no significant difference in the extent of herbivory between less-defended dusky territories and better-defended threespot territories. This may reflect the high variance within territories (Fig. 1) or may suggest that there is no significant difference in intensity of territoriality between damselfish species.

The implications of damselfish territories for *Thalassia* grass populations appear be very localized, given the extensive herbivory in controls placed immediately outside territories. Damselfish territories tend to be found in patchy coral habitats. Undefended areas within these habitats serve as preferred refuges of parrotfish and urchins and have higher herbivore densities. This might explain why large, open turtle grass beds without patchy coral habitats and with lower herbivore densities are able to persist, and yet 76% of the leaf area in our control treatments in these patchy coral habitats were herbivorized. Nonetheless, even the localized protection apparently afforded *Thalassia* within damselfish territories may show diel variation. Having observed high densities of nocturnally-active urchins in the patchy coral habitat, one might expect that at night, when damselfish are not active, these urchins easily herbivorize *Thalassia* in territories. Future studies should focus on diel herbivory patterns as well as herbivory rates in patchy versus open areas.

EFFECTS OF PRIOR HERBIVORY ON PARROTFISH SELECTION OF *THALASSIA* BLADES

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Abstract. Prior herbivory was studied as a cue potentially affecting the selection of *Thalassia* blades by parrotfish. Prior herbivory may indicate to parrotfish that a blade is nutritious and worth foraging upon. Beyond some level of herbivory, however, selecting leaves by this criteria may no longer increase foraging efficiency due to the reduced biomass of leaf available and increased time devoted by the parrotfish to travel between leaves. Grazing occurred more frequently on leaves with greater amounts of simulated herbivory. Though herbivory declined somewhat on leaves with the greatest number of simulated bites, there does not appear to be a threshold above which *Thalassia* is no longer subject to herbivory. Therefore, parrotfish herbivory may exert substantial selective pressure on *Thalassia* to delay initial contact with herbivores.

Key Words: Thalassia, *Scaridae, herbivory, cues*

Introduction

Turtle grass (*Thalassia testudinum*) is a marine spermatophyte covering large areas of substrate in shallow coastal waters of the Caribbean. This species is important in resisting erosion and in providing habitat and food for numerous organisms (Randall 1965). *Thalassia* beds are also a significant source of nutrients for the coral reef community. Leaf matter that is removed from the beds may be deposited as fecal matter by herbivores that take refuge in the structural complexity of the reef when not foraging. Grazing by herbivores is a major factor determining the distribution and abundance of plants in seagrass beds (Foster 1987) and, therefore, patterns of foraging may have significant implications for the seagrass bed community and the reef community as a whole.

Due to relatively low abundances of the long-spined sea urchin (*Diadema*) in Discovery Bay, Jamaica, grazing by coral reef fishes (Scaridae) represents the most significant source of herbivory. Prior studies indicate that parrotfishes preferentially select *Thalassia* leaves with high epibiont loads (Lobel and Ogden 1981). Parrotfish may use epibionts as a cue (Berry *et al* 1994) or they may use prior herbivory as an indicator of more nutritious forage (Bykowski *et al* 1994). Given the variability of herbivory observed within *Thalassia* beds, it is unlikely that fish respond uniformly to all degrees of prior herbivory. If a portion of a blade has been consumed, this may be a cue to a potential grazer that the blade is nutritious and worth the energy required to forage upon it. With increasing herbivory, however, the leaf may no longer be worth the foraging effort. If fish select leaves with substantially reduced leaf material, time spent eating would decrease while time spent searching for forage would increase, contradicting the requisites of optimal foraging. Therefore, we expected to observe a threshold of prior herbivory beyond which further herbivory should rapidly decline. This behavior in parrotfish would provide *Thalassia* with a "refuge" from severe herbivory and cause grazing pressures to be distributed more evenly across the *Thalassia* community.

Methods

The effects of previous herbivory on subsequent herbivory were studied in *Thalassia* beds in the west back reef of Discovery Bay, Jamaica on Feb 22, 1996. Whole *Thalassia* blades were collected haphazardly from various beds in the bay. Low, medium, and high levels of herbivory were simulated by punching 2, 7 or 15 half circles along the upper 10 cm of the blades edges respectively. Each blade was cut from the bottom to a standard 18 cm in length. Ten replicates of six blades each were made for the 3 herbivorized treatments and an un-herbivorized control treatment by securing the *Thalassia* blades with a clothespin attached to a bolt. Weighted flagging tape was used to mark a 20 m transect through the center of a dense *Thalassia* bed. Samples were placed approximately six inches to the right and left of the flagging tape every 0.5 meters at 0930, and were retrieved at 1630. For each replicate, the proportion of blades with any herbivory was assessed. Differences in herbivory between treatments were analyzed with a Chi-square test.

RESULTS

Simulated previous herbivory on *Thalassia* blades increased the frequency of subsequent herbivory ($X^2 = 20$, df = 3, $p < 0.005$; Fig. 1) Low levels of simulated herbivory had little effect on the frequency of further herbivory (60% vs. control = 55%). Blades with medium levels of simulated herbivory exhibited the highest frequency of subsequent herbivory (91%). Blades with heavy levels of simulated herbivory exhibited slightly less subsequent herbivory (78%) than those with medium levels of simulated herbivory, but much more than control leaves.

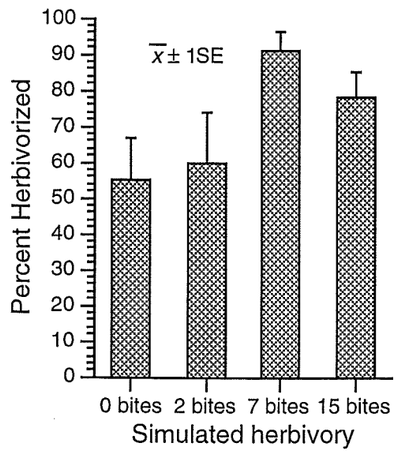

Fig. 1. Percentage of *Thalassia blades* with one or more bites for four levels of simulated herbivory (n = 10 replicates of 6 blades for each treatment).

DISCUSSION

The greater herbivory observed on leaves with simulated prior herbivory suggests that fish use prior herbivory as a cue in selecting *Thalassia* blades when foraging. There was little evidence for a significant threshold past which herbivory decreases. The frequency of herbivory decreased slightly when a leaf had 15 bites in it as opposed to 7, but it was still 41 % greater than herbivory on intact leaves despite the fact that 10-20% of the leaf area was missing (Figs. 1 and 2). It appears, then, that there is no "refuge" in herbivory for *Thalassia*. Plants which have experienced significant herbivory are still more likely to be eaten. This is consistent with the abundant *Thalassia* blades visible in our treatments and in nature, which have been consumed almost to the leaf base.

This may have implications for population dynamics, productivity, and evolution of *Thalassia*. Individuals which for some reason experience herbivory sooner than others will have leaves consumed at much higher rates. This may influence survival or reproduction; McGlathery (1996) showed that parrotfish herbivory in the West Indies is responsible for patterns of *Thalassia* distribution. If so, there should be strong selective pressure for mechanisms to reduce the likelihood of herbivory. These might involve decreased nutrient content in leaves and mechanisms to reduce epiphyll growth. Taller leaves appear to suffer greater herbivory on the reef (pers. obs). If in fact fish tend to forage on taller leaves (as opposed to taller leaves being older and hence showing more herbivory), herbivory might also select for reduced rates of leaf extension once leaves reach a certain length. Alternately, plants may maintain leaf area and reduce epiphyte cover by increasing growth rates. Plants which experience early herbivory may increase allocation to growth and hence show increased growth rates and decreased reproductive effort.

The use of prior herbivory as a foraging cue by fish may have important implications for *Thalassia*, but prior herbivory does not appear to be a primary cue for fish. Even in our control treatment 55 percent of leaves experienced herbivory within 7.5 hours. Research should consider whether epiphyll cover is a more important cue, or whether fish leaf choice may often be haphazard with respect to the leaves. Further investigation should also determine how much variation in rates of tissue loss to herbivory occurs in plants, and the effects of these differences on plant productivity and fitness.

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