factors that would increase herbivory: higher nitrogen content in the blades, higher epiphyte growth, higher nitrogen content in the epiphytes, and a lower blade turnover time. It is difficult to separate whether the herbivory preference is due to a higher epiphyte load or to possible phenotypic variation within *Thalassia*.

Our data suggests that epiphyte load is important in fish preference, but sheds no light on possible phenotypic differences in *Thalassia* between the two sites. It is possible that although nitrogen levels in the leaves can vary according to the aquatic nutrient levels, this seems to have little effect on fish preference. Past studies also seem to indicate no change in chemical defenses from high to low nitrogen sites. This would suggest little variation of fish preference due to phenotypic changes caused directly by higher nutrient levels; but still, differences in growth rate for *Thalassia* could occur between habitats due to increased shading caused by higher epiphyte loads in the high nutrient waters.

Thalassia distribution may be controlled by the interaction between nutrient and herbivore effects, as the bottom-up effects of nutrient levels influences the preference of fish predators. Predicting that *Thalassia* would incur highest predation in high nutrient waters is consistent with past studies that indicate that *Thalassia* is outcompeted and shaded by macroalgea in high nutrient waters. This could have broad implications for the abundance and distribution of *Thalassia* in our increasingly eutrophic costal waters.

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SPATIAL DISTRIBUTION EFFECTS ON HERBIVORY OF *THALASSIA TESTUDINUM* BY PARROTFISH (SCARIDAE)

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Abstract. Ogden (1976) showed that *Diadema* greatly impact the distribution patterns of seagrass. We investigated how herbivorous parrotfish grazing on *Thalassia testudinum* varies with relative distribution of the seagrass. We found that most herbivory on *Thalassia* occurred in the sandy, halo region between seagrass patches and the reef crest, and the least herbivory occurred in the middle of seagrass patches. These results suggest that parrotfish affect *Thalassia distribution* in a way similar to *Diadema*, though further study needs to examine the role of other biotic and abiotic conditions on the distribution of seagrass.

Key Words: Thalassia testudinum, *herbivory, halo region*

Introduction

Thalassia testudinum is common in the back reef area of Discovery Bay, Jamaica. Many studies have attempted to determine factors affecting herbivory on this grass. Parrotfish (Scaridae) and sea urchins (Echinoidea) are the primary herbivores on *Thalassia* , though the abundance of both herbivores differs with proximity to reefs and shelters. Based upon Ogden's (1976) explanation of the role of herbivores in the region between patch reefs and seagrass beds (called a halo), we hypothesized that the extent of herbivory on implanted *Thalassia* will vary both within a seagrass patch and within the halo region. Specifically, we predicted that herbivory will be greatest in the sandy halo region, due to the visually-feeding parrotfish easily locating the *Thalassia* against a white sand background. In addition, we predicted herbivory to be lowest in the middle of a *Thalassia* patch, due to the great abundance of grass blades, without a correspondingly high number of herbivores. We tested our hypothesis by recording herbivory rates over a seven hour period in each of these three habitat types in Discovery Bay's back reef.

Methods

We collected 180 blades of *Thalassia* (primarily ungrazed) from the back reef area of Discovery Bay, Jamaica. All blades were trimmed from the base to the same size and any previous signs of herbivory were removed from each blade by clipping the tip just below where the herbivory occurred. A blade was discarded if it displayed extensive herbivory. Epiphyte load was consistent across blades. We then clothespinned 30 sets of 6 *Thalassia* blades in a fanned-out bunch to mimic live *Thalassia* and securely attached 2 clothespins to a large bolt. We placed 5 bolts, or 10 sets of 6 *Thalassia* blades in each of 3 distinct back reef spots in ≈ 2 m of water: in a sandy halo area, without any other *Thalassia* ; on the edge of a large sea grass patch; and in the middle of the same large sea grass patch. Our 3 treatments were placed between 0845 and 0915 on 22 February, 1996 and were collected seven hours later.

We quantified the percent of herbivory on each experimental blade to the nearest 5 %. We then arcsine transformed our data for normalization, and used a one-way ANOVA to test for differences in herbivory between the three sites.

Results

Percent herbivory differed significantly between the sandy, halo area, the edge area, and the middle of the patch ($F = 19.98$, $df = 2, 12$, $P < 0.0002$; Figure 1). Herbivory was greatest in the sandy area, with an average of 32.6%. Herbivory was much lower in the other treatments with 7.6% and 0.6% of the leaf lost on the edge and in the middle of the patch. Herbivory was highly clumped on some clothespins and was attributed to parrotfish due to the rounded bite marks observed.

Discussion

The results supported the hypothesis that herbivory on *Thalassia* would change depending upon the loca

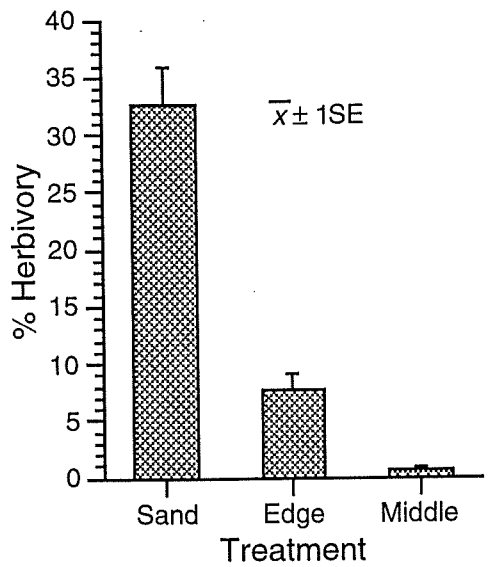

Figure 1. Percent herbivory on implanted *Thalassia* leaves in each of three treatments: sandy, halo area without other grass, edge of a grass patch, and the middle of a dense grass patch in Discovery Bay, Jamaica.

tion of a turtle grass blade in a turtle grass bed. The prediction that an individual blade outside the turtle grass would have a higher likelihood of suffering some herbivory was also supported. This pattern of herbivory intensity can be explained by evaluating three factors. Because the sandy area was close to the back reef, where many fish find refuge, there was a high likelihood that the grass treatment would fall within the visual search pattern of herbivorous fish. Because the sandy halo region is relatively close to the fish refuges, the cost of travel to the small clumps is reduced. The probability for one blade experiencing herbivory is higher outside the sea grass bed, where there are fewer total blades. Herbivory intensity is therefore concentrated on a few leaves as opposed to within the patch, where herbivory can be deflected across many blades.

Damselfish territories, which had their highest concentration within turtle grass beds (pers. obs.), may have caused increased edge feeding and feeding outside the bed so that herbivorous fish would avoid the costly evasion of these territories. This idea would help explain the benefits of swimming further to individual blades versus the costs of remaining in the bed and avoiding damselfish. Further study could examine herbivory along a gradient away from damselfish territories. Further study could also look at the role herbivorous fish have in creating a halo region similar to that induced by *Diadema* herbivory (Ogden, 1976), or whether burrowing shrimp and other biotic and abiotic factors play a larger role in influencing *Thalassia* distribution patterns.

The ecological implications of this study suggest that relatively large *Thalassia* beds are important for maintenance of this important back reef resource. One would predict that large turtle grass patches would increase in size and small turtle grass patches would remain the same size or become smaller because the large patches would suffer less herbivory per individual leaf. Individuals within these patches would thus have higher fitness.

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