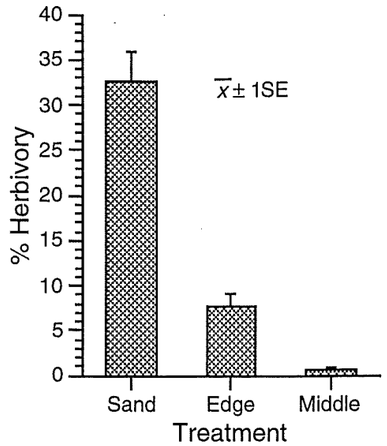

Figure 1. Percent herbivory on implanted *Thalassia* leaves in each of three treatments: sandy, halo area without other grass, edge of a grass patch, and the middle of a dense grass patch in Discovery Bay, Jamaica.

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.

Literature Cited

Ogden, J. C., 1976. Some aspects of herbivore-plant relationships on Caribbean reefs and seagrass beds. Aquatic Botany **2**: 103-116.

EFFECTS OF DAMSELFISH TERRITORIALITY ON *THALASSIA* HERBIVORY

Christy Hansel, Matthew K. Little, and E. Hank Taliaferro

Abstract. Thalassia testudinum may be found in high abundance in dusky and threespot damselfish territories because of the effective protection these fish provide against parrotfish, urchins, and other herbivores. To test for the existence of turtle grass refuges, experimental *Thalassia* plants were placed on coral reef sites inside and outside damselfish territories. *Thalassia* within damselfish territories sustained less herbivory than *Thalassia* outside territories. There was no significant difference between the amount of herbivory on *Thalassia* within threespot and dusky damselfish territories. These results suggest that damselfish territories serve as effective refuges for *Thalassia*.

Key Words: Herbivory, refuge, Stegastes fuscus, Stegastes planifrons, Thalassia testudinum

Introduction

Turtle grass (*Thalassia testudinum*) serves as a primary food source for parrotfish and urchins at Discovery Bay, Jamaica. It has been proposed that the high rates and spatial distribution of herbivory sustained by *Thalassia* might determine the distribution and abundance of this species in the coral reef environment. We observed that damselfish territoriality creates environments in which herbivores are excluded, and therefore hypothesized that these territories serve as effective refuges for *Thalassia*. Specifically, we predicted that *Thalassia* placed within the territories of dusky damselfish (*Stegastes fuscus*) and threespot damselfish (*Stegastes planifrons*) would suffer less herbivory than those placed outside the territories. We also predicted that since threespot damselfish appear to be more territorial (pers. obs.), *Thalassia* placed within these territories would sustain less herbivory than those placed within dusky damselfish territories.

Methods

On 22 February 1996, 180 uneaten *Thalassia* leaves were collected from the back reef at Discovery Bay, Jamaica. These were cut to uniform lengths of 17 cm, and ten leaves were grouped together with a clothespin to simulate a *Thalassia* plant. A bolt was tied to the clothespin to serve as an anchor, and a plastic bottle was attached to the opposite end of the clothespin to mark the plant locations and to keep the leaves standing upright. A total of 18 experimental "plants" were prepared: six replicates each for the dusky damselfish, threespot damselfish, and control treatments.

On 23 February 1996, a circular area of 20-m diameter and average depth of 1.5 - 2.0 m in the back reef was selected for study based on the presence of *Thalassia* and threespot and dusky damselfish territories. Individual damselfish were observed for five minutes to note the extent of their territories, and then a simulated *Thalassia* plant was placed in the center. The controls were placed in areas where no damselfish were witnessed during a five-minute observation period. In general, the control areas were more open and contained fewer coral patches than the damselfish territories, although both contained *Thalassia* populations. The experimental plants were placed on the reef between 0930 and 1000 and were retrieved at 1600.

Herbivory on the leaves was quantified by measuring the proportion of leaf area consumed during the day. For each replicate, the average amount of herbivory on the ten leaves of the experimental plant was determined, and these percentages were arcsine transformed for statistical analyses. An ANOVA was used to compare difference in the percent herbivory among the controls and in the dusky and threespot damselfish territories. Pairwise comparisons were employed to determine differences in total herbivory observed between the three treatments.

Results

Both dusky and threespot damselfish served as effective barriers to herbivory on *Thalassia* when these plants are harbored in their territories. Herbivory by parrotfish and urchins was greater in the control areas than in both the dusky and damselfish

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.

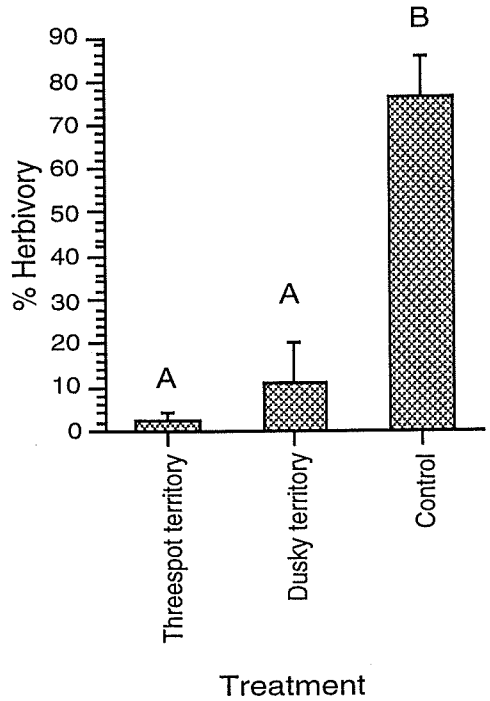

Figure 1. Percent area removed by herbivory (mean ± 1 SE) on *Thalassia* leaves within threespot and dusky damselfish territories and outside territories in the west back reef, Discovery Bay, Jamaica (n = 6). Treatments with the same letter are not statistically different (alpha = 0.05).

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.