DENSITY DEPENDENT HERBIVORY ON *THALASSIA TESTUDINUM*

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Abstract . We studied the effects of turtle grass patch density on herbivory by urchins and parrotfish. Optimal foraging theory predicts that in order for an herbivore's total energy intake to exceed the energy output required to locate, attack and ingest prey, herbivores should eat more biomass from individual food patches in areas of low patch density than in areas of high patch density. We found that both parrotfish and urchins ate more turtle grass from each grass patch in areas of low turtle grass patch density than high patch density. Parrotfish ate more than urchins in low density areas but both herbivores ate the same amount in high density areas, suggesting important differences in the foraging behavior of these herbivores. Our results also suggest that one of the advantages gained by *Thalassia testudinum* in vegetative propagation is the resultant high patch density that reduces the amount of herbivore damage to each individual grass patch.

Key words: density-dependence, resource limitation

INTRODUCTION

Turtle grass, *Thalassia testudinum*, is one of the most abundant plants in the Caribbean's shallow waters, and its primary production is important in sustaining tropical marine ecosystems (Colin 1978). In Discovery Bay, Jamaica, turtle grass beds sustain a large population of herbivores, including the sea urchins *Diadema antillarum, Lytechinus variegatus,* and *Tripneustes ventricosus* and the parrotfish *Scarus croicensis* and *Soarisoma viride* (Ogden et al. 1973, Bizarro et al. 1992, Bizarro and Shabel 1992). Some of these individuals migrate from the coral reef into the turtle grass beds during their preferred feeding times. Parrotfish feed on turtle grass primarily during the day by cropping the blades with their beak-like fused teeth (Stokes 1984). Turtle grass blades in Discovery Bay have highly variable lengths, and most display typical parrotfish rounded bite marks and/or urchin jagged blade tip damage, suggesting that turtle grass is under high herbivory pressure from both herbivore types there (pers. obs.). Both parrotfish and urchins have also been cited as potentially highly destructive herbivores of turtle grass that create "halo" areas void of turtle grass around coral reefs (Ogden et al. 1973, Stokes 1984, Hender et al. 1995).

Marked variability in grass clump densities exists within turtle grass beds. Turtle grass is an angiosperm, but it is also capable of clonal growth. As the rhizome buried in sediment grows from the terminal end, it gives rise to progressively more clumps of grass blades. If the terminal end of the rhizome is damaged, the plant ceases to grow in length. Mechanical damage to the rhizome as well as availability of sediment are responsible for the patchy turtle grass distribution within established beds (Colin 1978).

We studied density dependent herbivory on turtle grass clumps in both high and low patch density areas within a turtle grass bed. In order for an organism to survive, total energy intake must exceed energy output required to locate, attack and ingest prey. In herbivores, most energy is expended in the location of food (McNaughton and Wolf 1973) because movement between food sources is costly. Therefore, Optimal Foraging Theory predicts that herbivores should eat more from each food patch if patches are spaced far apart than if patches are closely aggregated. Defining each clump of grass as a patch, we predicted that herbivores would remove more blade area from grass patches in areas of low patch density than high patch density. In order to control for herbivore type, we also characterized the type of grass blade damage observed as parrotfish or urchin grazing. We expected both parrotfish and urchin grazing to be higher in grass patches in areas of low patch density than high patch density.

METHODS

We conducted our experiment on 23-24 February 1997 at Discovery Bay Marine Laboratory in Jamaica, West Indies. On the afternoon of the 23rd, we collected blades of living turtle grass from the bay and cut each blade to 17 cm in length, an average length of grazed and ungrazed blades in the field. We created 50 patches of 5 blades each by fastening the blades together with clothespins and attaching a small weight to the patch to anchor it to the substrate securely.

In the lagoon in the West Back Reef, halfway between the shore and the reef crest, we set out a 50 m transect parallel to the reef crest. We randomly

selected ten 1.2 m^2 plots within a 50x2m^2 area of the sea floor by swimming along the transect and searching for areas of low and high patch density. Five were high density plots, defined as approximately 75-100% turtle grass cover, and five were low density plots with 0-25% turtle grass cover. Based on visual inspection, the high density plots had evenly distributed grass patches spaced within 20 cm of one another, whereas the low patch areas were mostly covered by sand and contained only isolated grass patches. We placed five patches of grass in each plot (Fig. 1), oriented so that all blades faced upwards and waved naturally in the water.

On the afternoon of the 24th of February, after approximately 20 hours of exposure, we collected all fifty grass patches and counted the number of blades grazed in each patch. Of those blades that had been damaged by herbivory, we measured the amount of blade area removed and we recorded the type of herbivory exhibited. We classified an even top-down munching of the blade as urchin herbivory and semicircular bite marks as parrotfish herbivory (Fig. 2).

RESULTS

We found more grass blades exhibiting signs of herbivory in low density patches (1.53+ 0.1 leaves) than in high density patches (1.0+0.01 leaves; t-test, t=3.7, df=24, P=0.001). Of the grazed patches, we found more leaf area removed by all herbivores per patch in low density areas (9.18 + 3.18 cm2) than high density areas (0.28+ 0.09 cm2; t-test, t=2.74, df=45, P=0.009). We found that urchins consumed more per patch in low density plots (4.2+ 1.7 cm2) than high density plots (0.44+ 0.12 cm2; t-test, t=2.37, df=9, P=0.04). Parrotfish also consumed more in low density plots (14.9+ 4.5 cm2) than high density plots (0.54+ 0.22 cm2; t-test, t=2.42, df=17, P=0.027; Fig. 3).

Of the herbivory found in the low density plots, we found a trend towards more herbivory by parrotfish than by urchins (t-test, t= 1.5, df=15, P=0.16). In the high density plots, we found no difference between the amount of herbivory by parrotfish and by urchins (t-test, t=0.37, df=11, P=0.72).

DISCUSSION

Optimal foraging theory predicts that more herbivory occurs in the low than high density areas. Search time is likely to be greater in low density areas, and herbivores must graze more on each of the few patches they encounter to maximize energy intake. In high density areas, herbivores can maximize energy intake by eating a small amount from a greater number of patches and therefore consume only the most nutritious parts of the grasses, the tips. It is possible that herbivores consume more total biomass in the high than low density areas; however, we did not measure total biomass lost from the areas.

Although both parrot fish and urchins consumed significant amounts of *Thalassia* biomass, parrot fish consumed more biomass per patch than urchins in the areas of low patch density. Because parrot fish are visual predators and more mobile than urchins, they could take better advantage of the conspicuous patches in areas of low density. It would be harder for urchins to locate and move to these patches. It is also possible that parrot fish are the primary consumers of *Thalassia* in this area and simply eat a greater biomass of *Thalassia* than do urchins.

Bansak et al. (1993) found that more herbivory

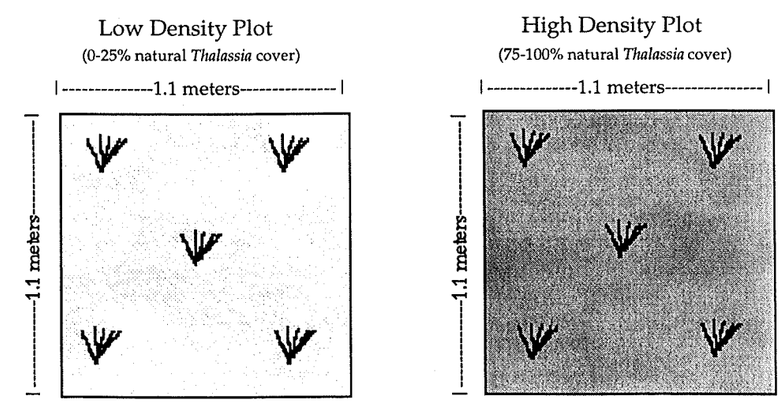

FIG. 1. Diagram of experimental setup.

occurred on patches located in low density areas outside and on the edge of the *Thalassia* beds than on patches in high density areas within the beds. They attributed this differential herbivory to a migration of herbivores from the reef towards the beds. We found that there was increased herbivory on patches in low density areas within the grass bed as well, suggesting that the pattern found in the 1993 study may be due more to density dependence than to a migratory pattern of herbivory.

Density dependent herbivory on *Thalassia* could be a factor influencing its distribution and reproductive strategy. *Thalassia* reproduces both sexually and by vegetative propagation. Vegetative propagation, which results in areas with high patch density, may be especially beneficial to *Thalassia* in areas of high predation pressure. The grass growing in dense beds would most likely be at an advantage over those growing in vulnerable isolated clumps.

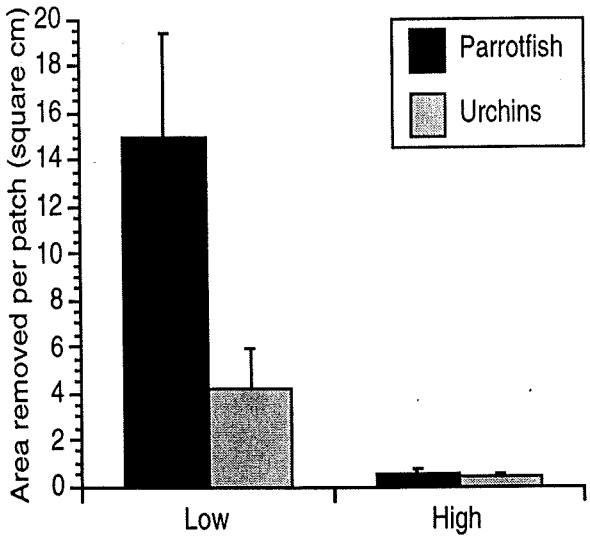

FIG. 3. Differential herbivory damage by parrotfish and urchins in low versus high density *Thalassia testinudum* areas.

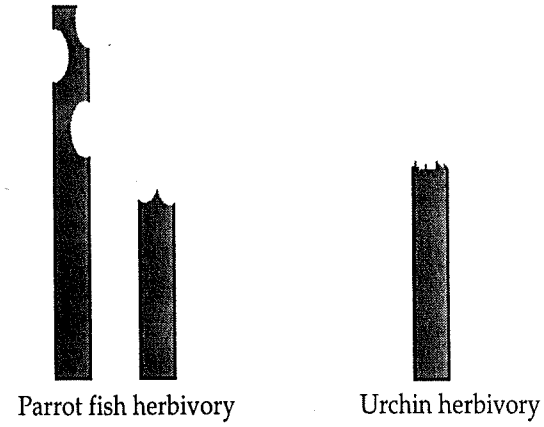

FIG. 2. Classifications of herbivory types.

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