Discussion

During the day, juvenile balloonfish schooled in the shallow, low salinity water around the mangroves. Their configuration parallel to the roots and their relative inactivity may make them less conspicuous and help to camouflage them from passing predatory fish that enter the mangroves during the day. Their schooling behavior could also serve to confuse predators and reduce the risk of any one individual to predation. Additionally, schooling could indicate that there are certain microclimates within the mangroves that juvenile balloon fish prefer.

The low salinity of the shallow water may also help to protect the fish from predation. Lower salt concentrations negatively effect most marine fish by increasing the osmotic gradient between their gills and the water. Many reef fish avoid areas with lower salinity to prevent this physiological stress (Cowen 2002). Additionally, the fierce defense of benthic macro-algal lawns by three-spot damselfish during the day could also influence balloonfish juveniles to move up into the shallow mangrove roots.

At night when predation pressure and damselfish aggression may be reduced, the juvenile balloonfish descend into the macro-algal beds to feed. The relative similarity between night and day census numbers suggests that most of the balloonfish forage within the lagoon at night. They are slow swimmers, and this may prevent them from traveling far from their daytime schooling locations. Additionally, we sampled early in the evening (19:30-21:30), and it is possible that they moved further from the mangroves and into the surrounding water later that night. Future studies that investigate other refuges of juvenile balloonfish in the backreef closer to the reef crest, the fidelity of juvenile balloonfish to their daytime schools, and the movements of balloonfish at other life stages would improve our understanding of balloonfish behaviors.

The behavior of juvenile balloonfish is one example of the important link between coral reefs and other surrounding habitats. Almost all of the balloonfish we found in the mangroves were approximately 7-10 cm in length. This suggests that the mangroves may play an important role in this stage in balloonfish development. Habitats surrounding coral reefs may play a critical role in the early life stages of reef fish and should be included in plans for coral reef preservation.

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Are mangrove roots a refuge habitat for some algal species?

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Abstract: We studied spatial variation in herbivory in a mangrove habitat at Discovery Bay Marine Laboratory, Jamaica, W. I. *Spyridia filamentosa*, a highly palatable, fragile red alga, occurs on the roots of mangroves but not elsewhere in the area. It has been suggested that this species survives only on mangrove roots not because of physiological or morphological characteristics but because of intense grazing pressure in the surrounding waters. We tested the hypothesis that mangrove roots provide a refuge from herbivory for macroalgae. We used the seagrass *Thalassia testudinum* to compare herbivory at the mangrove roots to the open area surrounding the mangrove. We did not observe any herbivory on the grass placed among the roots, but herbivory was high on grass placed in the open area surrounding the mangrove. We also found higher herbivory near the bottom than near the surface in the open area. Our results support the hypothesis that mangrove roots provide refugia for macrophytes from herbivory. Further studies should investigate explanations for reduced herbivory in mangrove root areas.

Key Words: herbivory, Spyridia filamentosa, Thalassia testudinum

Introduction

Marine grazers are known to exert strong control over the structure of benthic algal communities (Hay 1981; Littler et al. 1987). Algae have developed various defenses to combat herbivory, such as the production of toxins, morphological defenses, temporal or seasonal escapes, associational escapes, and spatial escapes or refuge habitats (Pfister and Hay 1988). Refuge habitats are defined as areas where an organism's fitness is high relative to other locations because of the non-uniform impact of mortality agents such as herbivory (Pfister and Hay 1988).

We studied spatial variation in herbivory in a mangrove lagoon. Fleshy red algae of the species *Spyridia filamentosa* are found on the roots of these mangroves, sometimes close to the surface in the low light environment provided by the shade of the trees. These algae are highly palatable and have been shown to be spatial generalists (Taylor et al. 1986). Taylor et al. (1986) concluded that herbivores, rather than physiological or morphological constraints, may restrict this species to hanging roots, suggesting that mangroves may provide refugia from herbivory for macroalgae. We tested the hypothesis that mangrove roots provide a refuge habitat, using turtlegrass (*Thalassia testudinum*), which is commonly employed as a bioassay because it is easy to move and is eaten readily by a wide variety of herbivores (Hay 1981). We predicted that there would be more herbivory on *T. testudinum* placed in open water surrounding the mangroves than on *T. testudinum* placed among the mangrove roots. We further predicted that there would be less herbivory closer to the surface in both areas because herbivorous fish tend to live near the bottom.

Methods

We used the seagrass *T. testudinum* as a bioassay to measure spatial grazing patterns between the root zone and the open area in a lagoon surrounded by mangroves approximately 50 m west of the dock at Discovery Bay Marine Laboratory, Jamaica, W. I. The area is bordered by mangrove trees with roots hanging into the water along the shore. The bottom of the open water in the center of the lagoon is rocky and supports a large fish community. The root zone is a low light habitat as a result of mangrove shading, while the open water receives full sunlight. We conducted a general survey of the lagoon habitat to assess the microhabitat use of *S. filamentosa* and the numbers and locations of potential herbivores.

We collected seagrass without evidence of herbivory from the open area of Discovery Bay. We attached three grass tips each 10 cm long to a clothespin tied to a piece of string. We tethered these strands at five different sites in each of four habitats (surface roots, bottom roots, surface open, bottom open). In the root habitat the clothespins were tied directly to the roots. In the open area the clothespins were anchored to the bottom with a weight. We placed the high grass 10 cm from the surface and the low grass 10 cm from the bottom. We left the seagrass exposed for a total of 72 hours. We visited each treatment every 24 hours and recorded evidence of herbivory. We grouped herbivory into the categories of 0%, 1-25%, 26-50%, 51-75%, and 76-100% area lost on the seagrass blade. We tested whether herbivory varied with habitat using contingency analysis.

Results

We observed *S. filamentosa* only on mangrove roots. No other macroalgal species were found on these roots. Very still water and low light due to mangrove foliage shading characterized the mangrove root habitat. We observed only balloon fish in the root habitat, whereas a variety of fish species were observed in the open area of the mangrove. Damselfish territories, which were abundant in the open area, appeared to stop before the edge of the mangrove root habitat.

We observed no herbivory on *T. testudinum* located on the mangrove roots, either near the surface nor near the bottom (Fig. 1). In the open water we found significantly more herbivory near the bottom than near the surface ($\chi^2 = 13.86$, $P = 0.01$). Herbivory was lower on the surface root treatments than in the open area at the bottom

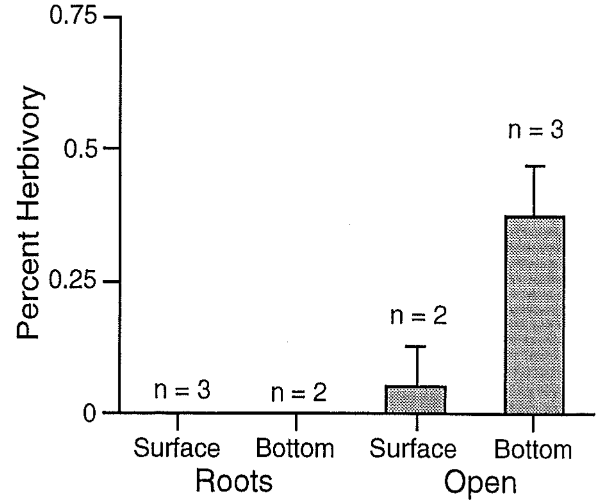

FIG. 1. Mean percent herbivory over 24 hours on *Thalassia testudinum* in mangrove root habitat and in open mangrove habitat, Discovery Bay, Jamaica. Herbivory data were collected 10 cm below the surface and 10 cm above the bottom in each habitat. Data represent means of 5 sites +/- SE. n = 2 for roots bottom and open surface, n = 3 for roots surface and open bottom.

($\chi^2 = 13.86$, $P = 0.003$). These are the two habitats we tested where algal substrates naturally occur.

Discussion

The lack of herbivory on *T. testudinum* in the mangrove roots suggests that mangroves provide a refuge habitat for some algal species. *S. filamentosa* has higher nutritional value and lower structural and chemical defenses than macroalgae found in open areas (Taylor et al. 1986), where herbivory pressure is much higher (Fig. 1). Our results support Taylor et al.'s hypothesis that *S. filamentosa* survives in mangrove root habitat because of reduced herbivory pressure.

The protective effect of the mangrove roots does not appear to be correlated with depth, as we did not observe any herbivory among the mangrove roots at any depth. However, lower herbivory at the surface than at the bottom in the open habitat suggests that herbivory pressure may be lower near the surface across habitats. Mangrove roots may be a refuge for algae in part

because they provide a substrate near the water surface, where fish are not as abundant.

Mangrove roots may also provide a refuge for *S. filamentosa* by reducing competition for space with other macroalgae. We did not observe any other species of macroalgae on mangrove roots, possibly because of low light under mangrove foliage and low salinity. It is also possible that *S. filamentosa* has developed mechanisms to harvest nutrition or other benefits from mangrove roots, increasing its competitive advantage. For example, *S. filamentosa* could grow roots penetrating the mangrove roots themselves.

Our results demonstrate that herbivory pressure is reduced in mangrove root habitats, but the mechanisms for this pattern remain unknown. Possible explanations include low light and high physical complexity, which may reduce the feasibility of visual feeding. Low salinity in these relatively shallow habitats may also be a deterrent to many fish by causing osmotic stress (Donovan et al. 2003).

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