INFLUENCE OF TURTLE GRASS (*THALASSIA TESTUDINUM*) ON ZOOPLANKTON DISTRIBUTION IN THE WATER COLUMN OF A SHALLOW BACK REEF

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Abstract: Some marine zooplankton seek refuges in the benthos during the day to avoid visual predators, and migrate into the water column at night, when predation risk is lower, to feed on phytoplankton in surface layers. Large zooplankton are more conspicuous to predators than small zooplankton, and consequently are more likely to exhibit this behavior. We hypothesized that zooplankton in beds of *Thalassia testudinum* in the shallow back reef at Discovery Bay, Jamaica, would use turtle grass beds as a refuge during the day and would migrate into the water column at night. We used a tow net to sample zooplankton above and within three turtle grass beds during the day and night. Zooplankton were more abundant within than above turtle grass, but did not differ in abundance between day and night. Large copepods were more abundant within than above turtle grass during the day, but were equally distributed between these habitats at night. Small copepods were equally distributed between the two habitats during the day and at night. Our results suggest that zooplankton may use turtle grass as a refuge, although food resources available in turtle grass beds or other factors may also drive the observed patterns in zooplankton abundance. Large zooplankton seem to use turtle grass as a refuge during the day, when predation pressure is higher, while small zooplankton do not exhibit this pattern, presumably because they are under less predation pressure.

Key Words: amphipods, copepods, decapod larvae, diel migration, ostracods

INTRODUCTION

Many zooplankton living on coral reefs exhibit diel vertical migration behavior, remaining in sediments or refuges within coral or macroalgae during the day and emerging into the water column at night to feed on phytoplankton, which is abundant in surface waters (Madhupratap et al. 1991a, Madhupratap et al. 1991b, Fagan et al. 2002, Iwamoto et al. 2003). This behavior allows zooplankton to reduce predation by planktivorous fish, which are visual predators and consequently are more effective at capturing prey during the day (Ohlhorst 1982, De Robertis 2000). Zooplankton that remain in the water column by day are generally smaller than those that migrate vertically, probably because small zooplankton can more easily avoid predators (Porter and Porter 1977).

Prior research has shown that zooplankton abundance is greater in the water column above macroalgal beds than above coral at night, presumably because macroalgae provide better daytime refuge from predators (Schoen and Close 2002). We examined the distribution of zooplankton in the water column within and above beds of an abundant submerged macrophyte, *Thalassia testudinum*, or turtle grass. We expected that zooplankton would use grass blades as a refuge from predation by planktivorous fish during the day, and mi-

grate into the water column during the night to feed. We predicted that (1) during day, abundance of zooplankton would be greater within turtle grass than in the water column above turtle grass, and (2) at night, abundance of zooplankton would be greater in the water column above turtle grass than within turtle grass. We also predicted (1) and (2) would be due mostly to migration of large zooplankton, because small zooplankton experience lower predation pressure, and hence less pressure to seek refuge during daylight. We expected that large zooplankton would be more abundant in the water column than in turtle grass at night because large zooplankton should migrate out of turtle grass and into the water column to feed when predation pressure is reduced.

METHODS

On 23 February 2005, we sampled zooplankton in three haphazardly-selected beds of turtle grass in the back reef near the marine laboratory at Discovery Bay, Jamaica. We collected samples with a zooplankton tow net (153 μm mesh, 26 cm diameter) by swimming back and forth three times along a 10 m transect laid haphazardly through each turtle grass bed. The depth of each bed was approximately 1.5 m. In each bed, we first sampled above the grass, towing the net just below the surface of the water, followed by sampling within the grass blades (approximately 2-4 cm above the sediment). Sampling was performed in this order at every bed to avoid contaminating surface samples with sediment stirred by the tow net. We sampled each bed twice, once during the day (1045 to 1215) and again at night (2145 to 2245).

Samples were passed through a 153 μm mesh and standardized to a volume of 18 ml with filtered seawater. They were then preserved with 2 mL 95% isopropyl alcohol. We homogenized each sample, removed two 5% (by volume) subsamples from each, and identified and counted all zooplankton in those subsamples under magnification. For each sample, zooplankton abundances for the two subsamples were averaged. All zooplankton were grouped into one of the following categories: copepods (adults and copepodites) < 0.5 mm, 0.5-1 mm, > 1 mm; nauplii (mostly

Table 1. Abundance of zooplankton taxa in 12 samples taken from turtlegrass patches on the back reef at Discovery Bay, Jamaica. Data from day and night sampling were summed to find total abundance of each taxon in samples obtained from above and within turtlegrass patches. The total number of zooplankton counted in 12 samples was 2088 organisms.

Taxon	Above grass	Within grass	Taxon total	% of total sample
Copepods	188	1532	1720	82.4
Ostracods	18	154	172	8.2
Amphipods	12	71	83	4.0
Decapod larvae	23	30	53	2.5
Polychaete larvae	10	18	38	1.8
Formaniferans	2	15	17	< 1.0

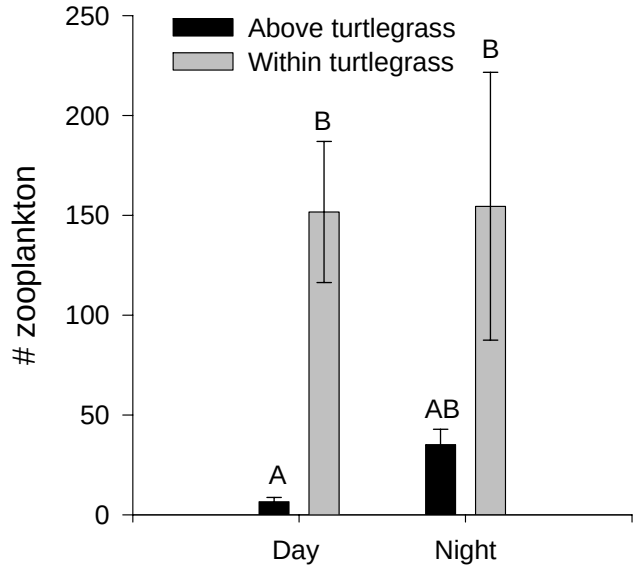

Figure 1. Abundance of zooplankton as a function of time of day and location in the water column with respect to turtle grass. Error bars are ± 1 SE. Letters above columns represent means that are significantly different at α = 0.05, Tukey's HSD post-hoc test

copepod); amphipods < 1 mm, 1-2 mm, > 2 mm; decapod larvae < 1 mm, 1-2 mm, 2-3 mm; ostracods < 0.5 mm, > 0.5 mm; polychaete larvae < 1 mm, 1-2 mm, > 2 mm; and foraminiferans. Foramaniferans are not generally planktonic, but may have been resuspended from the sediments during sampling. Because copepods were the most abundant organisms in our samples, and other taxa were rare (Table 1), we used only copepod data to evaluate the effects of zooplankton size on distribution in the water column. Preliminary analysis revealed that trends for intermediate (0.5-1 mm) and large (> 1 mm) copepods were similar, so we pooled these data. "Large" therefore refers to copepods > 0.5 mm, and "small" refers to copepods < 0.5 mm.

All statistical analyses were performed using JMP 4.0.0. Data met or were logarithmically transformed to meet all assumptions of parametric tests.

RESULTS

We used a two-way ANOVA to assess changes in zooplankton abundance as a function of time of day (i.e., day or night), location in the water column (i.e., above or within turtle grass), and the interaction between these factors ($F = 11.67$, df = 3, 8, $P = 0.003$). There was a significant interaction between time of day and location in the water column (2-way ANOVA, $F = 6.68$, df = 1, 8, $P = 0.03$); during the day, there was a greater difference between samples taken above and within turtle grass than there was at night, due to an increase in the number of zooplankton above the turtle grass at night. There were significantly more zooplankton within than above turtle grass (2-way ANOVA, $F = 26.16$, df = 1, 8, $P = 0.0009$). There was no difference in zooplankton abundance between day and night (2-way ANOVA, $F = 2.16$, df = 1, 8, $P = 0.18$; patterns for separate orders described in Appendix A). A Tukey's HSD post-hoc test was performed to assess the differences among the four groups ($\alpha = 0.05$; Fig. 1).

To assess the relationship between zooplankton size, time of day, and distribution in the water column in turtle grass beds, we examined data on copepods, the most abundant taxon in our sample. We performed a three-way ANOVA with the predictors size class (i.e., small or large), location in the water column (i.e., above or within turtle grass), time of day (i.e. day or

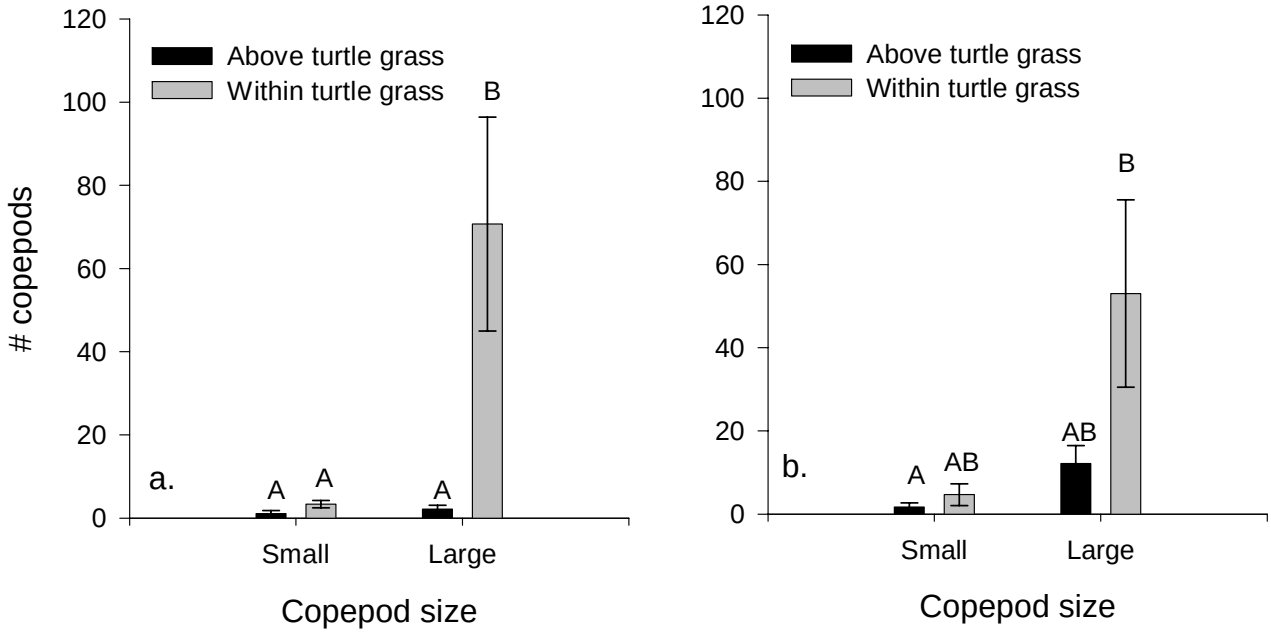

Figure 2. Number of copepods of two size classes (small, < 0.5mm; large, > 0.5 mm) found within and above turtlegrass beds during (a) day and (b) night sampling periods. Error bars are ± 1 SE. Letters above columns represent means that are significantly different at α = 0.05, Tukey's HSD post-hoc test.

night), the two-way interactions between these factors (i.e., size class*location, size class*time of day, location*time of day) and three-way interaction between these factors (i.e., size class*location*time of day). The model predicting copepod abundance with these factors was significant ($F = 9.32$, $df = 6, 29$, $P < 0.0001$). The three-way interaction was not significant ($F = 1.34$, $df = 1, 28$, $P = 0.26$), and was consequently excluded from the model.

The interaction between location in the water column and size class was significant ($F = 4.59$, $df = 1, 28$, $P = 0.04$); there were greater differences in copepod abundance between samples taken above and within turtle grass for large copepods than samples taken above and within turtle grass for small copepods. The few small copepods that occurred in our samples were equally distributed between the two habitats. The number of large copepods occurring above turtle grass was equal to the number of small copepods occurring in either habitat, but the number of large zooplankton occurring within turtle grass was greater than any of these three values. The interaction between location in the water column and time of day was marginally significant ($F = 3.92$, $df = 1, 28$, $P = 0.06$); the interaction was driven primarily by the increase in copepods above turtle grass at night. The interaction between size class and time of day was not significant ($F = 0.21$, $df = 1, 28$, $P = 0.65$). Copepod abundance was greater within turtle grass than above it ($F = 16.77$, $df = 1, 28$, $P = 0.0003$) and there were more large than small copepods ($F = 20.56$, $df = 1, 28$, $P < 0.0001$). There was no difference in copepod abundance between day and night ($F = 0.37$, $df = 1, 28$, $P = 0.55$). A Tukey's HSD post-hoc

test was performed to assess differences among the groups (Fig. 2).

Discussion

Our results supported our hypothesis that turtle grass may serve as a refuge from predation for zooplankton during the day, when visual planktivores are more effective. While zooplankton were significantly more abundant within than above turtle grass during the day, they were evenly distributed between these two habitats at night. The significant interaction between time of day and location in the water column suggests an increase in the number of zooplankton above the turtle grass from day to night. This supports our prediction that, when darkness decreases predation risk, zooplankton may migrate into the upper water column, where phytoplankton are more abundant. However, the increase in zooplankton abundance above turtle grass at night does not appear to be as substantial as we predicted.

During our night sampling, the moon was nearly full, which could have provided enough light for nocturnal planktivorous fish to prey on zooplankton. However, assuming that the light difference between day and night resulted in more predation pressure during the day, the high abundance of zooplankton within turtle grass at night suggests that any of the following explanations may be true: (1) turtle grass remains an important refuge for zooplankton even when predation pressure is reduced at night, (2) phytoplankton at the surface does not play an important role in the diet of these organisms, or (3) some other factor, such as greater food resource availability, causes zooplankton to remain within turtle grass at night.

Because many zooplankton feed on detritus, and turtle grass both accumulates and produces detritus, high resource availability in turtle grass beds may drive patterns of high zooplankton abundance in these beds. An experimental study could assess the extent to which each of these factors (i.e., refuge and resource availability) influences patterns in zooplankton abundance in turtle grass beds. Another alternate explanation for the observed pattern is that zooplankton tend to remain lower in the water column, irrespective of the presence of sea grass. Since we did not measure zooplankton abundance above bare substrates, we cannot rule out this explanation. The fact that we found benthic organisms (i.e. foramaniferans) in our within turtle grass samples suggests that there may have been some contamination of these samples. However, because foramaniferans constituted less than 1% of the total number of zooplankton we counted, and because care was taken to avoid stirring sediment with the tow net, contamination probably did not substantially influence our results.

At night, zooplankton may migrate horizontally, or be swept into the water column above turtle grass by currents moving in from other parts of the bay or reef. The fact that zooplankton abundance did not differ between day and night, however, suggests that the trends we observed

were due to vertical migration of zooplankton within each turtle grass bed, rather than to import zooplankton from outside of the beds.

Our hypothesis predicted that the abundance of copepods would depend upon copepod size class, location in the water column and time of day, with large copepods migrating from turtle grass beds into the water column at night, when predation pressure is reduced. Because small copepods are unlikely to experience similar predation pressure due to their small size, we expected to see equal numbers of small copepods above and within turtle grass during both day and night. However, the three-way interaction between size class, time of day and location was not significant.

While small copepods were evenly distributed above and within turtle grass habitats during the day and at night, large copepods were more abundant within than above turtle grass during the day, and evenly distributed between these habitats at night. Additionally, the abundance of large copepods above turtle grass was greater at night than during the day (Fig. 2). Large zooplankton are especially susceptible to predation due to their inherent conspicuousness (Porter and Porter 1977). With decreased predation, pressure on large zooplankton to seek refuge may decline at night, resulting in a more homogenous distribution of large zooplankton through the water column in turtle grass beds. Patterns in the distribution of large and small copepods suggest that the trends we observed for total zooplankton were driven primarily by the migration patterns of large organisms.

Our results suggest that changes in the abundance of turtle grass, and potentially other sea grass species, may influence zooplankton abundance in the back reef at Discovery Bay by either providing or removing refuge from predation, and hence reducing or increasing predation rates. Future research could assess alternate explanations for the patterns found in this study, and examine the effect of changing macrophyte cover on zooplankton abundance.

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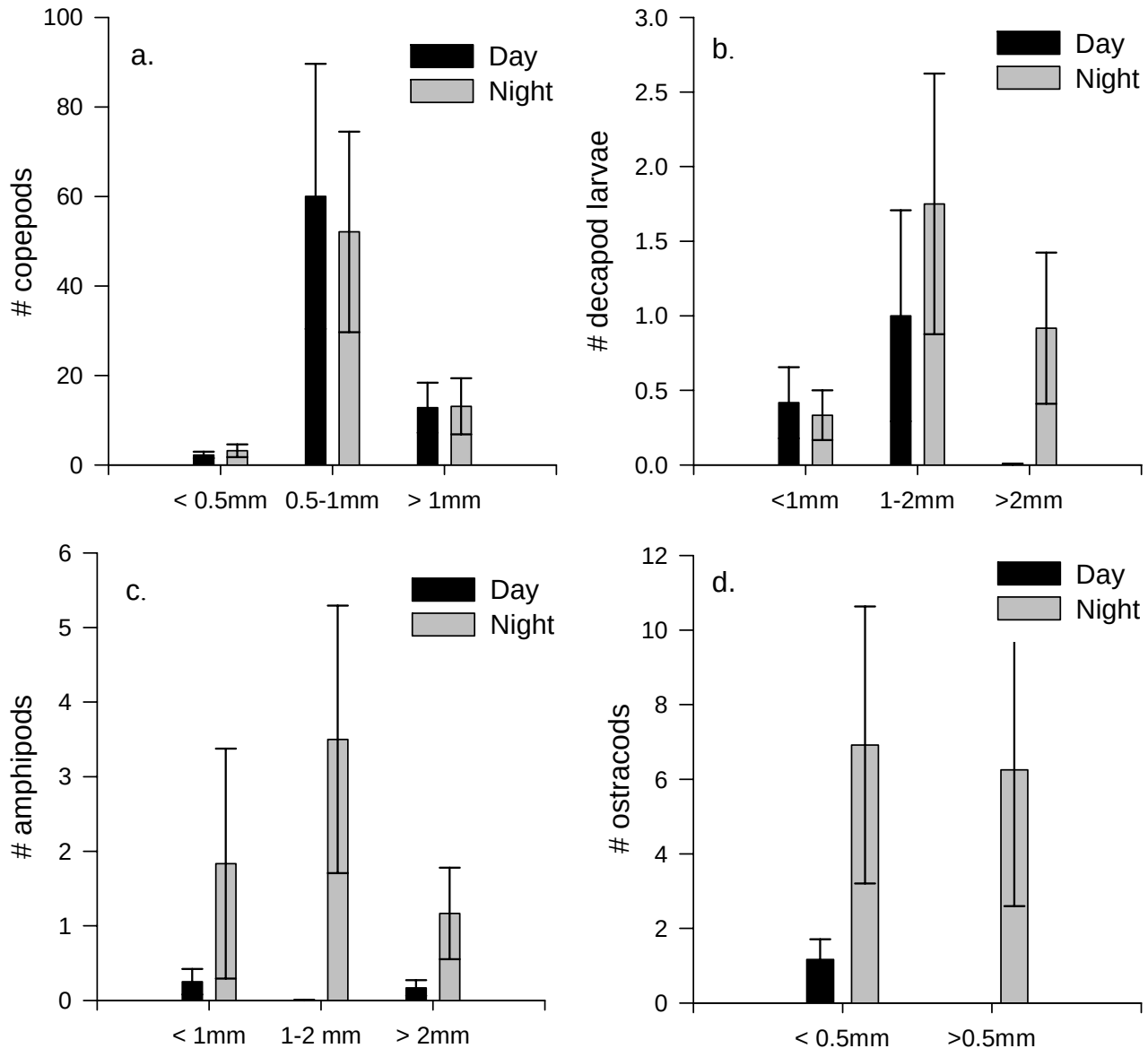

Appendix A. Effect of time of day and zooplankton size on the abundance of four zooplankton orders, pooled from samples taken within and above turtle grass: (a) copepods, (b) decapods, (c) amphipods, and (d) ostracods. Error bars are ± 1 SE. There were no significant interactions for any zooplankton order (P > 0.41).

A) The number of copepods differed among size classes (F = 9.74, df = 2, 30, P = 0.0006), but did not differ between day and night (F = 0.39, df = 1, 30, P = 0.54).

B) The number of decapods also differed among size classes (F = 2.74, df = 2, 30, P = 0.08), but did not differ between day and night (F = 2.62, df = 1, 30, P = 0.12).

C) The number of amphipods differed between day and night sampling periods (F = 9.78, df = 1, 30, P = 0.004), but did not differ among size classes (F = 0.40, df = 2, 30, P = 0.67).

D) The number of ostracods also differed between day and night sampling periods (F = 7.28, df = 1, 20, P = 0.01), but did not differ between size classes (F = 0.81, df = 1, 20, P = 0.38).

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SITE FIDELITY AND FOOD RESOURCES OF THE FOUREYE BUTTERFLYFISH

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Abstract: Butterflyfish are often associated with specific home ranges, though the costs and benefits of living in these home ranges are unclear. We studied site fidelity of the foureye butterflyfish, *Chaetodon capistratus*, in the back reef at Discovery Bay, Jamaica and examined how feeding behavior and vulnerability to attacks by aggressive damselfish changed with distance traveled. We monitored 10 fish over the course of three days. Foureye butterflyfish occurred as pairs or as individuals in non-overlapping home ranges with radii less than three meters. With increased distance traveled, *C. capistratus* suffered increased attacks from damselfish, but benefited from increased foraging attempts.

Key Words: Chaetodon capistratus, *clumped distribution, damselfish, foraging*

INTRODUCTION

Coral-reef fish are often associated with specific home ranges on reefs and are relatively sedentary compared with other vertebrates (Sale 1991). In previous studies a fish's home range has been defined as the area in which a fish spends 95% of its time (Parsons 2003). The foureye butterflyfish, *Chaetodon capistratus*, is thought to live in a specific home range with one monogamous mating partner for long periods of time, possibly for its entire life. Foureye butterflyfish are most often found alone, but they can also be found less commonly in pairs, and rarely in larger groups of up to 12 individuals (Deloach 1999). The foureye butterflyfish forages on almost every bottom substrate, but eats mostly anthozoan polyps (Deloach 1999).

We studied site fidelity, the tendency for an individual to remain in one specific area throughout its life, in the foureye butterflyfish in the back reef at Discovery Bay, Jamaica. We hypothesized that foureye butterflyfish would be site faithful and could be found in the same area repeatedly over a three-day period. We examined some of the costs and benefits of site fidelity in the foureye butterflyfish to better understand why coral reef fish might be faithful to specific sites; specifically, we observed feeding behavior and frequency of damselfish aggression