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

CHELSEA L. WOOD AND ANNA R. NOWOGRODZKI

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

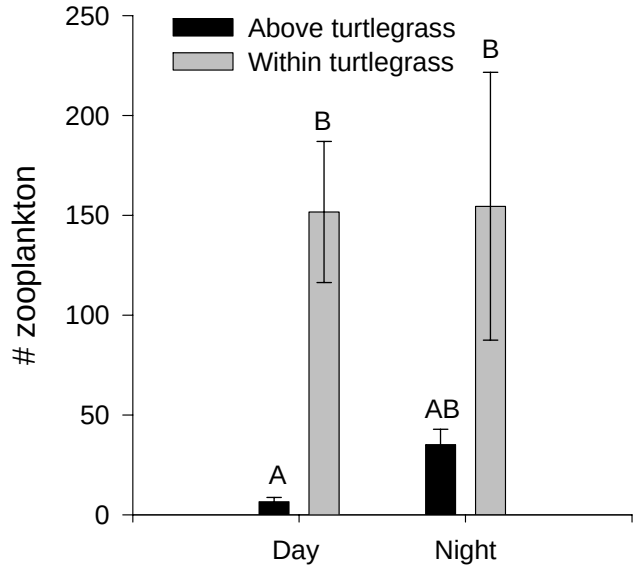

Figure 1. Abundance of zooplankton as a function of time of day and location in the water column with respect to turtle grass. Error bars are ± 1 SE. Letters above columns represent means that are significantly different at α = 0.05, Tukey's HSD post-hoc test

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

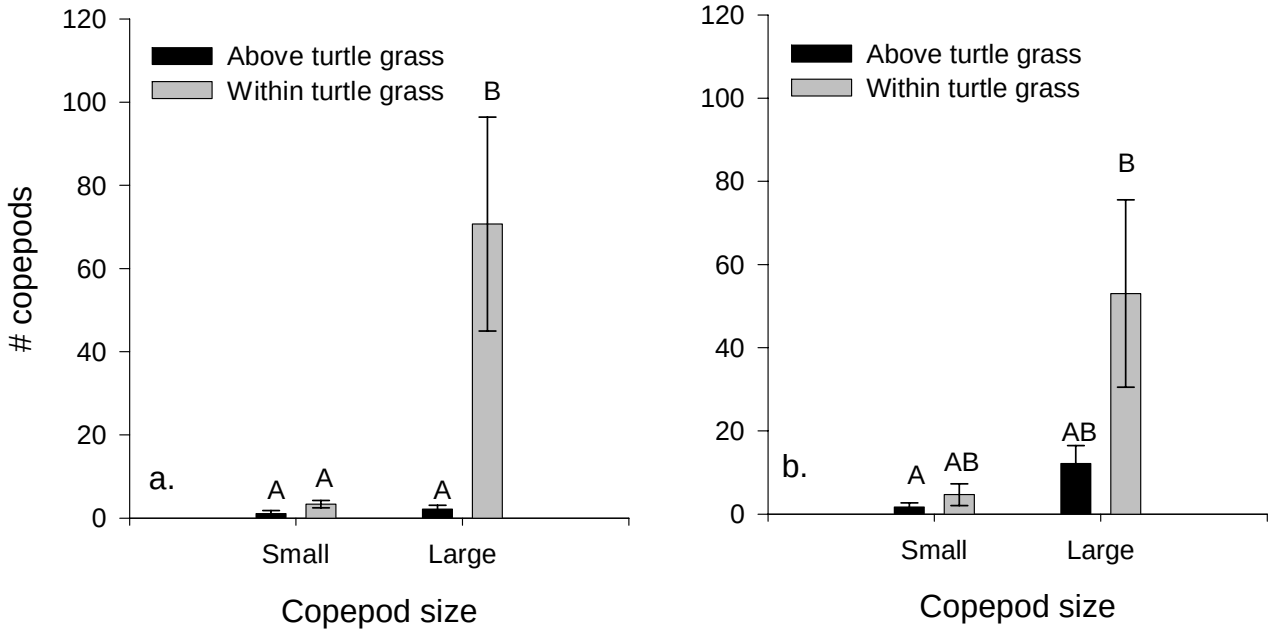

Figure 2. Number of copepods of two size classes (small, < 0.5mm; large, > 0.5 mm) found within and above turtlegrass beds during (a) day and (b) night sampling periods. Error bars are ± 1 SE. Letters above columns represent means that are significantly different at α = 0.05, Tukey's HSD post-hoc test.

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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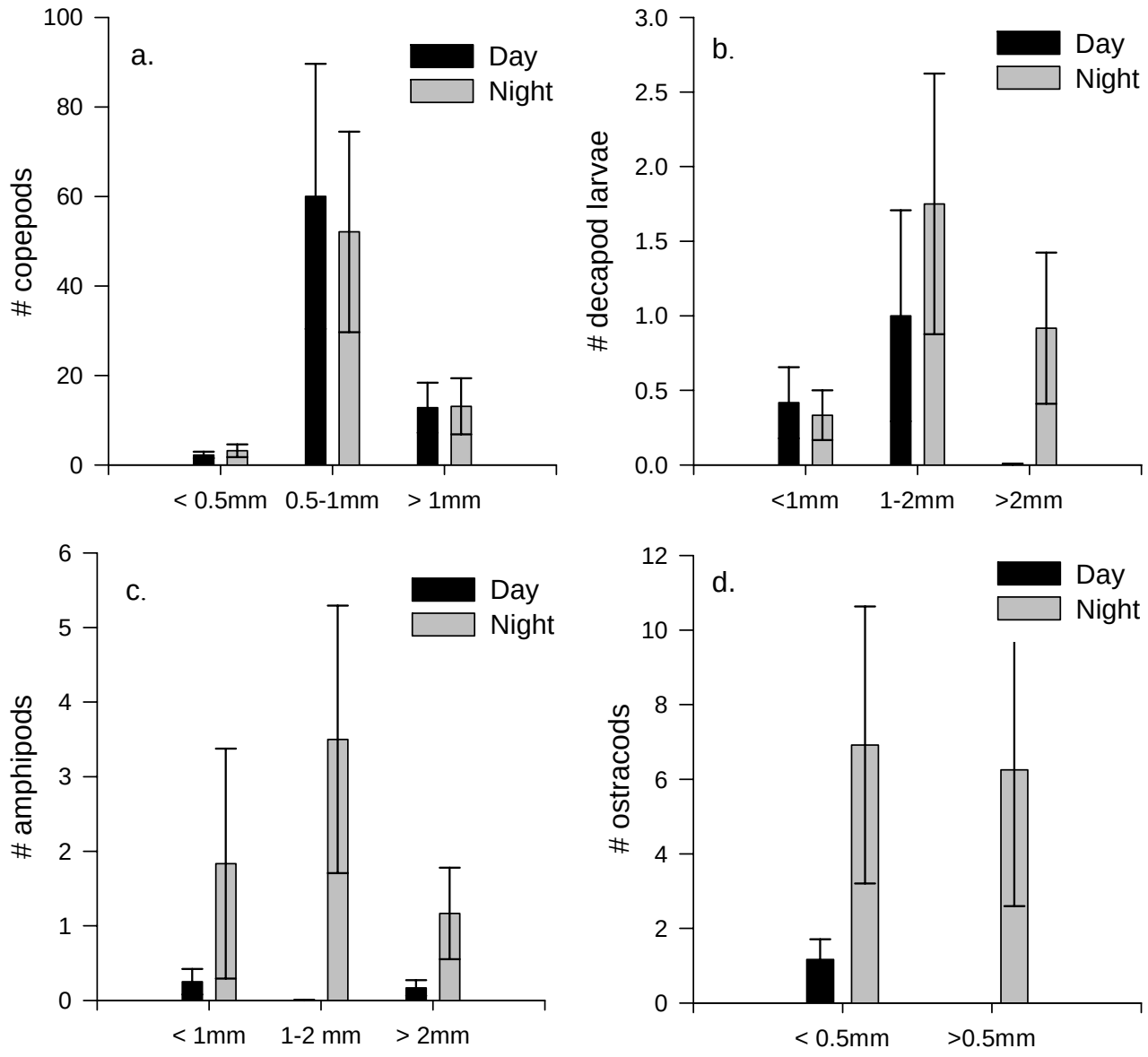

Appendix A. Effect of time of day and zooplankton size on the abundance of four zooplankton orders, pooled from samples taken within and above turtle grass: (a) copepods, (b) decapods, (c) amphipods, and (d) ostracods. Error bars are ± 1 SE. There were no significant interactions for any zooplankton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

Madhupratap, M., C. T. Achuthankutty, and S.R. Sreekumaran Nair. 1991b. Zooplankton of the lagoons of the Laccadives: diel patterns and emergence. Journal of Plankton Research, 13: 947-958.

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SITE FIDELITY AND FOOD RESOURCES OF THE FOUREYE BUTTERFLYFISH

DANIEL J. MADIGAN, CHAD M. VALDERRAMA AND GABRIEL H. CALVI

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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

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towards butterflyfish. We hypothesized that for foureye butterflyfish, as total distance moved increases, the number of attacks from damselfish would increase, and foraging efficiency would decrease.

METHODS

Our study was conducted from 24 - 26 February 2005 in the back reef of Discovery Bay, Jamaica (Fig. 1). Snorkeling, we located a total of 10 foureye butterflyfish in 6 different locations (Table 1). When a focal fish was located on a patch of reef, the site was marked and revisited every subsequent morning (0800-1000) and afternoon (1400-1600) throughout our study. Only seven fishes were located during the first observation period (Fishes 6, 9, and 10 were located during the second observation period, Table 1). During each visit, fish were recorded as present or absent. If the foureye butterflyfish was visible from the marked reef patch, within approximately 3 m of the marked location, it was recorded as present; if not seen over the two hour period of observation, it was recorded as absent. We define home range as the 3 m radius area that consistently contained the focal foureye butterflyfish. We compared the arcsine transformed proportions of times fish were present to times fish were absent to assess site fidelity in the foureye butterflyfish (JMP 5.0.1).

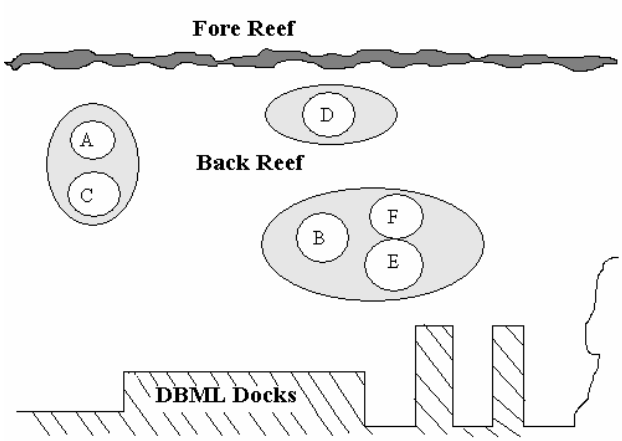

Figure 1. Locations of foureye butterflyfish (n = 10) in the back reef at Discovery Bay. Small circles with letters (A-E) represent non-overlapping 3 m radius home ranges of individuals or pairs that were followed for 10-minute observational periods and monitored over three days. Large shaded ovals represent 'clumps' of foureye butterflyfish observed within the reef.

We conducted 18 ten-minute observation periods of the 10 focal foureye butterflyfish. We recorded maximum distance traveled from marked home range center, number of feeding bites, and number of attacks by damselfish (attacks were any act of damselfish aggression which elicited a response in the observed foureye butterflyfish). We performed a linear regression on the number of feeding attempts and number of attacks by distance traveled to assess the effects of travel distance on feeding efficiency and damselfish attacks (JMP 5.0.1).

RESULTS

Fish were most often found in the locations where they were first sighted ($F = 8.41$, $df = 18$, $P = 0.001$; Table 1). Foureye butterflyfish always occurred alone or in pairs. Fishes 1 and 2 were the only fish that were never found paired with conspecifics (Table 1; they are the only fish found at locations A and B respectively). Our defined home range size seems to accurately reflect fish behavior since at each visit focal fish were never sighted beyond this range and most fish were found re-

peatedly within the marked areas where we first observed them. These home ranges were non-overlapping, but appeared to be aggregated in clumps, approximately 15-25 m in diameter, within the back reef (Fig. 1).

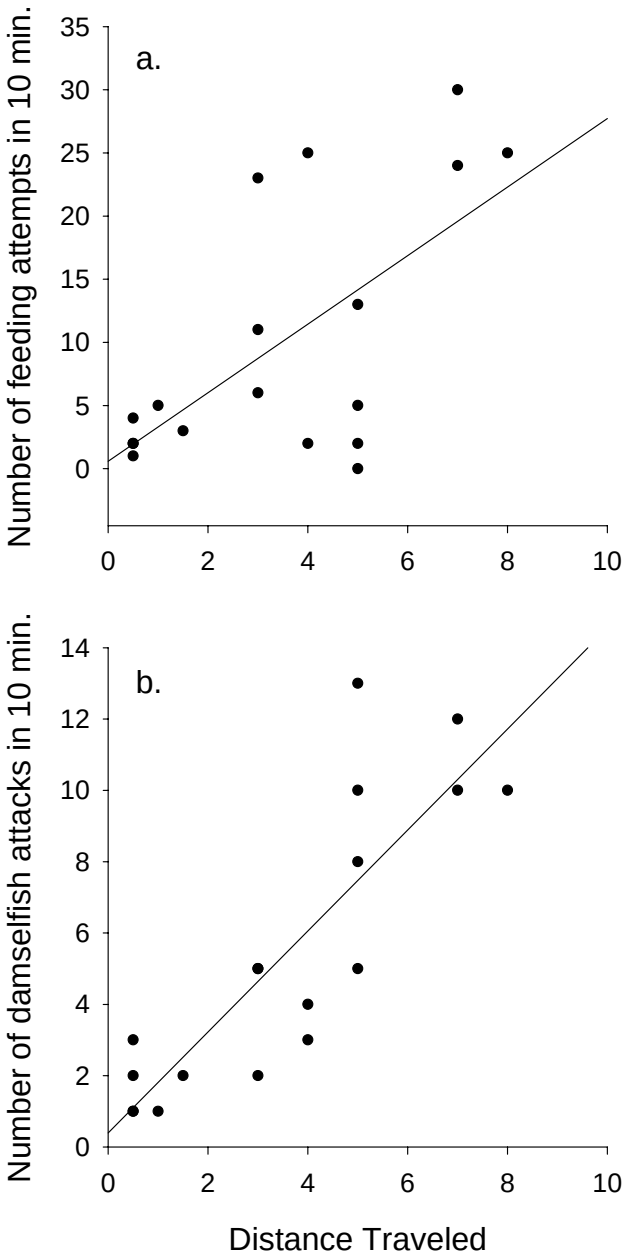

Figure 2. Feeding efficiency and damselfish attacks vs the maximum distance traveled away from the home range. a) Number of feeding attempts vs distance traveled by foureye butterflyfish in 18 ten-minute observation periods ($F = 43.03$, $df = 17$, $P < 0.0001$). b) Number of damselfish attacks increases with distance travelled for foureye butterflyfish ($F = 11.14$, $df = 17$, $P = 0.004$).

Within 10-minute observation periods, butterflyfish traveled distances ranging from 0.5 to 8.0 m. As distance traveled increased, the number of feeding attempts and the number of damselfish attacks increased (Fig. 2). When butterflyfish traveled greater than 1 m, they foraged on coral, algal, and sand substrates with no apparent preference for any specific substrate. When foureye butterflyfish traveled less than 1 m, they were often inactive within a rock recess, emerging only to feed on a nearby damselfish algal territory when the damselfish was occupied chasing another fish.

DISCUSSION

Most foureye butterflyfish were site faithful to home ranges within the back reef at Discovery Bay. However, fish were not always within marked sites, and in most cases one member of a pair was more site faithful than its pair-mate (Table 1). We propose five possible reasons for the absence of fish at marked sites: 1) Inaccurate home range size definition. Home ranges of some foureye butterflyfish may be larger than the 3 m radius circles that we defined for our study; Chapman and Kramer found that the banded butterflyfish have a home range of about 100 m (1998). 2) Initially observing a focal fish while outside of its home range. Foureye butterflyfish in Discovery Bay may travel outside of home ranges. This is supported by fish in our study that traveled greater than 6 m, thus out of their home ranges as we defined them. Locations may have been marked

when fish were traveling outside of their home range, and fish presence at the marked spot upon revisiting would be unlikely. 3) Chance observations at times when focal fish were foraging outside the home range. Marked locations may have been fish home ranges, but fish were foraging outside of this range at one or more of our visits. 4) Some foureye butterflyfish in Discovery Bay may not be site faithful. If this is true, it would imply that site fidelity by the foureye butterflyfish is facultative and not obligate. 5) Pairs may facilitate a distribution of tasks. One fish may 'stay home' and another may explore for better resources. Such behavior would lead to the unequal site fidelity in a pair which we observed in our study.

Consistent with our hypothesis, damselfish attacks increased with increasing foureye butterflyfish travel distance. This suggests that as foureye butterflyfish travel greater distances within or outside of their home ranges, they will expend more energy averting damselfish aggression. However, feeding bites increased with time traveled, suggesting that as a foureye butterflyfish travels further within or outside of its home range, its feeding efficiency increases even as damselfish attacks increase.

Continual use of home ranges could allow foureye butterflyfish to become familiar with the physical structure and damselfish territory locations within home ranges; this could lead to higher foraging success within home ranges than outside of home ranges (Marnane 2000). We observed this type of behavior in individuals that traveled short distances and emerged from rock recesses to feed when a nearby damselfish left its territory to defend against other foragers. However, the increase in foraging efficiency with travel distance suggests that food resources are not the only benefit to home ranges. It is

Table 1. Foureye butterflyfish presence and absence at 10 locations in Discovery Bay. Distinct locations are indicated by letters; two fish found at one location are considered a mating pair, indicated by subscript 2; solitary fishes are indicated by subscript 1.

Fish	Location	Times Present		Times Absent	
		Number	Percent	Number	Percent
1	A_1	4	80	1	20
2	B_1	4	80	1	20
3	C_1	5	100	0	0
4	C_2	5	100	0	0
5	D_1	4	80	1	20
6	D_2	3	75	1	25
7	E_1	1	20	4	80
8	E_2	2	50	2	50
9	F_1	1	25	3	75
10	F_2	3	75	1	25
Mean	-	3.2	68.5	1.4	31.5

possible that since the back reef at Discovery Bay has relatively low coral populations and relatively high algal cover (informal observations), algal mats are not a limiting resource for foureye butterflyfish. If this is true, they could easily forage on algae while avoiding damselfish territories. This limits the value of having familiarity with within-home-range damselfish territories. Since foureye butterflyfish have been shown to feed preferentially on coral polyps (Deloach 1999), they may be traveling greater distances to find this relatively rare food resource on the reef.

Familiarity with a home range may facilitate predator avoidance (Deloach 1999). We observed schools of night-feeding grunts that consistently aggregated in the same areas of our study sites, suggesting that these fish may convene in the same location for protection when they are not actively feeding (Partridge 1982). This may be a benefit that foureye butterflyfish derive from maintaining a home range, although we didn't directly observe any predation within or outside home ranges. Future studies should observe how predation changes as distance from home range increases.

Since many observed fish were in pairs, and foureye butterflyfish are believed to be monogamous, familiarity with home ranges may also facilitate mate location. Since foureye butterflyfish have been shown to forage outside home ranges, if a mating pair were separated while foraging, they would be able to relocate their counterpart by returning to a home range.

While the use of home ranges seems to be common in foureye butterflyfish in Discovery Bay, our results suggest that feeding efficiency is unlikely to be the only reason for this behavior. Longer term studies could examine the usefulness of home ranges in mating success and predator avoidance to better understand the benefits of having a home range.

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DIFFERENTIAL PATTERNS OF DISPERSION AND ABUNDANCE IN SEA URCHINS *TRIPNEUSTES VENTRICOSUS* AND *LYTECHINUS VARIEGATUS*

LAKSHMI NARAYAN AND JONATHON C. RAFFENSPERGER

Abstract: Differing physical attributes and behaviors may affect patterns of dispersion and abundance in taxa utilizing similar resources. Here, we examine these patterns in the *Tripneustes ventricosus* and *Lytechinus variegatus* sea urchins inhabiting turtle grass beds and rocky habitats in the back reef of Discovery Bay, Jamaica during both the day and night. We hypothesized that differences in grazing pressure, structural constraints, and other behavioral habits, would lead to differential abundance and dispersion not only between these two urchin species, but also within species depending on habitat and time of day. We found that in the turtle grass *T. ventricosus* was overdispersed during the day and near random at night, while *L. variegatus* remained near-randomly distributed regardless of time of day. In the rocky habitat, both *T. ventricosus* and *L. variegatus* were aggregated to some degree both during the day and at night. Habitat type seemed to be a better predictor of abundance than time of day for both species, as *T. ventricosus* and *L. variegatus* abundances varied more between habitats than between day and night. Further studies are needed to determine the forces driving habitat selection and dispersion in both urchin species.

Key Words: Discovery Bay, food limitation, habitat preference, nocturnal migration

INTRODUCTION

Two species of sea urchin, *Tripneustes ventricosus* and *Lytechinus variegatus,* coexist in the lagoon and back reef of Discovery Bay, Jamaica. Although these species are present in roughly the same area, taxon-specific behaviors and physical constraints that drive their habitat selection may lead to differences in their dispersion and abundance. Because the dominant forces behind habitat selection may shift over space and time, we examine distribution and abundance in two adjacent habitat types, turtle grass beds and rocky habitats, during both the day and night.

Both *L. variegatus* and *T. ventricosus* are grazers of turtle grass, *Thalassia testudinum,* although the former tends to select decayed blades (Monteque 1991) while the latter prefers live leaves (Klumpp 1993). This partitioning of turtle grass resources may reduce interspecific competition for food and promote the coexistence of these two species. Because *T. ventricosus* sometimes overgrazes turtle grass (Lilly 1975), which is also eaten by *L. variegatus,* food may be limiting for both of these species. We predict that both *T. ventricosus* and *L. variegatus* should be overdispersed in turtle grass habitat during both day and night in order to minimize intra - and inter - specific competition.

T. ventricosus is known to migrate from turtle grass beds to rock promontories when night falls, although the reasons for this movement are poorly understood (Todd and Kilmarx 1983, Tertschnig 1989).

We also observed that *T. ventricosus* tends to occupy patches of three-dimensional structure in rocky areas, which could generate an aggregated dispersion pattern of these urchins in rocky habitat. Thus, we predict that *T. ventricosus* would have an aggregated dispersion pattern in rocky habitat during both day and night, and should be more abundant on rocky habitat at night than during the day.

While *T. ventricosus* is found throughout the turtle grass lagoon and rocky back reef habitat, *L. variegatus* is less adept at attaching itself to substrates and thus cannot persist in areas of high wave action (Sharp and Grey 1962). *L. variegatus* is also intolerant of suspended silt and tends to abandon areas of high turbidity (Moore 1963). These findings suggest that *L. variegatus* should be largely absent from rocky, exposed areas of the back reef from which they would likely be dislodged, instead preferring the turtle grass beds where leaf blades slow water movement and cause silt to settle out of the water column (Gilbert, pers. comm.). Dispersion of *L. variegatus* is unlikely to change from day to night, as it avoids exposed rocky areas and does not exhibit diel migration, but we predict that *L. variegatus* will be less abundant in rocky habitats than it is in turtle grass beds.

METHODS

On 24–25 February 2005, we counted *Tripneustes ventricosus* and *Lytechinus variegatus* in 2 m^2, haphazardly-placed quadrats in turtle grass beds and rock habitats in the back reef of Discovery Bay, Jamaica. We sampled eight quadrats in each habitat type during one afternoon (1600) and one night sampling period (0400) for a total of 32 quadrats. As the urchins can be somewhat cryptic in both their appearance and their behavior, counts were made by two independent observers and averaged to more accurately determine abundance.

We used variance to mean ratios (VMR) to assess differences in dispersion patterns between species and substrate types at different times of day. A VMR equal to 1 indicates random dispersion, while a value > 1 indicates aggregation, and a value < 1 indicates overdispersion. We used two-way ANOVAs to determine how habitat type and time of day affect the abundance of each urchin species (JMP 5.0.1)

RESULTS

During the day, we found that *Tripneustes ventricosus* was clearly overdispersed in the turtle grass beds, while *Lytechinus variegatus* was only slightly overdispersed. In the daytime on rocky habitat, *T. ventricosus* was strongly aggregated and *L. variegatus* was slightly aggregated. Both urchin species were slightly aggregated in the turtle grass at night, and *T. ventricosus* was aggregated in the nighttime rocky habitat while *L. variegatus* was only slightly so (Table 1).

Location had a marginally significant effect on *T. ventricosus* abundance; this species was more abundant in rocky habitat than in turtlegrass ($F = 2.95$, $df = 3, 28$, P

= 0.097; Fig. 1). There was no effect of time of day (F = 0.87, df = 3, 28, P = 0.358), and no interaction between habitat and time of day (F = 0.48, df = 3, 28, P = 0.493). There were more *L. variegatus* in the turtle grass beds than in the rocks (F = 65.59, df = 3, 28, P < 0.0001; Fig. 1). Neither time of day (F = 0.22, df = 3, 28, P = 0.646) nor the interaction between time and location (F = 1.76, df = 3, 28, P = 0.195) affected *L. variegatus* abundance.

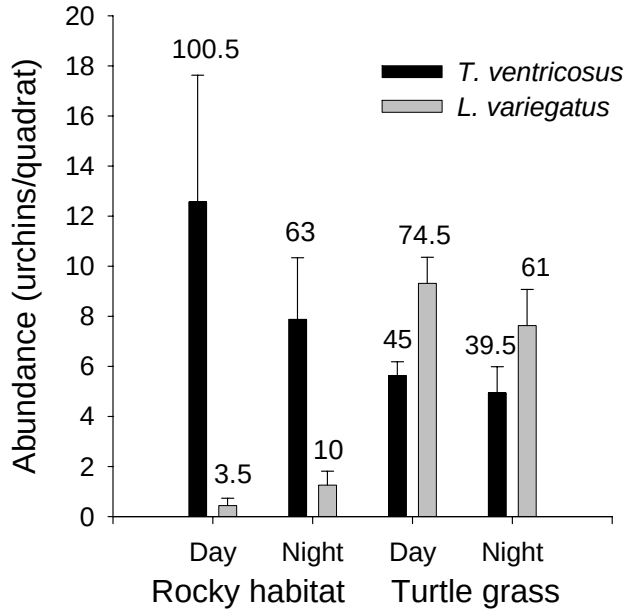

Figure 1. Day and night abundances of *Tripneustes ventricosus* and *Lytechinus variegatus* in turtlegrass beds and in rocky habitats. Error bars show mean ± 1 SE. Numbers indicate total urchins sampled in each habitat type and time of day.

DISCUSSION

Our results showed that *Tripneustes ventricosus* was strongly overdispersed in turtle grass habitat during the day and slightly aggregated in this habitat at night. Daytime grazing behavior could cause the overdispersion we saw in turtle grass beds during this time period. At night, urchins may not be grazing as actively, and thus would not overdisperse to reduce feeding competition. In the absence of grazing pressure, other factors such as mate location or distribution of predator refuges could lead to the more clumped dispersion pattern of *T. ventricosus* at night.

In rocky habitat, *T. ventricosus* was patchily distributed during both day and night. We observed that in rocky habitat, *T. ventricosus* was commonly elevated on rock promontories, rather than the benthos, suggesting that its distribution in this habitat may be driven more by preference for certain physical structures than feeding pressures.

Contrary to the finding that *T. ventricosus* nocturnally migrates to rocky habitat (Braden and Leander 2001), we did not find significantly more *T. ventricosus* in rocky areas or fewer in turtle grass beds at

Table 1. Dispersion patterns of *T. ventricosus* and *L. variegatus* in two habitats during the day and at night, as indicated by variance-to-mean ratios (VMR).

Urchin species	Time	VMR	
		Turtle grass	Rocky habitat
T. ventricosus	Day	0.44	16.33
	Night	1.77	6.15
L. variegatus	Day	0.92	1.54
	Night	2.18	2.00

night. One explanation for this result is that *T. ventricosus* may not move more than 8 m a day (Tertschnig 1989), and the patches we sampled were not close to the interface between rocky and turtle grass habitats. *T. ventricosus* distribution on rocky habitats was less aggregated at night than it was during the day, which is inconsistent with their observed migration patterns. Further study is needed to better understand the nocturnal migration and resulting dispersion patterns of *T. ventricosus*.

Our results showed that *Lytechinus variegatus* was close to randomly dispersed in turtle grass habitats during the day, which suggests that they may not experience the food limitation that we posit causes the overdispersion pattern in *T. ventricosus*. We found that *L. variegatus* was somewhat more aggregated in turtle grass at night, which might be the result of predation pressures or mating behavior. Lastly, we found that *L. variegatus* was slightly aggregated in rocky habitat at both day and night, but this result may be unreliable given the extremely low densities of this species in rocky habitats.

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HOMING AND AGGREGATING IN *DIADEMA ANTILLARUM*

RICHARD W. TRIERWEILER and S. ALLIE HUNTER

Abstract: The long-spined black sea urchin, *Diadema antillarum,* forages on algae at night and then aggregates during the day in coral crevice refuges. The urchins often return to their same crevices (homing). We hypothesized that because urchins receive many benefits from aggregating that , when isolated, they would return to a group. We also hypothesized that homing in *D. antillarum* occurs when the benefits of returning to a known area outweigh the costs of returning. If you increase the cost by moving groups of urchins farther from their reef patch, homing should decrease. We found that urchins do not return to their groups, perhaps because the cost of travel is greater than the benefits of being in a group. When entire groups of urchins were moved short distances from their patch, some individuals did return to their specific coral patch, but this behavior decreased as the distance to return to the patch increased. Our results suggest that there is a tradeoff between the costs and benefits of homing in *Diadema antillarum.*

Key Words: Discovery Bay, group benefits, Long-spined Black Urchin, travel cost

INTRODUCTION

Diadema antillarum, the long-spined black sea urchin, is an important circumtropical grazer of algae on coral reefs when the abundance of large herbivorous fish is low (Carpenter 1990). They exhibit a diel activity pattern, foraging from dusk to dawn and then aggregating in crevices throughout the day (Ogden et al. 1973). The benefits of being in these aggregations could be increased fertilization success since *D. antillarum* are dioecious external spawners and gamete release by an isolated individual often results in low success (Snyder 1970). *D. antillarum* also prefer to eat algal turf and crustose algae over mature macroalgae (Carpenter 1981) because the macroalgae has increased levels of calcification and secondary metabolites (Hay 1994). The maintenance of these algal turfs requires high levels of herbivory that might only be obtained by group grazing. Finally, the interlocking spines of a group of *D. antillarum* might decrease predation and dislodgement. We hypothesized that the benefits conferred to an urchin by being in a group would outweigh the cost associated with traveling to reach a group. We predicated that individual urchins, when removed from a group and placed by themselves, would return to the nearest group.

D. antillarum have been shown to return to the same crevice every morning for long periods of time (Carpenter 1984). This high tendency to home is due to the benefits received by having a known territory: having an adequate refuge when refuges are limited and are necessary to avoid predation (Carpenter 1984), increased surge protection (Morell 1981), and partitioning of food resources across the urchin population (Carpenter 1984). Traveling to return to specific sites costs the urchin in both the form of energy expenditure and

increased exposure to predators and surge while traveling (Carpenter 1984). We hypothesized that homing in *D. antillarum* occurs when the benefits of homing outweigh the cost. We predicted that the frequency of homing in a group of urchins would decrease as a function of increasing cost when we defined cost as the distance an urchin must travel to return to its original reef.

METHODS

We sampled on 23-25 February 2005 on the backreef of Discovery Bay, Jamaica. We established 10 patch reef sites varying between 1-3 m in diameter with *D. antillarum* present. At each of the sites we recorded urchin abundance on the patch reef (urchins within a half meter of the reef were counted as well). To test our first prediction that urchins would return to their original groups, we moved one individual from each site to another patch reef that was ≈5 m away. There were no other patches with *D. antillarum* that were closer than their original group. We chose 5 m because we wanted them to be isolated but capable of returning and *D. antillarum* have been observed to move up to 8 m during one night (Carpenter 1984). The following day we counted the number of urchins at each of our sites to see if the individual that was removed had returned.

To test the second prediction that groups of urchins would return to their original patch, we moved all the urchins from 10 patch reefs to another patch reef either zero, two, five, or ten m away. Each group ranged from 2 - 15 urchins. There were four 0 m replicates (control) and two sites for each distance treatment. The following day we counted urchins on the original patch reefs and on the treatment patch reefs to see if the urchins had returned to their original reefs or stayed on their new reefs. We used a linear regression to determine the relationship between the frequency of homing and the distance removed.

Table 1. The abundance of *D. antillarum* at different sites over time.

Site	# day 1	# day 2	Distance moved	# day 3 old rock	# day 3 new rock	Night 1	Night 2
1	9	8	2	1	8	.	.
2	5	4	0	4	.	4	3
3	16	15	0	15	.	12	8
4	10	9	5	0	9	.	.
5	5	4	10	0	5	.	.
6	12	11	0	11	.	3	2
7	5	4	0	4	.	3	3
8	3	2	2	1	1	.	.
9	6	5	5	1	3	.	.
10	6	5	10	0	2	.	.

Some urchins do not leave their crevice on any given night (Brosnahan 2002). We needed to establish that the urchins in Discovery Bay were moving. To determine if urchins were actually homing or simply never leaving their crevices, we surveyed the number of urchins on 10 patch reefs at both day and night. Urchins were considered to have moved off the reef if they were more than 0.5 m away. All data were analyzed using JMP 5.0.1.

RESULTS

Of the 10 individuals that we moved 5 m away from their original group and reef, none returned to the group and many remained where they were placed. However, when the entire group of urchins was moved, some urchins did return and there was a decreasing return rate with increased distance moved (Fig. 1). Most of the urchins in the group relocation experiment did not move; three unchins did return to their original reef, and four were unable to be located.

On the control reefs, 44% of the urchins moved off their reefs at night and all returned to their original reefs in the morning, so urchins are indeed capable of moving and homing under normal conditions.

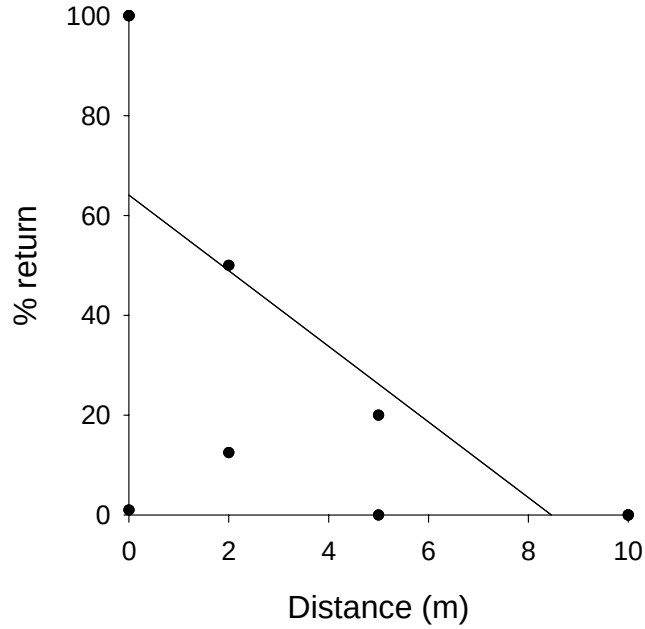

Figure 1. Effect of the distance *Diadema antillarum* was displaced from its original patch reef during the day on the percentage of individuals that returned the following day. Two points overlap at distance of ten and zero meters ($y = 0.82 - 0.1x$, $r^2 = 0.71$, df = 8, P = 0.002).

DISCUSSION

Since none of the urchins that had been removed singly from their groups returned to their groups, it appears that the cost of traveling back to join the group may be greater than the benefits derived from being with the group. The majority of the removed urchins did not even attempt to return, perhaps because our treatment distance was not far enough to remove the effect of group benefits such as maintenance of algal turfs and increased fertilization success. We only saw one urchin move 5 m so we do not know if the majority of this population of *D. antillarum* tends to only move distances less than 5 m, making our treatment level unrealistic.

The tendency of *D. antillarum* to return to their original patch reef when moved as a group supports the idea that there are benefits to homing, such as familiarity with refuges and the availability of known resources. Familiarity with a certain area has been shown to be an important factor in determining territoriality and homing in other species like gastropods (Cook 1979, Stimson 1973). However,

the sharp decline in homing with distance moved indicates that there may be a high cost to travel which eclipses the benefits of homing. Because we moved entire groups of urchins, which remained together at the new location, the benefit of being in a group was not altered. The cost for the whole group to return to the original site may be greater than the benefit to the group of returning to the original site.

Future studies could examine the effect of different levels of predation on the distance that urchins are willing to traverse to get back to their original reef. The effects of group size on *D. antillarum* homing should also be examined to see if certain group sizes provide optimum benefits to individuals in those groups, causing them to have a higher tendency to remain in the group. Additionally, more work is needed to quantify the benefits and costs associated with homing behavior.

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THE EFFECT OF ALGAL SPECIES AND SUBSTRATE TYPE ON INFAUNAL ASSEMBLAGES IN *PENICILLUS CAPITATUS* AND *PENICILLUS DUMENTOSUS*

EMILY L. SHARP AND CAYELAN C. CAREY

Abstract: Macroalgae provide important refuges for infauna from visual predators. We compared the infaunal communities in two algal species (*Penicillus capitatus* and *Penicillus dumentosus*) on two different substrates (*Thalassia testudinum* and sand). We hypothesized that large infauna would be more abundant in *P. dumentosus* because it has larger inter-filament spaces that would provide better refuge than the smaller inter-filament spaces in *P. capitatus*. We also hypothesized that sandy substrates would have higher total infaunal abundance because there is a greater need for refuge in this habitat. We collected samples of each algal species from the back reef at Discovery Bay, Jamaica and measured infaunal abundance and size of each organism. As predicted, we found more large infauna in *P. dumentosus* and more small infauna in *P. capitatus*. Total and large infaunal abundance did not differ between substrates, though more small infauna were found in the sandy patches. This may be due to the ability of small infauna to utilize grass as a refuge, reducing the need for a macroalgal refuge in this habitat.

Key Words: macroalgae, marine infauna, refuge, Thalassia testudinum

INTRODUCTION

Macroalgae provide important refuges for infauna (Glastris et al. 2001, Guidi 2003, Richardson and Nelson 1989, Shandro and Sohn 1997, Stoner 1985, Stoner 1986). The physical structure of the algae may be important in determining the abundance and composition of the infaunal assemblage (Glastris et al. 2001). The surrounding habitat of the macroalgae may also influence the infaunal assemblage by providing other possible refuges, thus reducing the need for a macroalgal refuge.

Penicillus capitatus, a common marine macroalga found in shallow reef waters, is an important infaunal refuge (Shandro and Sohn 1997, Stoner 1985, Stoner 1986). More infauna is found in the *P. capitatus* capitulum than in the surrounding habitat (Stoner 1985). *Penicillus dumentosus*, a similarly-structured macroalga, coexists with *P. capitatus* across multiple substrates. The two algae differ in filament size and abundance; *P. dumentosus* has fewer and wider filaments (400-800 μm) that are more spaced than *P. capitatus* (100-200 μm) (Dawes 1976). We hypothesized that infaunal communities would be different between *P. capitatus* and *P. dumentosus* due to the difference in capitula structure and inter-filament spaces in their capitula. We predicted that larger-sized infauna would be more abundant in *P. dumentosus* than *P. capitatus* because of the greater inter-filament space between filaments in *P. dumentosus*.

In *Thalassia testudinum* patches, grasses may provide a refuge from predation for infauna, reducing the need for a macroalgal refuge. In addition, predation pressure may be higher in sandy areas due

to a lack of refuge (Walters 1991). Therefore, we hypothesized that infauna face greater predation pressures within sandy patches than grassy patches, and would thus have a greater need for a macroalgal refuge. We predicted that there would be greater total infaunal abundance within the sandy patches than grassy patches.

METHODS

On 23 February 2005, we collected 16 algal samples (eight *P. capitatus* and eight *P. dumentosus*) from the back reef at Discovery Bay Marine Laboratory, Jamaica. Four samples of each alga were collected from sandy substrate patches and four samples of each alga were collected from *Thalassia testudinum* patches. All samples were collected from 1 m depth, and were located in the center of a patch of at least 4 m^2 to minimize infaunal variation from being near other patches and substrate types. We placed plastic bags around each alga underwater before removal to prevent any infauna contamination from the sediment, and loss of infauna from the alga. We attempted to choose algae that had capitula of similar sizes.

For each algal sample, we measured displaced volume and mass. Each algal sample was rinsed twice in both salt and fresh water to completely defaunate the alga. The rinsed water was filtered through a 153 μm mesh to remove all infauna. We preserved our infaunal samples in 10% formalin. Using dissecting microscopes, we counted and identified to order all infauna. We grouped the six most abundant taxa into large (> 1 mm) and small (< 1 mm) size classes.

We log-transformed our infaunal abundances to meet assumptions required for parametric tests. We used two-way ANOVAs to determine the effects of substrate, algal species, and their interaction on the large and small size classes of the six most abundant infaunal taxa (JMP 5.0.1). We used t-tests to compare the differences in capitulum mass and volume displacement between *P. capitatus* and *P. dumentosus*.

RESULTS

There was no difference in capitula mass or displacement volume between *P. capitatus* and *P. dumentosus* (t-tests, $F < 1.52$, $df = 1, 14$, $P > 0.24$). We counted and identified 1660 infauna in 13 orders. The two-way model with effects of substrate type, algal species, and the substrate/species interaction on total infaunal abundance was not significant (2-way ANOVA, $F = 1.08$, $df = 3, 12$, $P = 0.40$).

Within the six most common taxa (Amphipoda, Copepoda, Decapoda, Isopoda, Ostracoda, and Polychaeta) and large and small size classes (see Table 1), there was no significant interaction of substrate type and algal species on the abundance of small infauna per capitula (2-way ANOVA, $F = 0.001$, $df = 1, 14$, $P = 0.98$; Fig. 1a). There were more small infauna in *P. capitatus* than *P. dumentosus* (2-way ANOVA, $F = 7.51$, $df = 1, 14$, $P = 0.01$) and more small infauna in capitula above sandy substrates than in capitula above

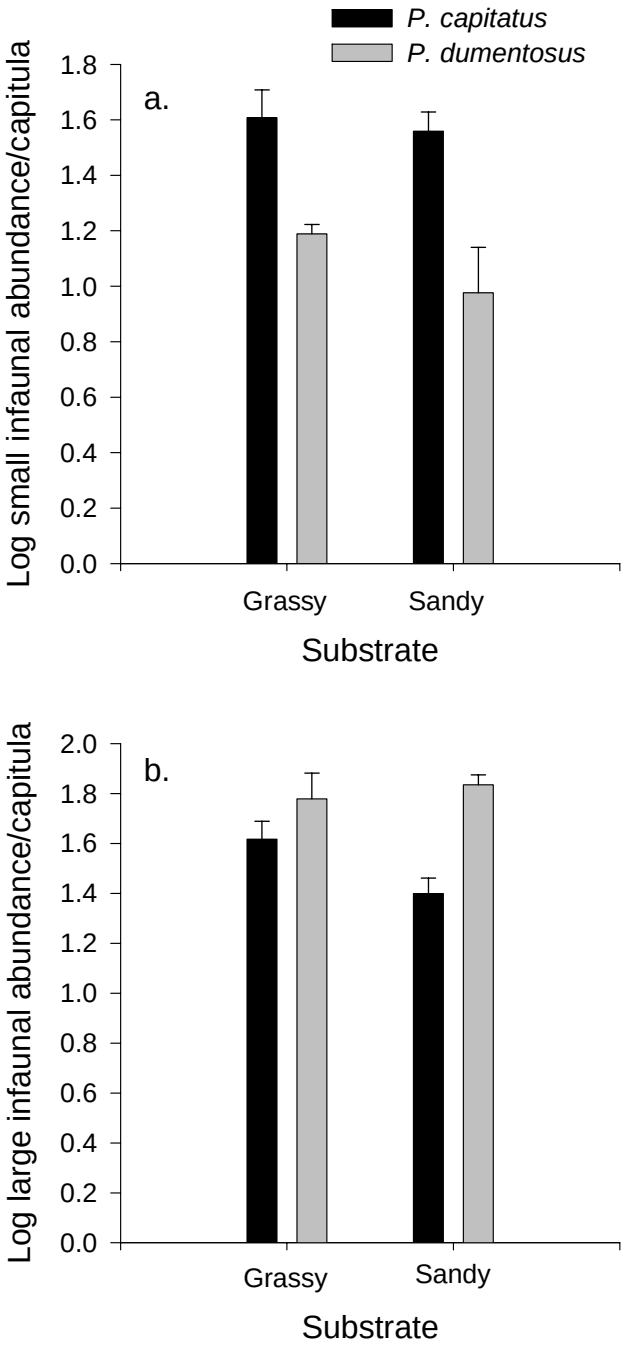

Figure 1. Effect of substrate type and algal species on infaunal abundance per capitula. A. Small infaunal abundance per capitula was higher in *P. capitatus* than *P. dumentosus* and in algae above sandy substrate than algae above grassy substrate. B. Large infaunal abundance per capitula was higher in *P. dumentosus* than *P. capitatus*, with no effect of substrate type.

grassy substrates (2-way ANOVA, F = 4.10, df = 1, 14, P = 0.06).

There was a significant interaction of substrate type and algal species on the abundance of large infauna per capitula (2-way ANOVA, F = 5.52, df = 1, 14, P = 0.04; Fig. 1b). There were more large infauna per capitula in *P. dumentosus* than *P. capitatus* (2-way ANOVA, F = 5.75, df = 1, 14, P = 0.03), but there was no significant effect of substrate type on large infaunal abundance per capitula.

DISCUSSION

We found the same abundance of total infauna in the four possible algal/substrate groups (grassy *P. capitatus*, sandy *P. capitatus*, grassy *P. dumentosus*, and sandy *P. dumentosus*), indicating that *P. capitatus* and *P. dumentosus* are utilized equally as refuges in both sandy and grassy substrates. There was no difference between *P. capitatus* and *P. dumentosus* in mass and displacement volume of the capitulum, so differences in faunal abundance are likely not a function of differences in capitulum size between the two species.

As predicted, *P. dumentosus* had more large infauna than *P. capitatus*, which may be due to its larger inter-filament spaces. The large organisms might only be able to fit inbetween the filaments of *P. dumentosus*, possibly competitively excluding small organisms from utilizing that alga as a refuge. The low abundance of large infauna in *P. capitatus* would then allow small organisms to dominate the infaunal

Table 1. Infauna taxa abundance per size class in *P. capitatus* and *P. dumentosus*. Small organisms are less than 1 mm in length, and large organisms are greater than 1 mm in length

Taxa	Size Class	Abundance in *P. capitatus*	Abundance in *P. dumentosus*
Amphipod			
	Small	147	28
	Large	110	356
Copepoda			
	Small	64	31
	Large	3	49
Decapoda			
	Small	0	0
	Large	146	98
Isopoda			
	Small	27	28
	Large	15	37
Ostracoda			
	Small	137	27
	Large	5	16
Polychaeta			
	Small	14	4
	Large	24	45
Total infauna			
	Small	389	118
	Large	303	609

assemblage in *P. capitatus*.

Contrary to our predictions, total infaunal abundance did not differ between those macroalgae in grassy substrates and those in sandy substrates. There were more small organisms in the macroalgae in sandy patches than in the grassy patches, but no change in abundance of large organisms between the two substrate types. If the small organisms could successfully use grasses as a refuge, then they would have less need to use macroalgae as a refuge in grassy habitat. This would explain their decreased abundance in the macroalgae surrounded by grass. Conversely, if large organisms faced similar predation pressures in both grassy and sandy areas but could not successfully utilize grass to evade predators, then we would expect them to utilize macroalgae equally in both substrates.

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DIURNAL PATTERNS OF PARROTFISH HERBIVORY ON *THALASSIA TESTUDINUM*

ELVINA C. CHOW

Abstract: Parrotfish are major herbivores of turtlegrass in coral reef systems. At Discovery Bay, Jamaica, these fishes exhibit diel behavior, with most activity concentrated during daylight hours. I hypothesized that herbivory on turtlegrass would change throughout the day due to changes in parrotfish activity. I predicted that herbivory would be greatest during the day, especially in the morning hours, and lowest at night when parrotfish are known to be inactive. I tested this hypothesis by monitoring herbivory rates in experimental turtlegrass patches at Discovery Bay through the day: morning, midday, evening, and night. Parrotfish herbivory was highest in the morning and lower for the remainder of the day. These results suggest that parrotfish feeding activity is concentrated in the morning hours, which is probably when they are most hungry, after a 12 h period of rest.

Key Words: day active fish, diel feeding, temporal differences, turtle grass

INTRODUCTION

Turtlegrass, *Thalassia testudinum*, is a major producer of primary biomass in coral reef systems, and its consumption is one of the main dynamics in tropical marine food webs (Kirsch et al. 2002). However, little has been done to identify the feeding behaviors of its consumers.

Parrotfish are one of the main consumers of turtlegrass in coral reef ecosystems. These fishes are diurnally active and are commonly found feeding on turtlegrass beds during the day. At night they rest and sleep, sheltering themselves with grass blades (Lobel 1981).

In this study, I investigated feeding rates of parrotfish in *T. testudinum* beds. Although parrotfish must forage during the day, I hypothesized that foraging rates during the daytime are not constant. More specifically, I predicted that parrotfish grazing would be highest in the morning because they require more calories after not eating during the night. After intense grazing in the morning, parrotfish may reduce their feeding rate over the course of the day because they become less hungry and have consumed enough to meet their dietary needs for the day.

METHODS

On 22-23 February 2005, I measured parrotfish herbivory rates in a large *T. testudinum* bed near the lagoon at Discovery Bay Marine Laboratory, Jamaica. The study site was located 150 m west of the Marine Lab in a turtle grass bed covering an area of approximately 3000 m^2 (Fig. 1).

I used *T. testudinum* implants to estimate grazing at different times of the day. Each implant consisted of three *T. testudinum* blade tips that had no visual evidence of herbivory trimmed to 12 cm in length. Each implant was clipped to a weighted clothespin. Turtle grass blades were taken from the dock area. Ten replicate groups

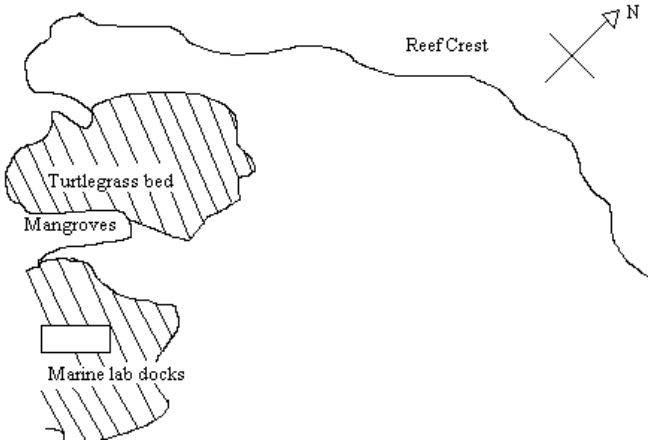

Figure 1. Turtle grass bed site used to test parrotfish herbivory patterns in Discovery Bay, Jamaica. Turtle grass bed is approximately 3000 m^2.

of four clothespins (12 leaves per group, 120 leaves total) were haphazardly placed within the *T. testudinum* bed. Clothespins within each group were placed approximately 0.2 m apart, and replicates were 5 m apart. Implants were left *in situ* for 4-hr periods during different times of the day: morning (0700 - 1100), midday (1100 - 1500), evening (1500 - 1900), and night (1800 - 2000). After each period, I collected the leaf implants and replaced them with new ones.

Herbivory was quantified at the end of each time period by measuring the percentage of areal leaf loss. Leaf losses to parrotfish grazers were estimated by subtracting the initial measurement of leaf area from leaf area remaining after 4 h. *Thalassia testudinum* blades that had been completely removed from the clothespin prior to my collection were counted as 100% herbivory. Percentage of herbivory was calculated as:

[(area of leaf loss/total area of blade) x 100]

Data were analyzed using JMP 5.0.1. A mixed model ANOVA was used to examine how parrotfish herbivory on *T. testidinum* changed over the course of the day with time of day as a fixed effect and patch as a random effect. Post-hoc comparisons were made using tukey's HSD.

RESULTS

Field observations over four hours at the study site revealed that parrotfish were the only fish grazing on *T. testudinum* blades. Furthermore, no sea urchins were observed in this area, and none of the collected blades were damaged by sea urchin grazing. All herbivory on *T. testudinum* implants in the study site was therefore attributed to parrotfish grazing.

Herbivory on *T. testudinum* ranged from 0.25 - 15.2% over the course of the day. The two-way ANOVA revealed that herbivory was a function of time-of-day ($F = 6.49$, $df = 1, 467$, $P < 0.001$; Fig. 2). Herbivory was greatest in the morning, and remained low for the rest of the day ($F = 24.0$, $df = 3, 467$, $P < 0.001$; tukey's HSD < 0.05; Fig. 2). There was no effect of replicate patches on the rate of herbivory ($F = 0.67$, $df = 36, 467$, $P < 0.74$). This indicates that the variation in herbiviory throughout the day was consistent across replicates.

DISCUSSION

Parrotfish grazing on *T. testudinum* was significantly higher in the morning, which supports my hypothesis that there is differential parrotfish feeding over the course of the day. This suggests that

parrotfish are probably most hungry in the morning after not eating in the night and require greater amounts of resources in the morning to be active during the day.

Although I did not expect to see any feeding at night, the night period had 0.25% herbivory on *T. testudinum* leaves. Since light may be the environmental cue for feeding, parrotfish may still be feeding as late as 1900, which was two hours into the "night" treatments. Future studies could quantify parrotfish feeding during periods of full darkness to determine if parrotfish do feed at night. Even with grazing in the night treatment, the morning treatment exhibited the highest level of herbivory. This result may be driven by several factors including hunger, predation, and competition.

It is possible that parrotfish may feed in the early morning to decrease predation activity. Although one cost of foraging throughout the day is expending energy, there may also be costs from increased exposure to predators, with the costs of day-time exposure exceeding the potential benefits of increased energy gains. However, this is highly unlikely in Discovery Bay given that this area has been heavily overfished, thereby decimating many fish populations including parrotfish predators. It is also inconsistent with the flurry of herbivory I observed in the morning, when predators are known to be inactive (Kirsch et al. 2002).

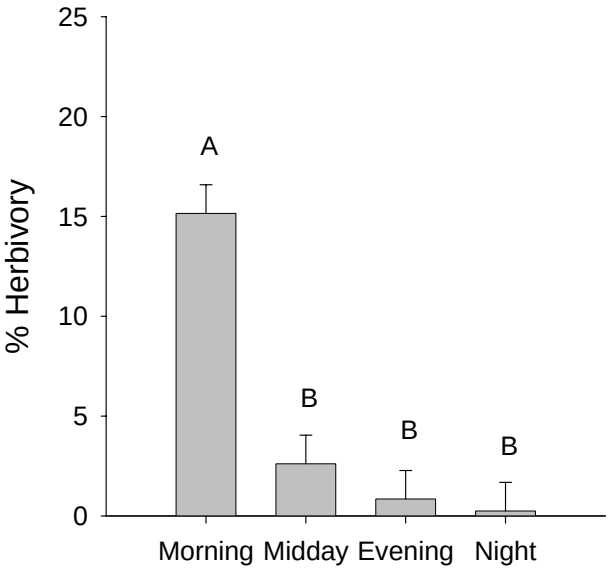

Figure 2. Percent of implanted *Thalassia testudinum* leaves eaten by parrotfish throughout the day.

The temporal changes of parrotfish grazing may also be attributed to competition for resources during the day. As sea urchins are major herbivores of *T. testudinum*, competition with these echinoderms may influence parrotfish grazing. There are three commonly occurring species of sea urchins at Discovery Bay. Only the West Indian sea egg, *Tripneustes ventricosus*, exclusively grazes on turtlegrass. This species of sea urchin grazes during the day and often moves out of turtlegrass beds at night to rest on rocks and rubble (Lawrence et al. 2001). Unfortunately, little is known about their grazing rates over the course of the day. An additional study could examine *T. ventricosus* herbivory rates during the daytime to determine if grazing patterns of *T. ventricosus* could contribute to the diel feeding pattern in parrotfish.

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DIURNAL CHANGES IN *TRIPNEUSTES VENTRICOSUS* COVERING RESPONSE IN *THALASSIA TESTUDINUM* SEA GRASS BEDS

JENNY E. JUN, TIMOTHY R. MATSUURA AND MELISSA A. BARGER

Abstract: The urchin *Tripneustes ventricosus* uses its tube feet and spines to cover itself with sea grass blades or other debris. We examined this behavior as a defense against solar radiation. We hypothesized that the degree of covering by *T. ventricosus* would change according to the degree of solar radiation over the course of the day. We predicted that covering would be highest in the afternoon, lower in the morning and evening, and lowest at night. Covering response may also be affected by available material. We predicted that *T. ventricosus* would cover itself more in areas of high-density sea grass than low-density sea grass. We measured percent cover in *T. ventricosus* individuals at different times of day in high- and low-density sea grass areas. Coverage was highest in the afternoon and lowest at night for both sea grass densities. Percent cover was significantly higher for urchins in high-density sea grass areas than in low-density areas for all times during the day, but not at night. These results indicate that *T. ventricosus* is able to detect and respond to changing levels of solar radiation by changing its percent cover.

Key Words: covering behavior, salt and pepper urchin, solar radiation

INTRODUCTION

Tripneustes ventricosus, the salt and pepper urchin, uses its tube feet and spines to cover itself with shells, sea grass blades and other debris (Lewis 1958). Several explanations have been suggested for this covering response, including protection from wave surge and predators (Kehas et al. 2004); however, there is strong evidence that the primary purpose for covering behavior is to screen solar radiation (Fierce and Lapin 2004, Kehas et al. 2004, Lewis 1958). When grass fragments are covering

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one half of the urchin and light is shown on the other half, the urchin will transfer the grass to the illuminated half (Lewis 1958). Additionally, when *T. ventricosus* in the lab were given the option of covering with black plastic strips or clear plastic strips, they chose the black strips (Fierce and Lapin 2004).

We examined covering behavior as a defense against solar radiation. Over the course of the day, there are changes in solar radiation with radiation being highest at midday, lower in the morning and evening, and negligible at night (Strickler 1999). We hypothesized that the degree of covering by *T. ventricosus* would change according to the degree of solar radiation. Therefore, covering should be low in the morning, peak at midday, decrease in the evening, and be lowest at night.

We also examined the covering behavior of *T. ventricosus* within different densities of turtle grass, *Thalassia testudinum*. We predicted higher coverage by *T. ventricosus* in high-density *T. testudinum* than in low-density turtle grass because there are more resources available for covering.

METHODS

On 24 February 2005, we observed the covering behavior of *T. ventricosus* in three *T. testudinum* patches in the back reef at Discovery Bay, Jamaica. Two patches were located in the west back reef; the third patch was in the central back reef near the reef crest. Water depth at each of these patches ranged from 0.5 - 1.5 m. We visually estimated percent cover for the first 40 *T. ventricosus* individuals encountered in each patch and noted covering material (i.e., seagrass blades, rocks, and shells). We also identified the *T. testudinum* density in which each urchin was found as either high or low. We sampled at three different times during the day: early morning (0800), late morning (1145) and evening (1700), and once at night (2230). Times were chosen to monitor changes in covering behavior across a range of solar radiation levels. During night sampling we found between 30 and 40 individuals; we were not able to find 40 individuals at all sites due to difficulties in locating individuals with flashlights.

All data met the assumptions of parametric tests, including normal distributions and equal variances. We used a two-way ANOVA to examine the effects of time of day, *T. testudinum* density, and their interaction on urchin covering.

RESULTS

We observed a total of 466 *T. ventricosus* individuals. All observed individuals that displayed covering behavior used only seagrass blades as covering material. Mean percent cover ranged from 7.8 ± 2.5 SE to 57.4 ± 3.7 SE across treatments (Fig. 1). The interaction between time of day and *T. testudinum* density on percent cover was significant (2-way ANOVA, $F = 9.29$, $df = 3, 3$, $P < 0.0001$; Fig. 1). Percent cover significantly changed over the course of the day, with highest cover occurring in the late morning for both high- and low-

density *T. testudinum* areas (2-way ANOVA, F = 48.51, df = 3, 3, P < 0.0001; Fig. 1). Percent cover was significantly higher for urchins in high-density *T. testudinum* areas than low-density areas for all times during the day, but not at night (2-way ANOVA, F = 94.74, df = 1, 1, P < 0.0001; Fig. 1).

DISCUSSION

We found that the degree of covering by *T. ventricosus* changed throughout the day and attributed this to changes in solar radiation. These results suggest that *T. ventricosus* is able to detect and respond to changing levels of solar radiation by changing its percent cover. At night, *T. ventricosus* sheds most of its covering material; this suggests that there is a cost associated with covering, and at night the costs of retaining the covering outweigh any benefits conferred by being covered. Covering may inhibit gas exchange through the aboral tube feet and thus decrease respiration or may inhibit release of feces and gametes into the water (Kehas et al. 2004).

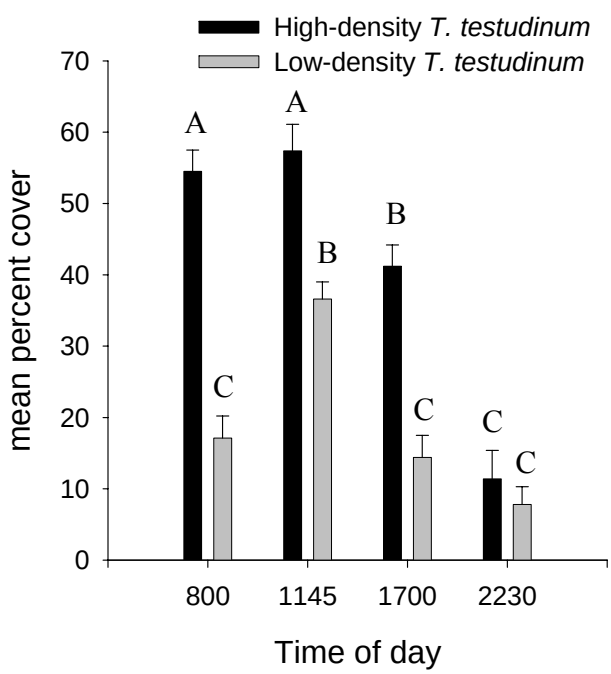

Figure 1. Mean percent cover of *Tripneustes ventricosus* at different periods during the day in high- and low-density *Thalassia testudinum*. Letters indicate significant differences in mean percent cover (Tukey test, α = 0.05).

Percent cover did not differ significantly between early- and late-morning treatments in high-density grass but did differ in low-density grass. Greater resource availability in the high-density areas may facilitate a quick covering response to increasing light intensity earlier in the day, whereas individuals in low-density areas may need more time to accrue covering materials. Sampling times for the early morning and late morning were also closer together than the evening sampling time (differences were 3.75 and 5.25 hours, respectively). It is likely that light intensity was more similar between the early- and late morning treatments, which further accounts for similarities between early- and late morning percent cover.

It is also possible that covering behavior may have evolved as a response to changing levels of light, but not specifically to damaging UV radiation. Although urchins do not respond directly to UV radiation (Butcher et al. 2002), responding to solar radiation allows them to avoid UV radiation as the intensity of UV radiation tracks the intensity of full spectrum solar radiation.

During the day, individuals covered themselves more in high-density grass areas than low-density grass areas. This is

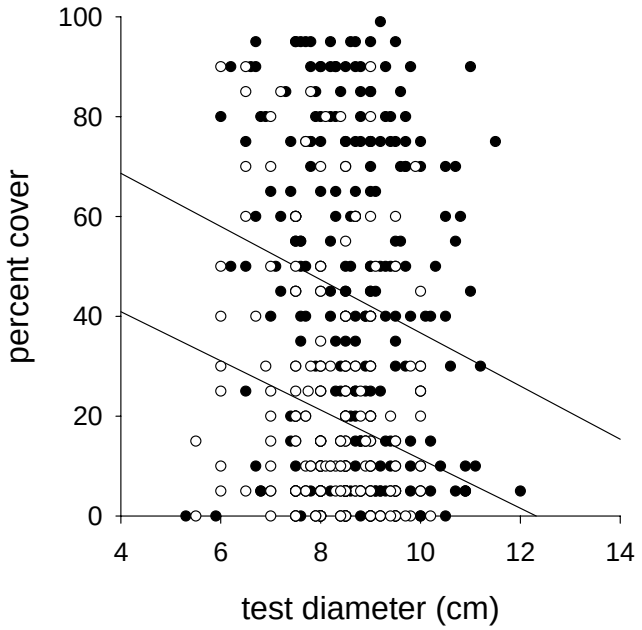

Figure 2. Relationship between percent cover in *Tripneustes ventricosus* and test diameter. Percent cover decreased with increasing diameter in both high density (closed dot) and low density (open dot) *Thalassia testudinum*. High density: y = -5.14x + 88.30; Low density: y = -5.14x + 62.47.

consistent with our prediction that higher density of *T. testudinum* would increase the availability of covering resources and would allow *T. ventricosus* to cover more fully. There was no effect of grass density on percent cover at night. High and low resource availability should not affect the ability to shed cover, only to acquire it. It follows that grass density would not affect the degree to which *T. ventricosus* sheds unnecessary cover at night.

Covering behavior may be augmented with a migration of individuals to different habitats as well as to deeper depths to increase avoidance of harmful radiation. Future studies could consider these aspects of *T. ventricosus* behavior.

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Addendum

We were also interested in the effect of sea urchin size on *T. ventricosus* covering behavior within the two *T. testudinum* densities. We measured test diameter for each *T. ventricosus* individual in our main experiment.

We examined the effect of urchin test diameter on percent cover between the high- and low-density *T. testudinum* using an indicator variables regression. The regression model was:

$$Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_1 X_2 + \varepsilon$$

where Y is the response variable (percent cover), X_1 is the urchin test diameter, X_2 is a binary indicator variable of analysis, β_0 is the intercept, β_1 is the slope, β_2 is the change in intercept between high- and low-density *T. testudinum*, and β_3 the change in slope between high- and low-density *T. testudinum* (Neter et al. 1996). We confirmed that data met the assumptions of normality and homogeneity of variances. Data were analyzed using JMP 5.0.1.

Percent cover decreased with increasing diameter in both high and low *T. testudinum* density areas. The high-density *T. testudinum* regression had an intercept significantly higher than that of the low-density *T. testudinum* regression ($P < 0.0001$), but no significant differences in slope were detected ($P = 0.8697$; Fig 2).

Small individuals in both grass densities covered themselves more than large individuals. Perhaps there is greater pressure on small individuals to cover due to greater susceptibility to radiation or inability to recover from damage. Additionally, there may be a greater risk of predation associated with being small, and a greater need to cover regardless of light intensity.

EFFECTS OF REFUGE SIZE AND DENSITY ON PREDATION AND HABITAT SELECTION IN BRITTLE-STARS

LAKSHMI NARAYAN, JENNY E. JUN AND ANNA R. NOWOGRODZKI

Abstract: Brittle-stars experience high predation pressure in coral reefs, and many use rocks as refuges from predators. We hypothesized that predation would be lowest on brittle-stars under large rocks, since they provide the greatest refuge area. Additionally, we hypothesized that predation would increase with brittle-star density, since brittle-stars may be forced into less protected spaces under rocks with higher densities. To test this hypothesis, we measured brittle-star abundance and predation levels under varying sizes of rocks in the backreef of Discovery Bay, Jamaica. Predation level was assessed by counting the number of lost or regenerating arms. We also conducted choice tests on *Ophiocoma echinata*, an abundant brittle-star species, between small and large refuges, and between refuges with high and low brittle-star density. The results of our field study showed a slight decrease in predation with increasing rock size and lower brittle-star densities. In the laboratory experiments, brittle-stars selected large refuges over small refuges, but did not select refuges based on brittle-star density. This suggests that brittle-stars may use refuge size, but not brittle-star density, as an indicator of refuge quality.

Key Words: Ophiocoma echinata, Ophiocoma pumilia, Ophioderma appressum, *Ophiuroidae*

INTRODUCTION

Many brittle-stars (Ophiuroidae) hide under coral rubble in tropical backreef ecosystems. High diurnal predation pressure restricts brittle-star activity to the night, when they may emerge or extend their arms from under rocks to deposit or filter feed (Casler et al. 2003, Sides and Woodley 1985). When attacked by a predator, brittle-stars use autonomy, self-amputation of one or more of their arms, as an escape mechanism. Arm regeneration occurs rapidly following a predation event (Hendler et al. 1995).

Given the consistently high predation pressure on brittle-stars in coral reef habitat, selection of suitable refuge is essential to brittle-star survival. To minimize predation risk, brittle-stars should select rubble refuges that provide the greatest protection. While patterns of brittle-star distribution under rubble are random in terms of species composition, abundance of individuals increases with rock size (Tran and Whited 2004). We hypothesized that this pattern is driven by higher brittle-star predation on small rocks. Larger rocks may provide better refuge for individuals because there is more hiding area available. Additionally, we hypothesized that predation should increase with brittle-star density, since brittle-stars may be forced into less protected spaces under rocks with higher densities.

We measured natural levels of pre-

dation on brittle-stars under rocks of varying sizes and brittle-star densities, with the prediction that predation on brittle-stars would decrease with increasing rock size but increase with increasing brittle-star density across varying rock sizes. We assumed that our predation measurements would reflect predation that occurred in the habitat where the individual was found, as brittle-stars tend to remain under the same refuge for up to three weeks at a time (Paine and Platt 1999). We also conducted lab experiments to examine how refuge size and density affect habitat selection by brittle-stars. We predicted that brittle-stars would prefer habitats that minimized predation in the wild, and, given the choice, would select refuges that were large and had a low density of other brittle-stars.

METHODS

Observational study

We conducted an observational study in the backreef of Discovery Bay, Jamaica, in areas near the reef crest that were approximately 1 m deep with abundant rock rubble on a substrate of sand and turtle grass. On 3-6 March 2005 we turned over 28 rocks ranging from 108 to 1770 cm^2 in base surface area, and collected all brittle-stars under each rock. Rock area (cm^2) and number of brittle-stars were recorded for each rock. For each brittle-star found, we recorded species and amount of predation, which we defined as the number of arms, out of five, that showed evidence of predation, including breakage and regeneration. Any arms broken off in the process of collection were not included as predation.

Lab experiment

We conducted a lab experiment that included two components: 1) a choice test between small and large rocks, and 2) a choice test between rocks with no conspecifics and rocks with a high density of conspecifics. Both experiments were conducted in opaque plastic tubs (66 cm long, 49 cm wide and 23.5 cm deep), set outside the wet lab at Discovery Bay Marine Laboratory and provided with running seawater. During the morning and early afternoon, all tubs were in partial shade, and during the late afternoon all tubs were in full shade. We used only the most abundant brittle-star species, *Ophiocoma echinata,* and all individuals were of similar size, with armspans ranging from 11 cm to 15 cm. To simulate small and large rocks, we used square glazed ceramic tiles 15.2 cm across (231.04 cm^2 in area) and 20.1 cm across (404.01 cm^2 in area), respectively. Tiles were raised on metal bolts 1.5 cm off the bottom of the tub to allow brittle-stars to seek refuge under them.

For the rock-size preference test, each tub contained one large and one small tile, placed 14.5 cm apart. For the conspecific-density preference test, each tub contained two small tiles, one with no brittle-stars under it and one with eight brittle-stars under it (which we had placed there previously). Tiles were placed 19 cm apart.

For each trial, we placed one brittle-star in the tub equidistant from the two

tiles. We recorded the individual's initial choice, and whether it had moved after one hour. For the conspecific-density test, we also recorded whether any of the other eight brittle-stars had moved after one hour. We conducted 12 trials of each of the two tests during the day (1030-1800), and 10 trials of each of the two tests during the night (1900-0030). Sunset occurred at 1820, so all day trials occurred in the light and all night trials in the dark.

We analyzed our observational data using linear regression and ANCOVA analyses. Lab experiment data were analyzed using contingency analyses, with α = 0.025, as determined by a Bonferroni adjustment to account for accumulated Type I error.

RESULTS

Observational study

We found a total of 161 brittle-stars under the 28 rocks sampled, with a mean density of 0.01 ± 0.001 SE brittle-stars/cm^2. Predation occurred at a rate of 1 ± 0.07 (mean ± 1 SE) arms/brittle-star, and ranged from zero to four arms lost. We found seven different species in total, with *Ophiocoma echinata* (82), *Ophioderma appressum* (48), and *Ophiocoma pumilia* (14) being the three most abundant species. We found a strong positive relationship between total brittle-star abundance and rock size (linear regression, r^2 = 0.74, df = 160, P < 0.001; Fig. 1), but no relationship between density and rock size (linear regression, r^2 = 0.03, df = 27, P = 0.39). Predation on brittle-stars decreased slightly with rock size (linear regression, y = 1.36 - 0.0004 x, r^2 = 0.05, df = 160, P = 0.005) and increased slightly with brittle-star density (linear regression, y = 0.6357127 + 30.827471x, r^2 = 0.02, df = 160, P = 0.05).

We found that predation on the three most abundant brittle-star species increased with density for each species (ANCOVA, F = 4.16, df = 1, 46, P = 0.05), but that there were no significant differences in the effect of density on predation between any of these species (ANCOVA; difference between *Ophiocoma echinata* and *Ophiocoma pumilia*: F = 1.61, df = 1, 46, P = 0.21; difference between *Ophioderma appressum* and *Ophiocoma pumilia:* F = 0.94, df = 1, 46, P = 0.34; difference between *Ophiocoma echinata* and *Ophioderma appressum:* F = 0.03, df = 1, 46, P = 0.86).

When we analyzed the differences in predation levels for the three most abundant brittle-star species, we found that *Ophioderma appressum* had significantly less predation than *Ophiocoma pumilia* (F = 5.09,

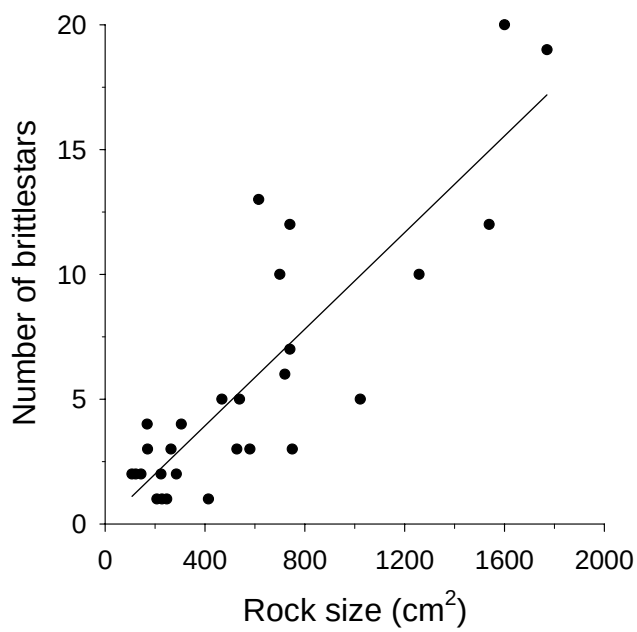

Figure 1. The number of brittle-stars under rocks increased with rock size (n = 28).

df = 1, 46, P = 0.03; Fig. 2) and marginally less predation than *Ophiocoma echinata* (F = 3.28, df = 1, 46, P = 0.08; Fig. 2). There was no difference in predation rates on *Ophiocoma echinata* and *Ophiocoma pumilia* (F = 0.91, df = 1, 46, P = 0.35; Fig. 2).

There was a marginally significant inverse relationship between rock size and predation for each of the three most abundant species (ANCOVA, F = 3.18, df = 1, 46, P = 0.08), and the effect of rock size did not significantly differ between any of these species (ANCOVA; difference between *Ophiocoma echinata* and *Ophiocoma pumilia*: F = 3.74, df = 1, 46, P = 0.06; difference between *Ophioderma appressum* and *Ophiocoma pumilia:* F = 0.24, df = 1, 46, P = 0.63; difference between *Ophiocoma echinata* and *Ophioderma appressum:* F = 2.08, df = 1, 46, P = 0.16).

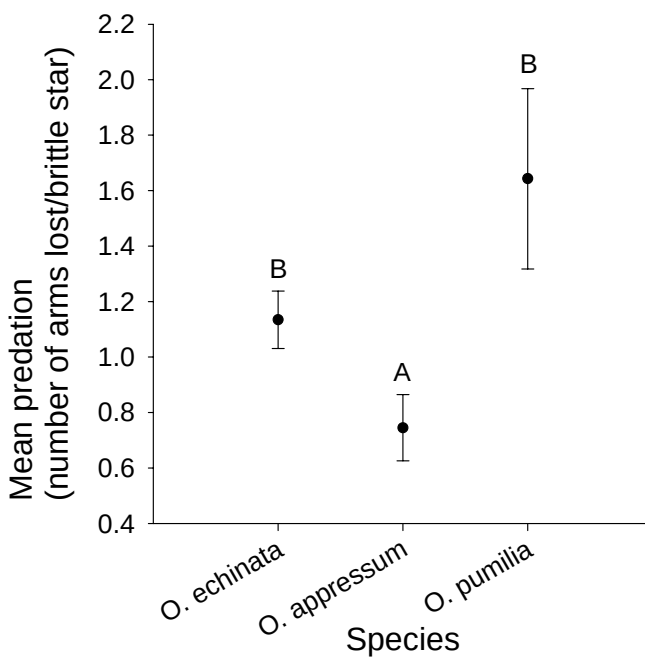

Figure 2. Mean number of arms damaged per brittle-star for *Ophiocoma echinata*, *Ophioderma appressum*, and *Ophiocoma pumilia*. Letters indicate significant differences in predation level. Values are mean ± 1 SE (n = 143).

Lab experiment

In our habitat choice experiments, we found that the final position of brittle-stars in the hour-long trials was strongly dependent on the habitat they initially selected, both for the rock size (χ^2 = 10.54, df = 1, 20, P = 0.001) and the brittle-star density (χ^2 = 14.67, df = 1, 20, P = 0.001) experiments. In most trials, brittle-stars placed in the middle of experimental tanks seemed to move towards the first tile they detected, and were found under the same tile at the end of the hour-long experimental period. The only exceptions occurred in the size-selection experiments, in which 4 out of 22 brittle-stars moved from small to large tiles.

The four occurrences of brittle-stars changing position in size-choice experiments all occurred at night, and contingency analysis showed that brittle-stars tended to select large tiles at night (χ^2 = 7.25, df = 1, 20, P = 0.007), with 9 out of 10 night brittle-stars selecting large tiles, compared to 4 out of 12 brittle-stars selecting large tiles during the day.

Tile selection in the density experiment was independent of time of day (χ^2 = 0.22, df = 1, 20, P = 0.64). Brittle-stars showed no clear preference for tiles with a high or low density of brittle-stars, with 12 brittle-stars selecting high density tiles and 10 selecting low density tiles.

Discussion

The results of our observational study showed that brittle-star abundance increased with rock size, indicating that

refuge size is an important determinant of brittle-star distribution. Although the relationships between predation levels, rock size and brittle-star density were weak, predation was lowest on individuals under large rocks with low densities of other brittle-stars, suggesting that these habitats provide the best refuge from predation. Therefore if brittle-stars are capable of selecting habitat, they should choose large rocks with low densities of other brittle-stars to minimize predation.

Although predation levels varied between the three most abundant species, the effects of rock size and brittle-star density on predation levels did not differ between taxa. If predation levels were disproportionately higher at high density for one species, this would suggest that this species was at a competitive disadvantage. Since this was not the case, it is likely that all three species had equal chances of being displaced from protective habitat at high brittle-star densities and none of these species were at a competitive disadvantage due to space limitation. Alternatively, species may not competitively displace each other in our study area, if space is not limiting for brittle-stars or if the three species occupy distinctly different areas under rocks. This may be the case, as microhabitat partitioning does occur between brittle-star species (Sides 1985).

Observed differences in predation levels between the three most abundant species could be due to differences in palatability or foraging behavior. Previous palatability studies found that *Ophioderma appressum* and *Ophiocoma pumilia* were more palatable than *Ophiocoma echinata*, but these results are inconsistent with the predation levels observed in our study for each of these species (Sides 1975, 1981 and Aronson 1988).

In our lab experiment, brittle-stars selected habitat based on refuge size but not brittle-star density. This suggests that brittle-stars recognize large rocks as better refuge than small rocks, but do not use density of other brittle-stars as an indicator of habitat quality. Large rocks may provide better refuges, which is consistent with the results of our observational study, in which predation was lower under large rocks. Our finding that brittle-stars did not choose habitats with lower brittle-star densities is inconsistent with our observational studies, which suggest that brittle-stars should choose habitats with low densities in order to minimize predation.

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BENEFITS OF MIXED SPECIES SCHOOLS FOR THREE FISH SPECIES

TIMOTHY R. MATSUURA, MELISSA A. BARGER, GABRIEL H. CALVI AND DANIEL J. MADIGAN

Abstract: The mechanisms that drive mixed species schooling are not well understood, and may vary with different fish species. We examined schooling behavior and the benefits of schooling in three fish species (spotlight parrotfish, doctorfish, and bluehead wrasse) at Discovery Bay, Jamaica. We followed individuals of each species, recording time spent schooling, average school size, feeding efficiency and damselfish attacks in and out of schools. Bluehead wrasse spent less time schooling than the other two species, although all species benefited from schools through increased foraging efficiency, decreased damselfish attacks, or both. Because food resources are neither limiting nor completely defended in Discovery Bay, we suggest that some mechanism other than increased foraging efficiency, such as predator avoidance, drives the amount of time each species spent schooling.

Key Words: bluehead wrasse, doctorfish, foraging efficiency, predator avoidance, stoplight parrotfish

INTRODUCTION

Forming heterospecific foraging associations is a common behavior of many tropical reef-fish species. These mixed-species schools comprise complex and relatively understudied interactions between species, and many mechanisms have been suggested to explain them. The main benefits of schooling include predator avoidance and increased foraging rates (Lukoschek and McCormick 2000). Other studies show that groups of fish can help fish circumvent the territoriality of competitors (Robertson 1976). A school of fish can swamp a damselfish territory and fish can graze on algae while the damselfish is occupied chasing other members of the school (Foster 1985), thus allowing an individual fish within a school to take more bites and receive fewer damselfish attacks.

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We chose three species of fish com-

mon in the back reef of Discovery Bay, Jamaica to compare the relative benefits gained by schooling across different fish species. Our three focal species were the stoplight parrotfish (*Sparisoma viride*), doctorfish (*Acanthurus chirurgus*), and the bluehead wrasse (*Thalassoma bifasciatum*). These fish are in different families and have distinct life histories, and all of these species are known to aggregate in loosely-knit feeding groups. Both the doctorfish and parrotfish are generalist feeders that consume algae, seagrass and microinvertebrates in the sediment. Terminal male bluehead wrasse forage upon invertebrates and zooplankton (Deloach 1999), and have been shown to prefer damselfish eggs when available (Foster 1987).

We wanted to assess any differences in schooling benefits between these species. We measured the differences in feeding rates and damselfish attack rates in and out of schools for each of these fish species. We also measured the proportion of time each fish spent in and out of schools. We predicted that the fish species with the greatest increase in feeding rate and the greatest decrease in damselfish attack rate would spend the greatest proportion of time schooling.

METHODS

We observed fish from 4-10 March 2005 on the west back reef at Discovery Bay, Jamaica. We located focal individuals of bluehead wrasse, stoplight parrotfish, and doctorfish by snorkeling over the reef until an individual was sighted in a mixed-species school. Since we were interested in schooling behavior, we chose fish that were initially in schools; any bias towards schooling should be seen across all three fish species and not affect the comparison between species. To control for size, all observed individuals fell into the following size ranges: bluehead wrasse, 9-11 cm (terminal male); stoplight parrotfish, 9-12 cm (juvenile); doctorfish, 9-12 cm (juvenile). Since size range and coloration were kept approximately equal for each fish species, the observed fish within each species were at approximately equal life stages.

We followed each fish for 10 min, recording the time spent in schools and time spent alone. We counted feeding bites and attacks by damselfish (damselfish attacks were any acts of damselfish aggression that elicited a response in the focal fish). We also counted the number of times an individual left and rejoined a school. Each time an individual joined a school, we recorded the number of individuals in the school; these values were averaged to obtain the mean school size for each individual during the observation period.

Proportion of time spent schooling, in-school and solitary feeding rates and in-school and solitary rates of attack by damselfish were compared for different species using one-way ANOVAs (JMP 5.0.1).

RESULTS

Bluehead wrasse spent significantly less time in schools than doctorfish and parrotfish ($F = 50.22$, $df = 2, 66$, $P < 0.001$,

Tukey's α = 0.05; Fig 1). Doctorfish and parrotfish did not differ in the proportion of time they spent in schools.

There was an effect of species and schooling on feeding rate (2-way ANOVA, F = 7.76, df = 5, 127, P < 0.0001; Species F = 8.76, df = 2, P = 0.0003; School F = 15.90, df = 1, P = 0.0001; Interaction F = 2.27, df = 2, P = 0.11; Fig. 2). The lack of an interaction shows there was no difference between species in the magnitude of the change between feeding rates in and out of schools. For each species, feeding rates were significantly higher when schooling than when solitary (Doctorfish F = 22.36, df = 1, 41, P < 0.0001; Parrotfish F= 2.02, df = 1, 42, P = 0.16; Bluehead Wrasse F = 3.71, df = 1, 44, P = 0.06; Fig. 2).

There was an effect of schooling, but not species, on rate of damselfish attacks (2-way ANOVA, F = 2.16, df = 5, 127, P = 0.06; Species F = 0.16, df = 2, P = 0.85; Schooling F = 5.34, df = 1, P = 0.02; Fig. 3). The magnitude of the change between damselfish attacks made on fish in and out of schools was the same for doctorfish and parrotfish but it differed significantly between these species and the bluehead wrasse (2-way ANOVA, Interaction F = 2.67, df = 2, P = 0.07; Fig. 3). Doctorfish and parrotfish both experienced a reduced rate of damselfish attacks when schooling than when solitary; there was no difference for bluehead wrasse (Doctorfish F = 3.11, df = 1, 44, P = 0.09; Parrotfish F = 7.28, df = 1, 42, P = 0.001; Bluehead Wrasse F = 0.27, df = 1, 44, P = 0.61; Fig. 3).

DISCUSSION

All three fish species showed benefits from mixed-species schools. Doctorfish and bluehead wrasse exhibited higher feeding rates in schools (Fig 2.), and the doctorfish and parrotfish experienced lower attack rates in schools (Fig. 3). The proportion of time spent schooling was not the same among the three species, with the bluehead wrasses schooling one-third as much as the doctorfish and parrotfish (Fig. 1).

The main benefits suggested for mixed-species schools are reduced risk of predation and higher foraging efficiency (Lukoschek and McCormick 2000). The proposed mechanisms by which foraging efficiency has been shown to increase in

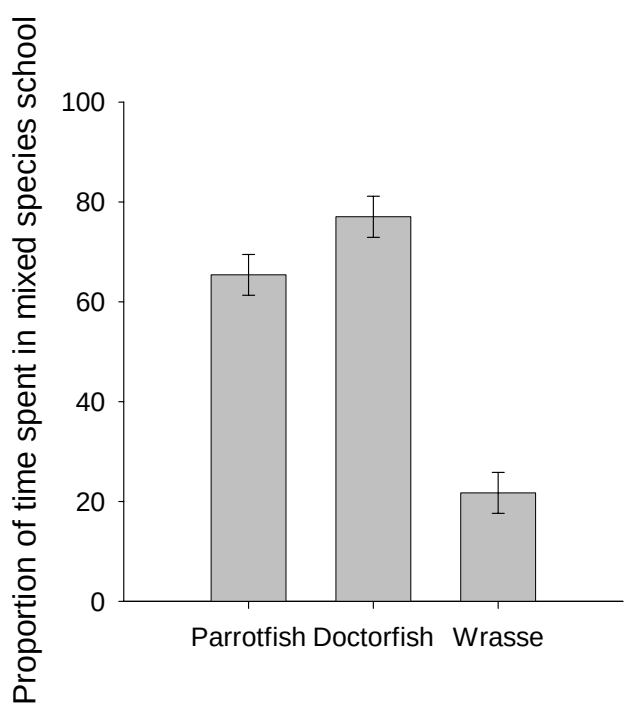

Figure 1. Proportion + 1 SE of time spent in mixed species schools. Doctorfish and Stoplight parrotfish spent more time in schools than out of schools. Bluehead wrasse spent more time out of schools than in schools.

mixed species schools are 1) resource location, in which school members expedite the finding of a rare or limited resource, and 2) swarming of territorially defended resources, such as fish eggs or damselfish algal mat territories (Foster 1985, 1987). In Discovery Bay, we saw doctorfish and parrotfish foraging on algal and turtle grass substrates, food resources that are neither limited nor entirely defended. Therefore, enhanced feeding is unlikely to be the only mechanism directly driving schooling behavior in these species.

Predator avoidance may be an important benefit of mixed-species schooling in these fish. Previous studies have shown that when in groups, fish spend less time showing 'vigilant' (predator-detecting) behavior, and thus more time foraging (Lukoschek and McCormick 2000). This was also supported by our behavioral observations of the doctorfish and parrotfish. In groups these fish fed in the open, but when solitary, they hid under rocks and fed little. This suggests that the doctorfish and parrotfish school to decrease their risk of predation, and that while schooling, decreased time is spent on predator detection, leading to increased foraging efficiency. This could be a response to naturally occurring predation threats; it is more likely to be an ingrained, evolutionarily-favored behavior, as predators are thought to be relatively uncommon at Discovery Bay (Ruel and Zug 1994).

The bluehead wrasse spent less time

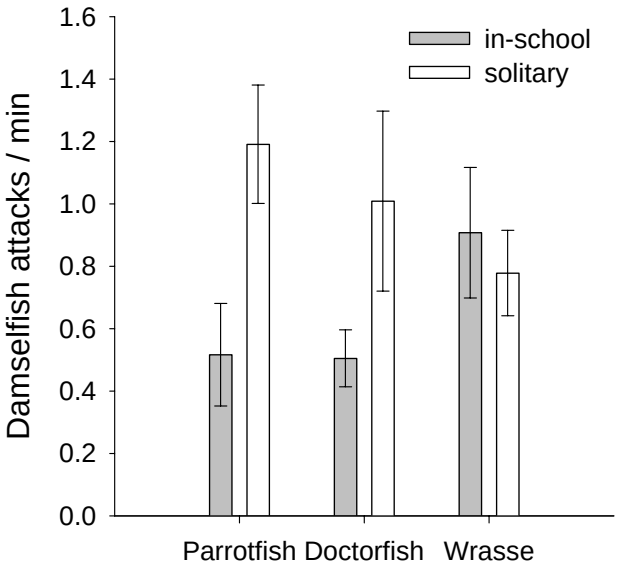

Figure 3. In-school and solitary damselfish attack rates + 1 SE for stoplight parrotfish, doctorfish, and bluehead wrasse in Discovery Bay, Jamaica (n = 69). Attack rates for parrotfish and doctorfish were higher when solitary. There was no difference in damselfish attack rates on bluehead wrasse while schooling or solitary.

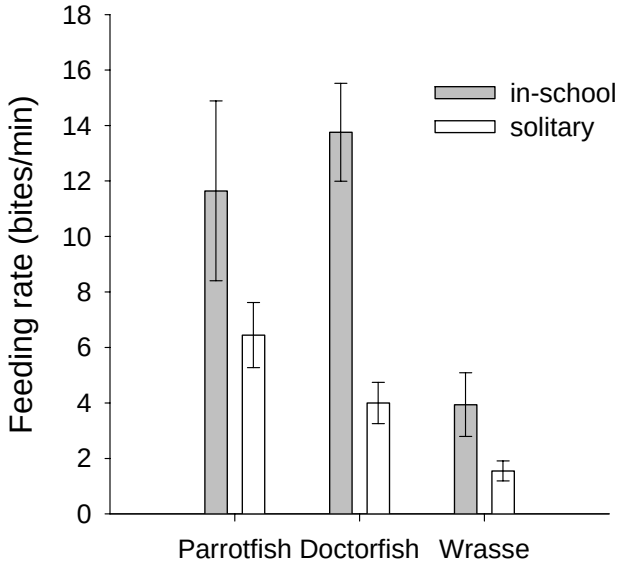

Figure 2. In-school and solitary feeding rates + 1 SE of stoplight parrotfish, doctorfish, and bluehead wrasse in Discovery Bay, Jamaica (n = 69). All fish showed greater feeding rates in schools than when solitary. There was an affect of species with parrot fish and doctorfish having higher overall feeding rates than bluehead wrasse (Tukey α = 0.05). There was no difference in the magnitude of change between in-school and solitary feeding rates across species.

in schools than doctorfish and parrotfish, though feeding efficiency increased while schooling. Solitary bluehead wrasse behavior was different from that of solitary doctorfish and parrotfish. While the latter two species were relatively inactive when alone, the solitary bluehead wrasses were highly active and seemed to forage often in damselfish territories. These wrasses may have been foraging for damselfish eggs, a preferred food resource (Foster 1987). If the acquisition of this resource was a priority for wrasses, blueheads may be more likely to leave the perceived safety of schools to search for damselfish eggs. We did not observe mixed-species schools swarming damselfish territories, and therefore schooling would not give the wrasse any advantage in egg foraging. Additionally, damselfish may target bluehead wrasses, as damselfish have been shown to defend specifically against egg-eating species (Foster 1987); therefore schooling would give bluehead wrasses no benefit against damselfish attacks.

Recent studies have indicated that several factors may encourage mixed species schooling, and these factors may be constantly changing with changing environmental conditions (Crook 1999). Our results suggest that although feeding efficiencies increased in schools for all three fish species, this may be an indirect effect of a behavior that evolved as a result of different benefits, possibly predator detection and avoidance.

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EFFECTS OF BAUXITE ON MARINE INVERTEBRATE POPULATIONS IN DISCOVERY BAY, JAMAICA

CHELSEA L. WOOD AND CAYELAN C. CAREY

Abstract: Bauxite mining is an economically important industry in Jamaica, and bauxite is often present in ecosystems in the vicinity of Jamaican mining facilities. This material contains heavy metal contaminants including Al, Fe, Mn, Pb and Zn; however, the influence of bauxite contamination on marine near-shore ecosystems in Jamaica has not been evaluated. Here we assess (1) whether abundance of infaunal invertebrates differs among sites that may have different contamination levels, and (2) whether bauxite can drive these differences. We sampled infaunal invertebrate communities of three sites at different distances from the Kaiser Jamaica Bauxite Company, Discovery Bay, Jamaica and found that abundance of infaunal invertebrates was lowest at the highest contamination site, and highest at the lowest contamination site. We also experimentally exposed mysid and brine shrimp to processed bauxite and sediments from these sites. Results from these experiments suggest that bauxite may increase mortality of mysid shrimp and may drive the differences in infaunal abundance observed in the field. In addition to increasing invertebrate mortality, bauxite may have sub-lethal effects. The influence of this contaminant on the behavior, growth, reproduction, and other physiological processes of marine organisms deserves further study because of its potentially harmful effects on benthic marine communities.

Key Words: brine shrimp, contaminants, infauna, invertebrate colonization, Mysidacae

INTRODUCTION

Waste from the processing of aluminum oxide (i.e. bauxite tailings, or "red sludge," and dust contaminated with Al, Fe, Mn, Pb, and Zn) is often present in ecosystems in the vicinity of bauxite mining facilities (Pagano et al. 2002). Exposure to bauxite reduces the abundance of freshwater macroinvertebrates (Fonesca 1998, Fonesca and Esteves 1999, and Laal and de Assis 2000). Bauxite also reduces the reproductive potential of sea urchins, and may otherwise negatively affect marine invertebrate communities (Pagano et al. 2002).

Bauxite dust from Kaiser Jamaica Bauxite Company is deposited at Columbus Park, Discovery Bay, Jamaica, by wind and spillage during transfer of bauxite to ships for transport (Quinn, *pers. comm.*). We hypothesized that the deposition of bauxite dust at Discovery Bay would have negative impacts on infaunal assemblages. We assumed that bauxite contamination decreases with distance from the Kaiser plant, and therefore predicted that there would be greater infaunal colonization of bristle brushes submerged at a site (i.e. West Back Reef) 1 km away from the Kaiser Jamaica bauxite loading wharf than at Columbus Park, due to decreased abundance of infaunal invertebrates at Columbus Park. We also expected that infaunal colonization would be greater at a site 6 km from the loading wharf (i.e. Pear Tree

Bottom) than at Columbus Park or West Back Reef.

We hypothesized that marine invertebrates experimentally exposed to bauxite and bauxite-contaminated sediments would have lower survivorship than invertebrates exposed to uncontaminated sediments. We expected that mysids exposed to bauxite would have the highest mortality, followed by those exposed to sediment from Columbus Park, West Back Reef and Pear Tree Bottom. We also predicted that brine shrimp eggs exposed to these treatments would show similar patterns in hatching rate.

METHODS

We selected three sampling sites, Columbus Park (CP), West Back Reef (WBR), and Pear Tree Bottom (PTB), at different distances from the Kaiser Jamaica bauxite loading wharf. CP, our contaminated site, was approximately 500 m from the loading wharf; WBR, our intermediate contamination site, is 1 km northwest of the wharf; and PTB, our uncontaminated site, is 6 km east of the wharf. On 3 March 2005, we laid a 10 m transect parallel to the shore on fine-grained sediment and at a depth of approximately 1 m at each site. At five randomly-selected points along the transect, we inverted a plastic container over the sediment, pressed the lip of the container 5 cm into the sediment, and scooped that sediment into the container (approximately 1.5 L). We also collected seawater from above the sediment at each site. We homogenized the sediment samples within each site. Because particle grain size can influence infaunal communities (Coull 1988), we wanted to ensure that mean grain size was similar between sediment treatments. We therefore sieved the homogenized sediment mixtures with coarse mesh to remove large sediment fragments and decrease the differences in average grain size among treatments. All seawater collected was strained with a 153 μm mesh to remove zooplankton. Bauxite was collected from outside the Kaiser Jamaica Bauxite Company.

We created five treatments for our mysid and brine shrimp experiments: uncontaminated (PTB sediment and PTB water), intermediate contamination (WBR sediment and WBR water), contaminated (CP sediment and CP water), bauxite (pure bauxite and PTB water), and a control (PTB water and no sediment). We collected mysids (genus *Mysidium*) for our experiments from WBR on 5 March 2005. In the mysid experiment, we filled plastic containers (approximately 2 L), excluding the control, with a 1.5 cm layer of the appropriate sediment (approximately 250 mL) and a 3.5 cm layer of the appropriate seawater (approximately 1 L). The control was filled with a 5 cm layer of PTB seawater. There were two containers per treatment and five treatments for 10 containers total. We used pipets to add 30 mysids to each container at 1100 on 5 March 2005. For 108 h, two independent observers counted the number of surviving mysids every 12 h. These counts were averaged for each container. We also made observations of mysid behavior. We used

one-way ANOVAs to compare mysid survivorship among treatments at 12 h, 36 h, 60 h, and 96 h .

In the brine shrimp experiment, we added a 1.5 cm layer of the appropriate sediment (approximately 38 mL) and 3.5 cm layer of the appropriate seawater (approximately 1 L) to each of five Nalgene bottles. Each container was continuously aerated with a bubbler and received lamplight for the duration of the experiment. We added approximately 3 mL of dry brine shrimp cysts (genus *Artemia*) to 10 mL of water, and added 2 mL of this mixture to each treatment on 5 March 2005. We counted the number of unhatched eggs, dead individuals, and live individuals in a 2 mL subsample, 48 hours after the addition of the cysts. A second replicate of these treatments began on 8 March 2005 and ran for 48 h. We calculated the proportion of live hatchlings to the total number of live hatchlings + eggs + dead hatchlings, and the proportion of dead hatchlings to the total number of live hatchlings + dead hatchlings. We used one-way ANOVAs to compare the means of these proportions among treatments.

For our invertebrate colonization experiment, we attached bristle brushes to bricks with cable ties and wire. We placed four of these bricks at 2 m intervals along the transects used for collecting sediment at each site (i.e., PTB, WBR, and CP) on 4 March 2005. Bristle brush colonization is a reasonable proxy for abundance of infaunal invertebrates (Iwamoto and Salant 2003). We retrieved the bristle brushes from each site after 72 h and immediately rinsed them in saltwater and freshwater to completely defaunate them. We preserved infauna in 10% formalin and counted and identified all specimens to order. Total abundance and individual taxa abundances as a proportion of total abundance were compared between the three sites with one-way ANOVAs.

RESULTS

At 12 h, mysid survivorship differed significantly among the five treatments ($F = 7.55$, $df = 4, 5$, $P = 0.02$). More mysids had died in the bauxite treatment than in the PTB and control treatments (Tukey's HSD post-hoc test, $\alpha = 0.05$, Fig. 1). Mysid survivorship in the CP and WBR treatments did not significantly differ from other treatments. At 36 h, 60 h, and 96 h, there was no significant difference in mysid survivorship among treatments ($F < 1.84$, $df = 4, 5$, $P > 0.26$). We observed a lower activity level and less swarming in the bauxite treatments relative to other treatments.

We found no difference in the proportion of live hatchlings in the total sample (i.e., [# live hatchlings]/[# live hatchlings + # eggs + # dead hatchlings]) among the treatments in the brine shrimp experiment ($F = 1.72$, $df = 4, 5$, $P = 0.28$). There was also no difference in the proportion of dead hatchlings in the number of animals that had hatched (i.e., [# dead hatchlings]/[# live hatchlings + # dead hatchlings]) among the treatments ($F = 0.27$, $df = 4, 4$, $P = 0.88$).

Abundance of infaunal invertebrates sampled from bristle brushes dif-

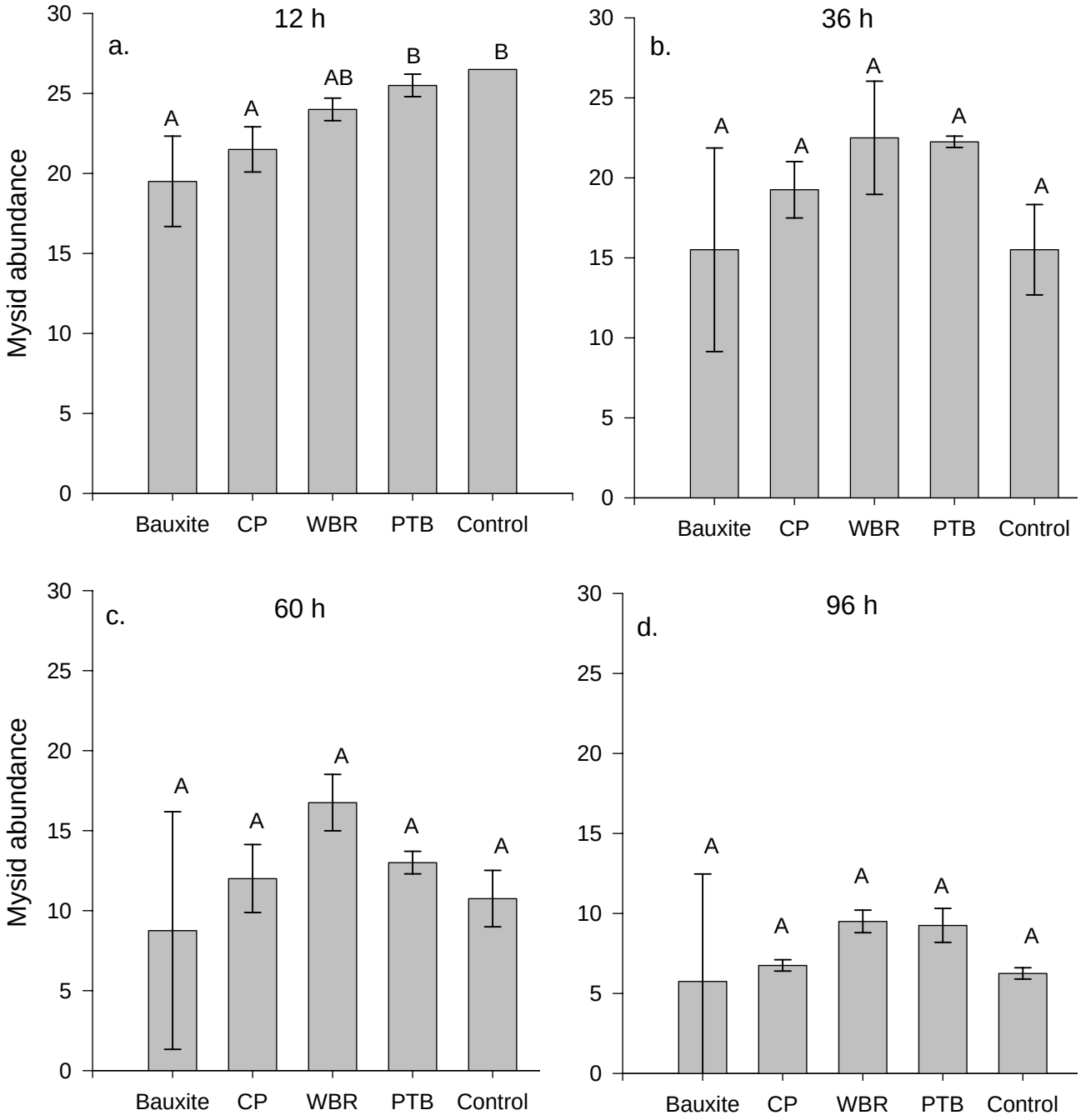

Figure. 1. The number of surviving mysids after (a) 12 hours, (b) 36 hours, (c) 60 hours, and (d) 96 hours in the five treatments: bauxite (pure bauxite), CP (high contamination sediment), WBR (intermediate contamination sediment), PTB (low contamination sediment), and control (no sediment, uncontaminated water). Error bars are ± 1 SE. Letters above columns represent means that are significantly different at $\alpha = 0.05$, Tukey's HSD post-hoc test.

fered significantly among the three sampled sites ($F = 11.81$, df = 2, 9, $P = 0.003$). Abundances at PTB and WBR were greater than abundance at CP (Fig. 2).

The proportions of copepods, amphipods, isopods, decapods, ostracods and polychaetes were similar among the three sites ($F < 2.11$, df = 2, 9, $P > 0.18$). The pro-

portion of gastropods was marginally higher at PTB than CP or WBR (F = 4.01, df = 2, 9, P = 0.06). However, a Tukey's HSD post-hoc test found no significant difference in gastropod abundance among the sites. The proportion of foramaniferans was greater at PTB than at CP or WBR (F = 15.22, df = 2, 9, P = 0.001).

DISCUSSION

Our results suggest that bauxite contamination may negatively influence marine invertebrate communities in Discovery Bay, Jamaica. Though results from our brine shrimp experiments did not support our hypothesis, data on mysid survivorship suggest that bauxite may increase the likelihood of death in exposed individuals. At 12 h, there were more surviving individuals in the control and low contamination treatments (i.e., control and PTB, respectively) than in the bauxite treatment. As expected, survivorship for individuals in the high contamination treatment (i.e., CP) was greater than that for individuals in the bauxite treatment and less than that for individuals in the intermediate and low contamination treatments; however, these relationships were not significant.

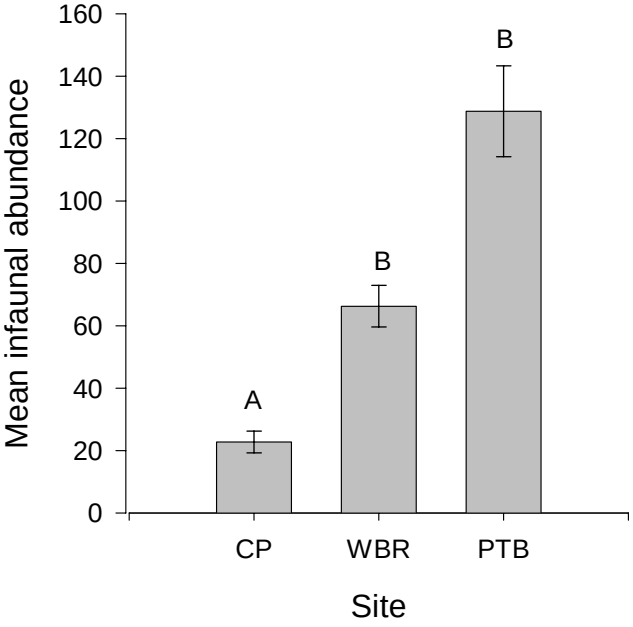

Figure. 2. Total infaunal abundance in bristle brushes at CP (contaminated site), WBR (intermediate contamination), and PTB (uncontaminated site) after 72 hours of colonization. Error bars are ± 1 SE. Letters above columns represent means that are significantly different at α = 0.05, Tukey's HSD post-hoc test.

At 36 h, 60 h, and 96 h, there was no significant difference in mysid survivorship among treatments; however, trends were in the predicted directions. The low and intermediate contamination sites (i.e., PTB and WBR) had higher survivorship than the high contamination site (i.e., CP), and the high contamination site had higher survivorship than the bauxite treatment. Given the low number of replicates (2) within each treatment, it is reasonable to conjecture that increasing replication might increase the likelihood of detecting significant differences among the treatments at the various time steps.

Surprisingly, individuals in the control treatment had a similar mean survivorship at 36, 60, and 96 h as individuals in the high contamination and bauxite treatments. The control treatment lacked sediment, and consequently may have also lacked food. This may explain the high rate of death in the control treatment relative to that in some of the other treatments, all of which contained sediment. The bauxite treatment contained only bauxite collected from the Kaiser Jamaica bauxite

processing facility, and consequently, most likely also lacked food. Survivorship of individuals in the bauxite treatment was lower than that for individuals in the control treatment, though this relationship was not significant. This indicates that there may be an effect of bauxite (i.e., toxicity) on mysids, other than lack of food, which caused greater mortality in this treatment. This is further supported by the significant difference in mortality between the bauxite and control treatments at the 12 h time step. The results of the mysid experiment provided some support to our prediction that survivorship would depend on the level of bauxite contamination in a treatment, and suggests that bauxite may negatively affect marine invertebrates.

Data from our study of invertebrate colonization rates at the three sites agree with our predictions and the results of our mysid experiments. We found fewer invertebrates in brushes collected from the high contamination site, CP, than in those from the intermediate and low contamination sites, WBR and PTB. There were more invertebrates in brushes collected at the low than intermediate contamination site, although this difference was not significant. Because bristle brush colonization is a reasonable proxy for infaunal abundance (Iwamoto and Salant 2003), these results may suggest that the abundance of infaunal invertebrates in the field decreases with increasing exposure to bauxite. We found no significant differences in the proportion of each taxa among the three sites, except a greater abundance of foramaniferans at PTB than at WBR or CP. No research of which we are aware suggests that foramaniferans are especially sensitive to environmental contaminants, and we therefore conclude that the observed difference is probably due to other site-specific factors. While bauxite may reduce the abundance of infauna, there is little evidence for an effect of bauxite on infaunal community composition.

The results of this study indicate that (1) bauxite is potentially detrimental to marine invertebrates, and (2) levels of bauxite contamination in Discovery Bay may be high enough to negatively influence invertebrate communities. Mortality, however, is not likely to be the only effect of bauxite contamination. Our observations of mysid behavior suggest that individuals exposed to bauxite are less active and less likely to exhibit swarming behavior. These effects could have important implications for populations of mysids and other marine invertebrates exposed to bauxite in the field. Effects of bauxite on behavior, growth, reproduction and other physiological processes in marine invertebrates deserve further study.

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DIFFERENTIAL EFFECT OF DEPTH ON MICROHABITAT SELECTION IN POLYCHAETE TUBE WORMS

JONATHON C. RAFFENSPERGER AND CHAD M. VALDERRAMA

Abstract: An appropriate microhabitat is particularly important to sessile filter-feeding organisms such as polychaete tube worms. Both Christmas tree and fanworms use cilia to filter water from the abfrontal to the frontal side of each radiole. Unlike the single layer of radioles posessed by fanworms, the radioles of Christmas tree worms are stacked in a spiral conformation and filter efficiently only when ambient current displaces water perpendicular to the axis of coiling and prevents re-filtration. Feeding efficiency in both species may be negatively affected by strong currents that could bend or damage their radioles. We hypothesized that polychaete worms are selecting microhabitats on substrata based on current velocity, which changes with depth and height from the benthos. We then examined the height distribution of Christmas tree worms and fan worms across depths at the west forereef of Discovery Bay, Jamaica and confirmed our prediction that relative height of Christmas tree worms would be positively related to depth, while relative height of fan worms be lower and would not change with depth. This suggests that larvae of Christmas tree worms may be able to control the height at which they settle on a coral surface, thereby maximizing their feeding efficiency.

Key Words: Christmas tree worm, fanworm, Spirobranchus giganteus

INTRODUCTION

Polychaete tube worms are common on the surface of rocks and live corals in the forereef at Discovery Bay, Jamaica. These filter feeders extend their radioles and use cilia to create a feeding current. Suspended particulate food is intercepted by the radioles and transported to the mouth. Most of these worms have one fan-like layer of radioles that take in water on their undersides and expel it above, separating incurrent from excurrent and thus preventing the inefficient re-filtration of water. The Christmas tree worm, *Spirobranchus giganteus*, is exceptional in that in still water, the stacked spiral arrangement of its radioles causes excurrent flow passing through proximal whorls to be taken up and re-filtered by distal whorls. Although it has a large filter area, it requires external current roughly perpendicular to its whorl of radioles to make full and efficient use of its feeding capacity (Strathman 1984).

The need for external current at least partially drives the distribution of *S. giganteus*, with Christmas tree worms most commonly found on corals in exposed areas with high current velocity (Waters and Smith 1987) and generally absent from depths below 24 m (Fouts and Woodson 1994). Excessive water movement may bend and compress the worms' spirals, however, reducing surface area and preventing efficient feeding (Strathman 1984). Christmas tree worm larvae should thus seek out sites with sufficient current to prevent re-filtration, but not so much current

as to interfere with the functioning of the filters.

As water velocity generally decreases with increasing depth (Waters and Smith 1987), we hypothesized that Christmas tree worms in deep water would be found at or near the exposed tops of coral masses, while at shallower depths they would be found further down the sides in locations more shielded from the surge and less exposed to potential predators. Fanworms, which do not require external current for efficient feeding, should at all depths be located lower down on non-living substrates where they are hidden from predators and shielded from disruptive currents. We thus predict a positive relationship between depth and relative height on corals for *S. giganteus*, while relative height of fanworms should not change with depth and should be lower on average than the mean relative height of Christmas tree worms.

METHODS

We sampled polychaete tube worms on the west fore reef of Discovery Bay, Jamaica from 2 - 9 March 2005. Using SCUBA, we sampled worms along north-south transects near the Caricom mooring at depths ranging from 20 to 2 m. We measured the depth at which each worm was found and recorded its type (Christmas tree or fan). We also measured height (cm) from the sea floor to the opening of the worm's tube, as well as the total height of the coral or substratum the worm was inhabiting. We used these two heights to calculate relative height (height of worm / height of substratum) of each worm. We sampled worms evenly across all depths. Relative height data were arcsine-transformed to meet the assumptions of normality and homogeneity of variance for parametric tests. For the two worm types, we analyzed the relationship between depth and relative height on coral using an indicator variables regression. The regression model was:

$$Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_1 X_2 + \varepsilon$$

where Y is the response variable (relative height), X_1 is depth, X_2 is a binary indicator variable that codes for worm type (christmas tree or fan), β_0 is the intercept, β_1 is the slope, β_2 is the change in intercept between worm types, and β_3 is the change in slope between worm types. Data were

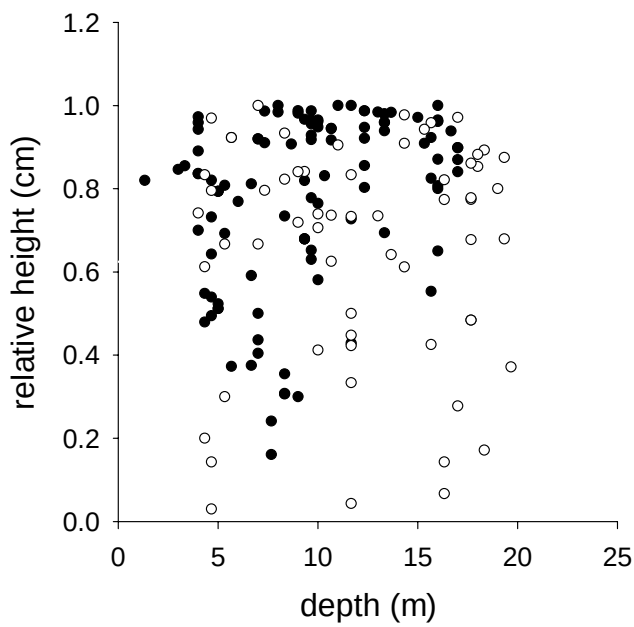

Figure. 1. Relative height on substratum of Christmas tree worms (closed circles) and fanworms (open circles) as a function of depth. For Christmas tree worms, there is a positive relationship between relative height and depth. The relative height of fan worms is independent of depth.

analyzed using JMP 5.0.1. All tests were performed on the transformed data.

RESULTS

As we expected, Christmas tree worms were always found on living coral and *Millepora*. Fanworms, however, were found on both living and non-living substrates. Variegated feather dusters (*Bispira variegata*) and yellow fanworms (*Notaulax occidentalis*) were only observed on non-living surfaces, while social feather dusters (*Bispira brunnea*) and star horseshoe worms (*Pomatostegus stellatus)* were most often found on live corals.

There was no relationship between water depth and the relative height on coral for fan worms ($Y = 0.001X + 0.745$; $r^2 < 0.00$, df = 1, 58, P for slope = 0.84, P for intercept < 0.01), but there was a positive relationship for Christmas tree worms ($Y = 0.010X + 0.705$; $r^2 = 0.12$, df = 1, 106, P for slope < 0.01, P for intercept < 0.01).

The rate at which relative height on substrata changed with depth (Fig. 1) was significantly different between fan worms and Christmas tree worms ($F = 5.04$, $P = 0.03$), and the y-intercept of the regression between depth and relative height was higher for fanworms than for Christmas tree worms ($F = 17.80$, $P < 0.01$).

DISCUSSION

As we predicted, relative height of *Spirobranchus giganteus* on coral masses increases with depth. In deep water, these polychaetes were found predominantly on promontories of knobby coral, where their spiraled radioles have maximum access to the relatively slow currents. As the water became shallower and currents became stronger, Christmas tree worms were found more frequently in sheltered areas lower on the sides of corals where they are less likely to be flattened by the surge. We informally observed there to be no *S. giganteus* in the back reef or lagoon, likely due to excessive surge and high sedimentation. Additionally, none were found deeper than 20 m, where water velocity probably is too slow for efficient filtration. Fanworms were most often found low on the sides of corals at all depths, avoiding areas of high water velocity and possibly decreasing their exposure to predation.

We found a number of exceptions to these general patterns of distribution in both Christmas tree and fanworms. Although most *S. giganteus* observed in shallow water occurred in relatively low positions, some occurred near the tops of coral formations where one would expect that their filter feeding would be continuously disrupted by high surge. These worms had much smaller filters than their low-current counterparts, however, and were found on bladelike pieces of *Millepora* coral that may act as a shield against moving water (Fierce and Campbell 2004). In deeper water, certain fanworms were observed growing on top of promontories in contrast to their apparent preference for protected areas. These sabellid fanworms, most likely *Bispira brunnea*, occur in clusters and are known to prefer areas with some water movement (Humann 1992). The clustering

of these worms could result in the overlap of their radiole crowns and lead to re-filtration, which may cause them to choose microhabitats similar to those preferred by *S. giganteus*. Additionally, the close proximity of other worms may help to reduce the disruptive impact of current on each individual.

S. giganteus is a broadcast spawner whose larvae swim in the plankton for 9 - 12 days before settling down to a sessile life on the surface of a live coral (Hunte et al. 1990). In the lab, these larvae exhibit an active preference for the coral species on which they most commonly occur (Hunte et al. 1990), suggesting that they select the coral substrate on which conditions for growth are likely to be best. Studies have also shown that *S. giganteus* larvae select corals with different morphologies at different depths, possibly due to the varying hydrodynamic properties of these corals (Dickenson and Douzinas 1998). Our results suggest that, in addition to differentiating between coral types and morphologies, larvae may be able to control the height at which they settle on the coral surface, therefore maximizing their feeding efficiency. Alternatively, it is possible that larvae settle on all areas of an appropriate coral surface and the ones that establish themselves in unfavorable positions simply die before reaching maturity. Further study is required to determine the nature and sensitivity of the mechanisms that generate the patterns of distribution and abundance for *S. giganteus*.

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EFFECTS OF PREY AND PREDATORS ON THE DISTRIBUTION AND ABUNDANCE OF *HERMODICE CARUNCULATA*

EMILY L. SHARP, S. ALLIE HUNTER AND RICHARD W. TRIERWEILER

Abstract: Here we examine the effects of prey availability and predation on the distribution and abundance of the bearded fireworm (*Hermodice carunculata*). We hypothesized that fireworm distribution would be related to the abundance of sea anemone prey, and that they would employ chemotaxis to detect prey at a distance. We also hypothesized that fireworms would be subject to increased predation pressure at night, so they would be more abundant under shelter at night than during the day. We also expected the fireworms to be clumped under larger rocks in order to hide from predators. We found no relationship between fireworm and anemone abundance, and we did not observe the fireworms to have any chemotactic ability. Neither predation on tethered fireworms, nor abundance beneath rock rubble was different between day and night samples. The abundance of fireworms was distributed randomly across rock sizes. These results suggest that prey abundance is not an important factor in generating patterns of *H. carunculata* distribution and abundance, although predation may be.

Key Words: Bunodeopsis antilliensis, *chemotaxis, fireworms*

INTRODUCTION

The amphinomid polychaete *Hermodice carunculata* (bearded fireworm) is found throughout the Caribbean in mud flats, turtle grass beds, and coral reefs (Kaplan 1982). It is an important determinant of coral-reef community composition because of its voracious appetite and expansive diet. Fireworms are omnivores that are known to consume zoanthids, sea anemones, ten species of scleractinian corals, hydrocorals, sponges, and gorgonians, as well as moribund creatures (Witman 1988, Vreeland 1989). They have been shown to limit the growth and distribution of species of *Millepora*, *Acropora*, *Plexaura*, and *Zoanthus* (Witman 1988, Vreeland 1989); however, few studies have looked at the effects of prey availability on fireworm distribution and abundance. We hypothesized that the abundance of fireworms in turtle grass beds is related to the abundance of a common prey item, the anemone *Bunodeopsis antilliensis* (Abram 1994). We predicted that with increasing anemone abundance there would be increasing fireworm abundance.

Fireworms are selective in which type of prey they choose to eat if multiple prey items are available (Witman 1988, Vreeland 1989). Once touching a prey item, they can identify the prey with an olfactory organ, the caruncle (Witman 1988). This organ may also aid in searching for and tracking prey across the habitat. We hypothesized that fireworms are able to use chemoreception to detect prey from a distance. We predicted that fireworms would orient toward prey items.

The distribution and abundance of fireworms could also be affected by preda-

tion. Fireworms feed throughout the day with peak activity around 1600, and then they take shelter under rubble and sediment during the night (Abram 1994, Lewis 1996). Most soft-body worms hide under rubble during the day to avoid predation; however, fireworms are commonly seen in the open during the day. They have venomous setae and bright coloration that might serve to warn diurnal predators that use vision for prey detection (Kaplan 1982). Warning coloration, however, may not be an effective predation deterrent at night, thus increasing predation risk. We hypothesized that fireworms would be more abundant under rubble during the night to avoid increased night predation. Similarly, we predicted that predation rates on tethered fireworms would be higher at night than during the day. Also, to decrease predation by satiation we predicted that fireworms would be aggregated under the rubble.

METHODS

To determine the effect of prey abundance on fireworm abundance in turtle grass beds, we compared the abundances of *B. antilliensis* and fireworms at four sites in the back reef at Discovery Bay, Jamaica, West Indies on 5-6 March 2005. We counted fireworms along 10 min swimming transects through areas dominated by *Thalassia testudinum.* Along each transect, we counted anemone abundance on *T. testudinum* blades in three randomly chosen 0.5 m^2 quadrats. Transects were placed at four sites; two deep sites in the east back reef (4-6 m) and two shallow sites in the west back reef (1-2 m), because anemone abundance increases with depth (Guerrerio 1992). There were six replicate transects at each site.

To determine if fireworms can locate prey from a distance, we placed fireworms in a tank within 25 cm of a food item and observed their behavior. The fireworms had been starved for 24 hours prior to the observational period. We observed 10 fireworms with a halved *Tripneustes ventricosus* and then 10 fireworms with two *B. antilliensis.* To ensure that the prey were palatable, each anemone and urchin was fed to the fireworms after all the observations had been completed.

To determine if fireworm distribution and abundance may be affected by predation, we tethered fireworms in the water column away from refuges. We used monofilament line to suspend worms from buoys in the water column in the back reef, approximately 0.5 m from the surface in order to minimize wave action. We assessed predation during both the night and the day, leaving a set of nine fireworms on the line for 12 hours, from 1800 - 600, and nine new fireworms from 600 - 1800 the following day. As a control to measure the fireworms' ability to get loose from the line, we tethered a set of fireworms in the wet lab where there were no predators. We counted fireworm abundance on the lines after each time period.

We compared fireworm abundances during the day and night under rubble refuges in the barren zone behind the reef crest in the west back reef on 7 March 2005. We searched under rocks and broken corals at 1500 and 2000, and recorded both the

surface area of the rubble and fireworm abundance. To determine the dispersion pattern of the fireworms under the rubble, we found the variance of the fireworm abundances among the rubble and divided this by the mean number of fireworms per rock (only rocks with fireworms were used). A variance to mean ratio = 1 indicates random dispersion, < 1 is over-dispersed, and > 1 is clumped.

All data were analyzed with one-way ANOVAs and linear regressions using JMP 5.0.1. The surface area of rocks was log-transformed; all other data met the assumptions for parametric tests.

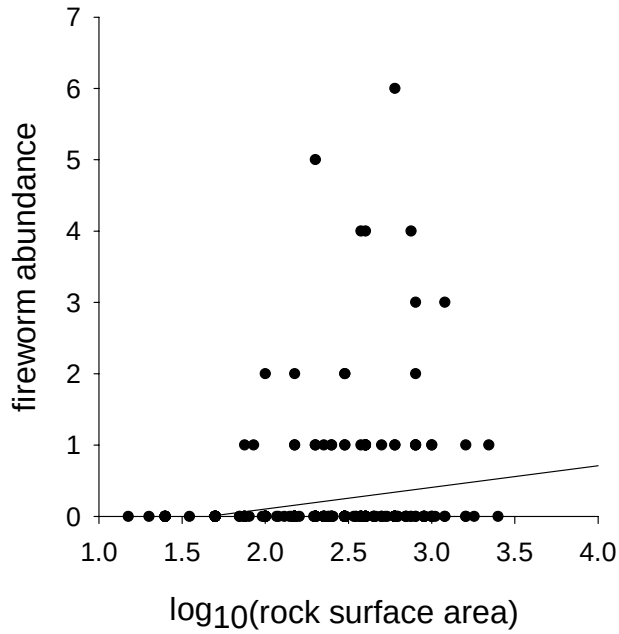

Figure 1. Rocks with more surface area have higher worm abundance.

RESULTS

In all 24 transects, we found a total of 14 fireworms (mean = 0.58 fireworms /10 minute transect) and 43 *B. antilliensis* (mean = 0.60 anemones /quadrat). There was no relationship between fireworm and anemone abundance ($r^2 = 0.08$, df = 1, 22, P = 0.19).

Our observational study of chemotaxis showed that the fireworms were unable to detect their prey before touching it. Fireworms that turned towards the food did not appear to actually sense the prey until they physically ran into it, often passing within millimeters of the prey without stopping or reacting. After the observational period, the fireworms that were offered the prey quickly ate it.

Predation on tethered fireworms was equal in the day and night; five of nine fireworms were absent in each time period ($X^2 = 0.22$, df = 1, P = 0.64). None of the fireworms in the lab were able to escape.

There was no difference in fireworm abundance under rubble during the day or night (t = 1.143, df = 311, P = 0.25). Because of this, both day and night samples were pooled for the remaining analyses. There were more fireworms under larger rubble ($r^2 = 0.03$, df = 311, P = 0.0012; Fig. 1). Worm abundance = -0.50 + 0.30 $\log_{10}$(rock surface area). Rubble without fireworms was smaller (mean area = 313.72 cm^2 ± 18.77 SE) than rubble with fireworms (mean area = 527.24 cm^2 ± 71.54 SE; F = 15.012, df = 1, 311, P = 0.0001). The index of dispersion was 0.98 showing that fireworms were randomly distributed across rocks. When we removed the rubble without fireworms present, we found no relationship between rubble size and fireworm abundance ($r^2 = 0.0057$, df = 36, P = 0.65).

DISCUSSION

Since there is no relationship be-

tween the abundances of *B. antilliensis* and *H. carunculata* in turtle grass beds, it seems that the distribution of anemones does not affect that of the fireworms. *H. carunculata* is not capable of chemotaxis and seems to find prey by stumbling upon it. It would be interesting to determine whether fireworms are even capable of foraging optimally due to their lack of ability to detect prey at any distance. The fireworm's inability to detect prey from a distance could be driving its expansive diet, because they can eat only what they stumble upon. Since fireworms have such a varied diet and have no chemotactic ability to detect prey, it seems unlikely that any one prey type should affect distribution of *H. carunculata*. Perhaps the total abundance of all prey types may influence the distribution or abundance of *H. carunculata*, and depth and substrate may as well.

Although we found slightly more fireworms under rubble in the day than during the night, the difference was not significant. We were not able to detect a difference in predation on fireworms between night and day. It appears that predation is constant through time, as is fireworm hiding behavior. Weather conditions were much rougher in the field than in the lab, so our fireworms might have escaped, and were not eaten.

Increased abundance of fireworms under larger rubble suggests that fireworms avoid smaller rubble. This may be because smaller rubble is less stable and may not provide the benefits of larger, more stable refuges. Contrary to our hypothesis, the number of fireworms was random with respect to rock size, for rubble with fireworms present. This indicates that they may not be clumping to avoid higher predation. Future studies could elucidate why the fireworms are present under the rubble, investigating whether they are foraging under the rocks, avoiding UV radiation, or seeking shelter from waves and predators.

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COMPETITIVE INTERACTIONS BETWEEN *DIADEMA ANTILLARUM* AND *TRIPNEUSTES VENTRICOSUS*

ELVINA C. CHOW

Abstract: Both *Diadema antillarum* and *Tripneustes ventricosus* use coral and other hard substrate at the top of coral promontories at night, which may create a potential conflict for space. The purpose of this study was to first examine the potential for competition between *T. ventricosus* and *D. antillarum* for substrate at night. I tested this by establishing twenty transects and documenting the abundance and distribution of *D. antillarum* and *T. tripnesutes* day and night. *D. antillarum* and *T. ventricosus* were spatially segregated during the day; *D. antillarum* was found on reefs and *T. ventricosus* was found on sand and grass habitats. At night, *T. ventricosus* densities on top of reef promontories were highest when *D. antillarum* populations were lowest, and *T. ventricosus* densities on top of coral promontories were lowest when *D. antillarum* populations were highest. This suggested competition for hard substrate at night. Then, I determined whether *D. antillarum* competitively excluded *T. ventricosus* from these habitats. I hypothesized that *T. ventricosus* would behaviorally respond to manipulated densities of resident *D. antillarum*. After removing *D. antillarum*, the number of *T. ventricosus* migrating to the top of promontories increased significantly. My findings suggest that competition exists between *D. antillarum* and *T. ventricosus* for reef substrate at night, and that *D. antillarum* may potentially be excluding *T. ventricosus* from these habitats.

Key Words: aggression, competition, exclusion, lottery hypothesis, sea urchins

INTRODUCTION

The spiny sea urchin, *Diadema antillarum*, and the West Indian sea egg, *Tripneustes ventricosus*, are abundant tropical sea urchins that potentially compete with each other for space. In Discovery Bay, Jamaica, both species are found in a heterogeneous environment of discrete patches of coral heads and turtlegrass beds. Reef patches are a combination of live coral and coral rock eroded by *D. antillarum*.

These two species are spatially segregated during the day with *D. antillarum* occupying coral reefs and *T. ventricosus* occupying turtlegrass beds; however, both *D. antillarum* and *T. ventricosus* inhabit patches of hard substrate at night when *T. ventricosus* migrates into these habitats. Williams (1981) suggests that *D. antillarum* migrates to the tops of reefs at night to graze on damselfish algal lawns while these fishes are inactive. Tertschnig (1988) documented that *T. ventricosus* in the West Indies migrates to coral patches at night to escape predation from fish and night-active helmet conchs. However, both of these potential predators are rare in Discovery Bay. Regardless, *T. ventricosus* at Discovery Bay still migrates to rocky outcrops at night (personal observation), which presents a potential conflict between *D. antillarum* and *T. ventricosus*.

The purpose of this study was to (1) examine the potential for competition between *T. ventricosus* and *D. antillarum* for

surfaces at night, and (2) determine whether *D. antillarum* competitively excludes *T. ventricosus* from these habitats. If competition exists between *D. antillarum* and *T. ventricosus,* then the abundances of these two species should exhibit an inverse relationship. If competition can be demonstrated, we can also address a secondary corollary question: is the nature of this conflict consistent with competitive exclusion of *T. ventricosus* by *D. antillarum* at night? I assumed that *D. antillarum* is a better competitor than *T. ventricosus* because it is actively aggressive via pushing, biting, and waving its spines (Ferrie et al. 2003). Therefore, I predicted that the densities of *T. ventricosus* would increase when *D. antillarum* was completely removed.

METHODS

All observations and experiments were conducted in the back reef at Discovery Bay, Jamaica on 4 - 9 March, 2005. The study site covered an area of approximately 3000 m^2 and was located northwest of the marine laboratory (Fig. 1).

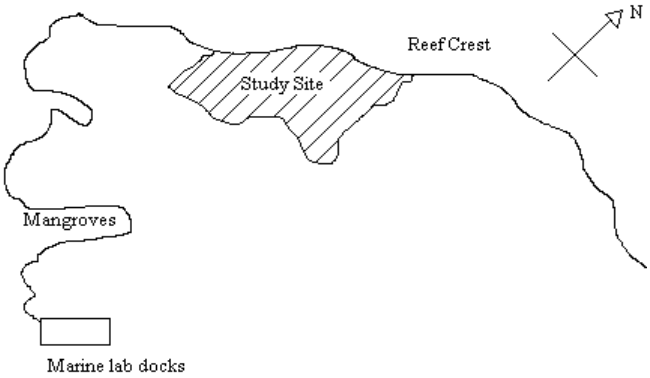

Figure. 1. Western end of Discovery Bay, Jamaica. All observational studies and experimental manipulations were conducted at the study site.

I. *Competition*

To test whether *D. antillarum* and *T. ventricosus* are spatially segregated during the day and use the same substrate at night, I established twenty 10 x 2 m belt transects in which all *D. antillarum* and *T. ventricosus* were counted both day and night. All transects were east-west, parallel to the reef crest, approximately 10 m from the reef crest at 1 - 2 m depth.

In each transect, I counted the total number of *D. antillarum* and *T. ventricuosus*, and the number of *T. ventricosus* up on coral and reef rock. At every 1 m interval, the substrate was categorized according to three habitat classes: 1) reef habitat: hard substrate with adequate hiding refuges for *D. antillarum*, 2) habitat dominated by *Thalassia testudinum* with little or no refuges, or 3) sand and rubble.

II: *Competitive Exclusion*

To determine whether the presence of *D. antillarum* competitively excludes *T. ventricosus* from reef substrate at night, I performed a removal experiment. Patches of coral and coral rock in the backreef provided discrete areas for removals of resident *D. antillarum*. From a total of 39 patches surveyed in day-night transects, 20 coral patches (3 x 3 m) were chosen randomly for this experiment. The size of each patch was standardized in both control and treatment groups. Each patch consisted of live coral and reef rock nested in a bed of turtlegrass or sand. Ten patches were randomly assigned as controls, and ten patches were manipulated. Control patches were areas with naturally occur-

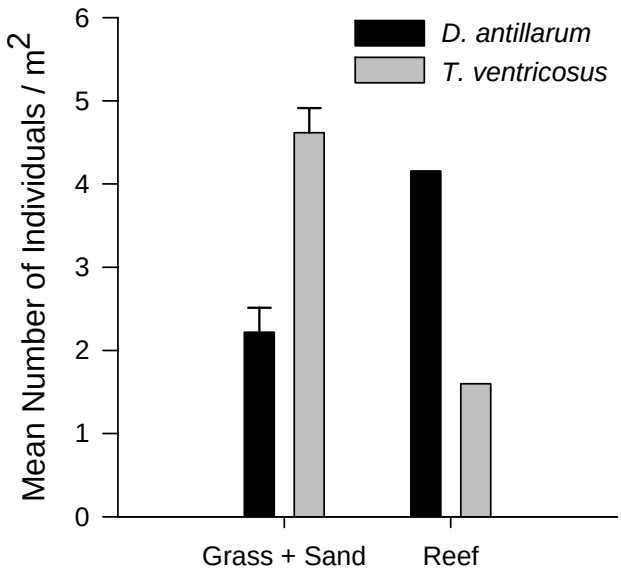

Figure 2. Day comparison of substrate preference in *Tripneustes ventricosus* and *Diadema antillarum*.

ring resident *D. antillarum* which I did not remove. Treatments were patches in which all *D. antillarum* were removed and placed at least 10 m away. I also monitored treatment patches daily and removed any *D. antillarum* there. I counted separately the total number of *T. ventricosus* surrounding the coral and coral rock, the number of *T. ventricosus* on top of the coral and coral rock, and the total number of *D. antillarum* in the patches for three consecutive nights.

RESULTS

I: *Competition*

The two-way ANOVA revealed that sea urchin abundances during the day were a function of the interaction between substrate type and species (2-way ANOVA, $F = 24.8$, df = 3, 36, $P < 0.0001$; Fig. 2). Total sea urchins (species were combined) were marginally more abundant on grass and sand substrate than on reef patches (2-way ANOVA, $F = 3.35$, df = 1, 36, $P = 0.0754$). There was no effect of species on abundance (2-way ANOVA, $F = 0.08$, df = 1, 36, $P = 0.78$).

At night, the number of *T. ventricosus* on the top of reef patches decreased proportionally with increasing numbers of *D. antillarum* ($r^2 = 0.57$, df = 1, 39, $P < 0.0001$; Fig. 3).

II: *Competitive Exclusion*

To determine the effects of *D. antillarum* removal on *T. ventricosus* usage on reef patches, I performed a one-way ANOVA comparing number of *T. ventricosus* on treatment v. control reefs. The number of *T. ventricosus* increased in patches when *D. antillarum* was removed compared to control groups ($F = 12.19$, df = 1, 18, $P = 0.00026$; Fig. 4).

DISCUSSION

Under natural conditions, high densities of *D. antillarum* were associated with low *T. ventricosus* densities. Experimental removals of *D. antillarum* from reefs of coral and coral rock at night resulted in significant increases in *T. ventricosus* on this space within 24 h. This provides strong evidence of competition for reef substrate between these two species of sea urchins at night, and suggests that this habitat type may be a limiting resource at night.

It is possible that urchin distributions may be influenced by priority effects.

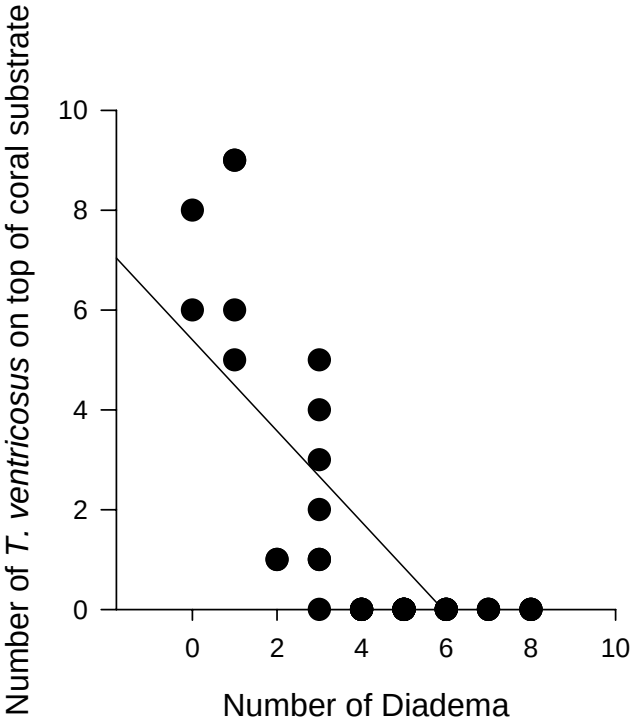

Figure 3. *Diadema antillarum* and *Tripneustes ventricosus* abundances on top of reef patches are inversely related (y = 5.40 – 0.91x).

One of the main assumptions of the lottery hypothesis is that vacant space is randomly colonized by organisms and randomly renewed as organisms die (Sale 1977, 1978). Since *D. antillarum* is found in reef patches during the day, *D. antillarum* may have an advantage simply because it is present on reef patches before *T. ventricosus*. This may explain why areas with high densities of *D. antillarum* have low densities of *T. ventricosus.* Recently, strong evidence of priority effects has been shown in similarly-sized gobies of different species on the Great Barrier Reef (Munday 2004). Munday attributed the coexistence of these coral-dwelling fishes to the priority effects of the lottery hypothesis. Therefore, it is possible that *D. antillarum* simply is able to secure and retain space on rocky outcrops excluding *T. ventricosus* which migrates away from the reef each day to forage in turtle-grass.

An alternative explanation is that *D. antillarum* may be physically superior to *T. ventricosus* in some way, thereby making it a superior competitor. *D. antillarum* may be competitively better because of its heavily armored body, its aggressive nature, and numerous long, thin, sharp spines. Though *T. ventricosus* bodies are larger than those of *D. antillarum* (approximately five centimeters greater), *D. antillarum* spines are double the length of *T. ventricosus* spines (Humann et al. 1997). The long spines of *D. antillarum* may deter *T. ventricosus* from venturing to outcrops when there are high densities of *D. antillarum*. In addition, Shulman (1990) found that *D. antillarum* exhibited biting and pushing behavior when placed next to an intruder. Studies between *T. ventricosus* and *D. antil-*

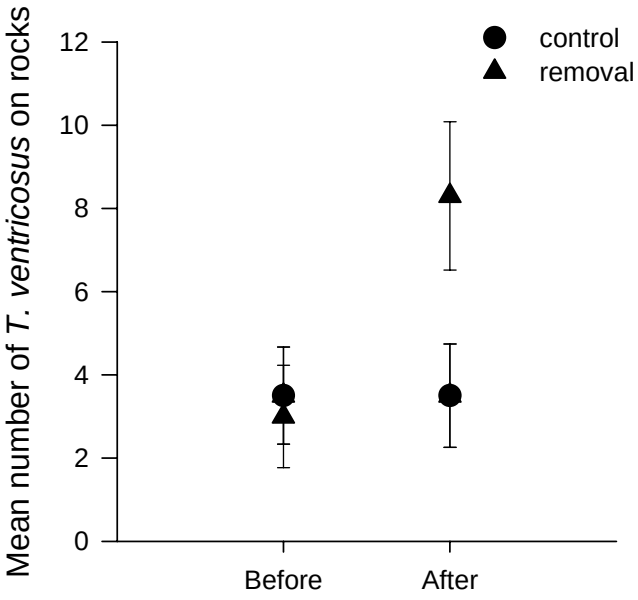

Figure 4. Comparison of *Tripneustes ventricosus* mean abundances on reef patches before removal experiment and after *Diadema* removal

larum have shown that *D. antillarum* is the more aggressive species (Ferrie et al. 2003). Therefore, *D. antillarum* most likely exhibits agnostic interactions with *T. ventricosus*. The attacks by *D. antillarum* may restrict *T. ventricosus* from the top of reefs at night.

Although my results provide strong evidence of competition between these two sea urchins, I did not measure active competition between *D. antillarum* and *T. ventricosus*. An additional study could examine the nature of direct interactions between *T. ventricosus* and *D. antillarum*, and could determine if the habitat use patterns observed in this study are the result of priority effects.

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DIEL ZOOPLANKTON ACTIVITY IN THE BACK REEF AT DISCOVERY BAY, JAMAICA

S. ALLIE HUNTER, CAYELAN C. CAREY, RICHARD W. TRIERWEILER,
SHARON J. MARTINSON AND THE 2005 FSP CLASS

Abstract: For many zooplankton populations, abundance in the water column increases at night, which is thought to maximize energy consumption in the water column while minimizing exposure to visual predators during the day. We predicted that zooplankton would have an increased abundance in the upper water column at night and that larger zooplankton, which are more subject to visual predation, would be proportionally more abundant at night. After sampling in the early afternoon and after sunset, we found both of our predictions to be correct.

Key Words: copepods, diel vertical migration, size distribution

INTRODUCTION

Many zooplankton populations exhibit diel vertical migration (DVM), a behavioral adaptation whereby zooplankton ascend into the water column at night to feed and then retreat to the benthos during the day (De Robertis et al. 2000, Jacoby and Greenwood 1988, Fagan et al. 2002, Iwamoto et al. 2003, Madhupratap et al. 1991, Pickhardt et al. 1999). This tradeoff probably maximizes zooplankton energy gain and provides protection from visual predators when the risk of attack is highest. If larger zooplankton are more vulnerable to predation because of their size, they may face greater pressure to engage in DVM behavior than smaller zooplankton (Iwamoto et al. 2003).

The stimulus for DVM is believed to be diel variation in light intensity (De Robertis et al. 2000). If light serves as a proximal cue for migration, it is possible that lunar irradiance may also affect the likelihood for DVM to occur (Jacoby and Greenwood 1988).

We hypothesized that the zooplankton population in the back reef of Discovery Bay, Jamaica exhibits DVM. We predicted that zooplankton would be more abundant in the surface water during the night than the day, and large zooplankton would be more likely to engage in DVM than small zooplankton. We also predicted that the presence of a full moon would decrease DVM behavior.

METHODS

A transect of 20 m was demarcated on 25 February 2005 approximately 12 m south and parallel to the reef crest in the west back reef of Discovery Bay, Jamaica. At 1400 and 2000 we collected samples for less than one hour. Five replicate samples were collected by swimming at a leisurely pace toward the west and then toward the east along the transect, for a total of 40 m. Zooplankton were captured with a 153 μm mesh net (26 cm diameter) held directly

beneath the water's surface (transect water depth was ≈0.8 m). The total volume of water filtered for each sample was calculated to be 2.12 m^3. Samples were preserved on site in 10% formalin.

All zooplankton in each sample were identified, counted, and measured within 24 hours, using dissecting microscopes. One-way ANOVAs were used to determine differences in abundance, average zooplankton size between night and day samples, and the dominant taxa for each time period. One night sample was accidentally destroyed, creating unequal sample sizes, but our abundance data met the assumptions of normality and homogeneity of variance after a log transformation, so we used standard F-tests to analyze our data.

RESULTS

There were more zooplankton in the samples collected during the night (1167 ± 101 organisms/m^3) than during the day (220 ± 91 organisms/m^3, $F = 48.42$, df = 1, 8, $P = 0.002$). The average size of the zooplankton in the night samples was larger (1.15 ± 0.02 mm) than in the day samples (0.71 ± 0.02 mm, $F = 192.8$, df = 1, 8, $P < 0.0001$). For decapods (Fig 1a) and copepods (Fig 1b), the abundance at night was greater than the abundance during the day in all size classes (decapods, $F = 50.47$, df = 1, 13, $P < 0.001$, copepods, $F = 38.10$, df = 1, 21, $P < 0.001$). The zooplankton collected were not uniformly abundant across all taxa (Table 1). There were significantly more copepods than any other group of organisms in the day samples, and at night both copepods and decapods comprised the majority of observed zooplankton (day, $F = 13.38$, df = 11, 119, $P < 0.0001$; night, F =

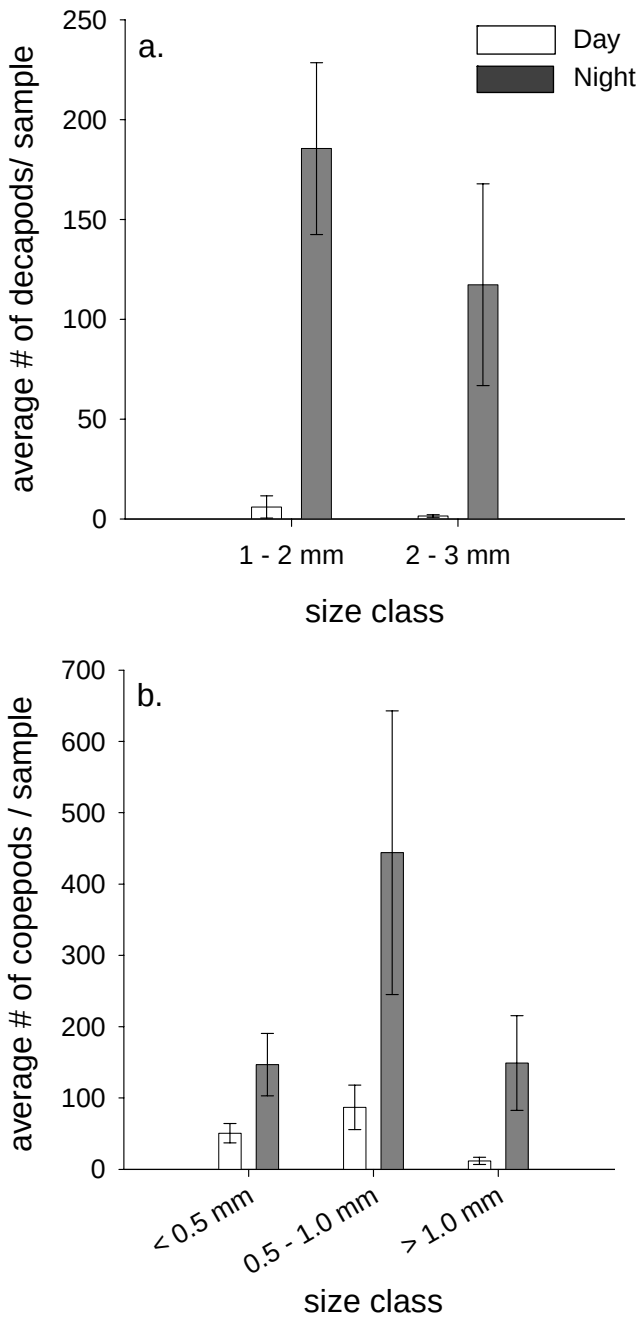

Figure 1. The average abundance per sample of decapods and copepods of different size classes between the day (clear bars) and the night (dark bars) (decapods, $F = 50.47$, df = 1, 13, $P < 0.001$; copepods, $F = 38.10$, df = 1, 21, $P < 0.001$)

13.18, df = 11, 95 , P < 0.0001, means compared with Tukey HSD test, $\alpha = 0.05$).

DISCUSSION

The increased abundance of zooplankton in the water column during the night indicates that zooplankton in the back reef at Discovery Bay are under pressure to partake in DVM. The presence of larger zooplankton at night is also consistent with the prediction that larger zooplankton are more vulnerable to visual predation, and thus are more likely to engage in DVM.

Copepods made up 63% of our night samples while in a past study they constituted 94% of the night samples (Iwamoto 2003), suggesting a shift in zooplankton taxa composition in two years. Although sampling occurred under a full moon, it was cloudy on sampling nights, so it is unlikely that lunar irradiance had any inhibitory effect on the zooplankton ascent. It would be interesting for future studies to investigate the effects of moonlight on zooplankton DVM. Future studies could test if zooplankton emerges earlier with heavy day cloud cover, as would be predicted if light intensity is the stimulus for DVM.

Table 1. Abundance of zooplankton taxa at day and night

Taxa	Day	Night
Copepods (<0.5 mm)	253	587
Copepods (0.5-1 mm)	434	1776
Copepods (> 1mm)	59	596
Decapods (1-2 mm)	24	742
Decapods (2-3 mm)	3	469
Amphipods (< 1 mm)	58	38
Amphipods (1-2 mm)	31	55
Amphipods (> 2 mm)	10	17
Isopods (< 1 mm)	46	28
Isopods (> 1 mm)	31	27
Fish larvae (< 2mm)	1	47
Fish larvae (> 2 mm)	2	151
Polychaetes	159	79
Other (Gastropods, Ostracods, Formanifera)	33	57
Total	1144	4669

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