originally made. Some blades were missing their top half – for these we counted the bites we could see and added five bites as an estimate of herbivory on the missing half. We considered this to be a conservative measure of bites taken on the half we couldn't see.

Table 1. Amount of herbivory on *Thalassia testudinum*. (total # bites/6-leaf-treatment [#leaves half gone])

replicate	I	II	III	IV
1	10	9[1]	1	0
2	0	10	1	0
3	6	15	0	1
4	25	8[1]	0	0
5	0	3[1]	0	0
6	3	9[3]	0	0
7	0	9	0	0
8	0	0	1	1
9	0	0	0	2
10	0	0	4	0
Total	44	63[6]	7	4

Treatments: (I) Epiphytes, not punched; (II) Epiphytes, punched; (III) Not scraped, punched; (IV) Scraped, punched.

RESULTS (JLB)

The presence of an epiphyte load on *Thalassia* leaves was shown to increase herbivory on these leaves (107 bites to 11 bites; $p<0.001$, Table 1). A two-way ANOVA performed on the two treatments found no interaction between the effects of epiphyte load and previous parrotfish bites ($p>0.05$, Table 2). Two tests were performed on the effect of parrotfish bite marks on herbivory. A two-way ANOVA found no significant effect on herbivory ($p > 0.1$, Table 2). A Wilcoxon 2-sample test comparing unscraped punched and unpunched leaves found no significant effect of previous bite marks on herbivory ($U=64.5$, $p > 0.1$).

Table 2. Results of ANOVA: punched vs. scraped leaves.

	F	p
A: punched	2.36	$0.25 > p > 0.1$
B: scraped	13.12	$p < 0.001$
A x B	3.26	$0.1 > p > 0.05$

DISCUSSION (CNO)

Our results demonstrate that epiphyte presence on *Thalassia testudinum* blades is the stronger factor affecting the amount of parrotfish herbivory. We might expect that it is more energetically efficient for the fish to forage on the nutrient-rich epiphyte-covered grass since the algae growing on the leaf surfaces, in combination with the leaves, provide the fish with higher nutrient levels than do the leaves stripped of epiphytes.

Although statistically insignificant, the differences between the amount of herbivory on punched and unpunched leaves shows a trend of parrotfish preference for punched leaves. The fish may use the punches as cues of previous herbivory. The increased herbivory on some leaves may also be due to differing palatability of *Thalassia testudinum* leaves. Better leaves will have more bites, signaling to other fish the quality of the food.

The area used in this study had an abundant supply of *Thalassia testudinum*. Our results might have shown more significance if the tests had been performed in a higher herbivory environment.

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COLOR ASSOCIATIONS OF *OPHIOTHRIX SUENSONII* WITH *HALICLONA RUBENS* AND *H. HOGARTHI* SPONGES

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Abstract. This study examined the relationship of two color morphs of *Ophiothrix suensonii* brittlestars and two species of finger sponge, *Haliclona hogarthis* (lavender) and *Haliclona rubens* (maroon). At Columbus Park, Discovery Bay, Jamaica, dark brittlestars are found almost entirely on maroon sponges, and pale brittlestars almost entirely on lavender sponges. Field tests showed that sponge color does not significantly influence brittlestar abandonment of sponges. However, laboratory trials indicated that pale brittlestars abandon maroon sponges more often than lavender sponges. Tests of predation in the field revealed greater predation on pale brittlestars tethered to maroon sponges. It appears as if pale brittlestars on maroon sponges react to greater predation pressure by abandoning these substrates. Our data fail to explain the non-random distribution of dark brittlestars in the field, and therefore other mechanisms, such as brittlestar color change, merit further investigation. (JLB, CNO, JVK)

INTRODUCTION (CNO)

Many studies have suggested that predation is the most influential factor affecting brittlestar behavior. A comparison of brittlestars in a Bahamian saline lake and nearby shallow coastal sites showed that those in the lake, where predatory fishes were absent, were found out in the open while those on the coast were most often hidden in sponges (Aronson and Harris 1985). A separate study showed that *Ophiothrix lineata* brittlestars on an open, sandy substrate were attacked more often by predatory fish than *O. lineata* on the outside walls of sponges (Hendler 1984). This suggests that sponges afford protection from visual predators by providing a cryptic background for brittlestars.

It appears that for brittlestars, substrate choice stems from this need to avoid visual predators. A preliminary study looking at predation of brittlestars on different sponges found a significantly greater number of pale shaded *Ophiothrix suensonii* depredated on maroon sponges (*Haliclona rubens*) than on lavender sponges (*Haliclona hogarthi*). There was no difference in the amount of predation on dark *O. suensonii* on maroon and lavender sponges (Gorman, et al. 1991).

Parrotfish and wrasse, the primary brittlestar predators (Hendler 1984) are common in our study site at Columbus Park, Discovery Bay. Because of the predatory pressures, the brittlestars in this area should maximize their fitness by blending in with the substrate, thus avoiding visual predators. Our study continued to explore the relationship between different shades of *O. suensonii* and the dark maroon sponge, *H. rubens*, and the paler lavender sponge, *H. hogarthis* (hereafter referred to as maroon and lavender sponges). We looked at color associations in nature, expecting to find mostly pale brittlestars on lavender sponges and dark brittlestars on maroon sponges. Secondly, we performed manipulations in the lab and in the field to determine whether the two shades of brittlestars set on the sponges would leave the two colors differentially. To maximize their fitness, dark brittlestars should move off of lavender sponges more often than they leave maroon sponges. Similarly, pale brittlestars should more readily leave maroon sponges than lavender sponges. Our final test examined the predation on the two shades of brittlestars tethered on the lavender and maroon sponges. Since they are visual predators, fish should be able to find and eat dark brittlestars on lavender sponges and pale brittlestars on maroon sponges more often than brittlestars that better match their host sponge color.

METHODS (JVK)

Physical arrangement. We conducted our study at the Discovery Bay Marine Laboratory, Jamaica, from 24 February to 3 March 1992. All field surveys, experiments, observations, and collections were done at Columbus Park with the aid of SCUBA for a total of 9.25 hours in 14 dives. To facilitate orientation and to locate sponges being used, we set up a 12m x 9m plot between depths of 30ft and 50ft using underwater buoys with the longer side of the area following the contour of the slope. This plot was then subdivided into twelve quadrats approximately 3m x 3m each.

We surveyed the number of dark and pale brittlestars found on all maroon and lavender sponges in or near our plot as we simultaneously collected them for our field and lab manipulation. Brittlestars were collected by flushing them from the sponges with a small squirt of bleach. We placed brittlestars in a mesh bag designated for the sponge color on which they were found. Only dark brittlestars from maroon sponges and pale brittlestars from lavender sponges were actually used in our experiments to reduce the number of variables studied. Brittlestars were judged as pale or dark by their disk and leg color based on a group concensus of what was obviously pale and dark.

Site fidelity field experiment. We collected brittlestars during three consecutive morning dives to be returned in the afternoon for our manipulation trials. Each brittlestar collected was tagged in the lab for immediate identification purposes. We tagged brittlestars by passing a threaded needle through the mouth and out the aboral disk and then knotting the thread ends together (Aronson 1988). Orange thread was used to identify 23 pale brittlestars and pink thread for 60 dark brittlestars used in this experiment.

We placed a pair of brittlestars (one dark and one pale) on the top half of either a maroon or lavender sponge. A flagged weight was placed next to the sponge being used so that we could easily find it again. After 24 hours we checked the sponges and noted the remaining brittlestars while also surveying the area to locate new positions of any absent brittlestars. Twelve maroon sponges and eight lavender sponges were used to test site fidelity. Due to the frequent absence of dark brittlestars collected, dark-dark pairs were also placed on four maroon sponges and three lavender sponges. Pairs were used to keep a consistent number of brittlestars on each sponge.

Sponge fidelity lab experiment. Lavender and maroon sponges of similar size and shape were collected from the

field. One unbranching sponge of each color was placed in a ten gallon glass tank filled with sea water. The sponges were tied to a support above the tank so that each stood at a similar angle. We placed a dark brittlestar on the maroon sponge and a pale brittlestar on the lavender sponge to see if they would leave or remain on the sponge. We considered a brittlestar to have left the sponge once its disk and at least four legs were lying on the bottom of the tank. Brittlestars that crawled up the sponge and onto the overhead support were also considered to have left the sponge. Initially a 5min time limit was given for each brittlestar to move off since we believed that this was sufficient time for a brittlestar to leave an unpreferred substrate. However, after our initial trials we discovered that the brittlestars had not changed their location between 3min and 5min, thus we used a 3min limit in our final trials. The brittlestars were then tested on the other color sponge so that each individual brittlestar was tested on both color sponges. A total of 25 dark and 27 pale brittlestars were tested (including preliminary trials).

Field predation trials. Additional brittlestars were collected during two separate dives and set out in the field on the next dive after tagging them in the lab with colored thread. A pair of brittlestars (one dark and one pale) was tethered with thread to the top half of either a maroon or lavender sponge. Seven pairs of brittlestars were placed on five maroon and two lavender sponges during one morning and checked that afternoon for signs of predation. An additional 16 pairs were placed on 7 maroon and 9 lavender sponges that afternoon and checked the following morning. Sponges used were flagged so that we could easily find them again. Brittlestars with missing legs or disk parts, and whole brittlestars absent (i.e., only thread remaining), were recorded as preyed upon.

RESULTS (JLB)

Our study data show a distinct color association between *O. suensonii* and sponges in the field, with 97% of brittlestars matching the sponge on which they were found (dark on maroon, pale on lavender; Table 1).

Table 1. Survey data: brittlestars observed on two species of finger sponge.

		sponge species	
		maroon	lavender
# brittlestars	dark	94 (99%)	1 (1%)
found	pale	6 (5%)	105 (95%)

Site fidelity field trials. Several chi-square tests were performed to determine the effect of sponge color on brittlestar behavior in the field (Table 2).

Table 2. Chi-Square results for field site fidelity trials.

dark on maroon	χ^2=1.84 p>0.1	χ^2=0.066 p>0.5	χ^2=0.43 p>0.5
	pale on maroon	χ^2=1.06 p>0.1	χ^2=0.203 p>0.5
		dark on lavender	χ^2=0.139 p>0.5
Brittlestar on sponge combinations			pale on lavender

No difference was found in the behavior (frequency of brittlestars leaving or staying) of dark or pale brittlestars on either maroon (χ^2=1.84, p>0.1) or lavender (χ^2=0.139, p>0.5) sponges.

Light brittlestars did not behave differently on maroon or lavender sponges (χ^2=0.203, p>0.5). Dark brittlestars also exhibited no difference on different color sponges (χ^2=0.066, p>0.5). In all cases, more brittlestars were absent from test sponges than remained (Appendix A). A comparison of matched pairs (dark brittlestars on maroon sponges, pale on lavender) showed no difference between them (χ^2=0.43 p>0.5). No difference was found between unmatched pairs (χ^2=1.06, p>0.1). Therefore, sponge color was found to have no effect on the frequency of brittlestar sponge abandonment.

Lab sponge fidelity trials. We found that sponge color did influence the clinging behavior of brittlestars in laboratory manipulations (Table 3). No difference in frequency of leaving sponges was found between dark and pale brittlestars placed on maroon sponges (χ^2=0.055, p>0.1). However, dark and pale brittlestars placed on lavender sponges showed nearly significant differences in behaviour (χ^2=3.57, p>0.05): 21% of dark brittlestars dropped versus only 4% of pale brittlestars (Appendix A). There was no significant difference in dark brittlestar behavior on maroon or lavender sponges (χ^2=0.80 p>0.1). However, pale brittlestars left maroon sponges significantly more often than lavender sponges (χ^2=11.20, p<0.005). Analysis of matched trials also showed that pale brittlestars left lavender sponges significantly less often than dark brittlestars left maroon sponges (χ^2=7.36, p<0.01). No difference was found between unmatched pairs (χ^2=2.69, p>0.1).

Table 3. Chi-Square results for laboratory sponge fidelity trials.

Brittlestar on sponge combinations	pale on maroon	dark on lavender	pale on lavender
dark on maroon	χ^2=0.55 p>0.1	χ^2=0.82 p>0.1	χ^2=7.36 p>0.01
pale on maroon		χ^2=2.69 p>0.1	χ^2=11.20 p>0.005
dark on lavender			χ^2=3.57 p>0.05

Field predation experiments. All results from field predation trials are shown in Table 4. Light brittlestars were depredated significantly more than dark brittlestars on maroon sponges (100% to 62%, G=7.4, p<0.01). No difference was found between color morphs on lavender sponges (60% to 60%, χ^2=0, p>0.975). Predation on pale brittlestars on maroon sponges was marginnaly significantly greater than on lavender sponges (G=3.45, 0.1>p>0.05). Predation on dark brittlestars on different color sponges was not significantly different (χ^2=0.004, p>0.9). A significant difference in predation was not found for either matched (χ^2=0.008, p>0.9) or unmatched (G=3.45, p>0.05) pairs; only pale brittlestars on maroon sponges were therefore found to experience increased rates of predation.

Table 4. Chi-Square and G-test results for field predation trials.

Brittlestar on sponge combinations	pale on maroon	dark on lavender	pale on lavender
dark on maroon	G_{adj}=7.4 p<0.01	χ^2=0.004 p>0.9	χ^2=0.008 p>0.9
pale on maroon		G_{adj}=3.45 p>0.05	G_{adj}=3.45 p>0.05
dark on lavender			χ^2=0 p>0.975

Due to the near significance of our predation data and our small sample size, we combined our data with data from predation experiments performed by Gorman, et al. (1991) to increase our effective sample size (Appendix B). The combined data shows a significant difference in predation on unmatched pairs, with pale brittlestars on maroon sponges experiencing more predation than dark brittlestars on lavenders sponges (G=4.84, p<0.05, Table 5). Predation on pale brittlestars on lavender sponges was significantly less than on maroon sponges (G_{adj}=5.34, p<0.025, Table 5). Light brittlestars were still found to be more heavily depredated than dark ones on maroon sponges (G_{adj}=5.65, p<0.025, Table 5).

Table 5. G-test results for combined data predation trials: Burnaford, et al. (1992) and Gorman, et al. (1991).

	dark on lavender	pale on lavender	dark on maroon
pale on maroon	G_{adj}=4.84 p<0.05	G_{adj}=5.34 p<0.025	G_{adj}=5.65 p<0.025

DISCUSSION (JLB, JVK, CNO)

Our field survey revealed that the majority of *O. suensonii* match the color of the sponge on which they are found. Two possible explanations for this phenomenon are (i) brittlestar choice of matching color substrate and (ii) differential predation on brittlestars on mismatched substrates. Both of these possibilities were examined in our study.

Field studies of site fidelity revealed that sponge color had no effect on brittlestar abandonment of test sponges. These results are difficult to interpret as the absence of any brittlestar from a test sponge could be due to either predation or voluntary abandonment. Although we did not quantify incidences of voluntary abandonment, field observations indicate that it does occur. We observed that two pale brittlestars had moved to a pale substrate (lavender vase sponge and pale coral) after having been placed on a maroon sponge 24 hours earlier.

Previous studies have shown that predation rates are greater for brittlestars on sand than for those on sponges and suggest that moving from a sponge carries some risk of predation (Hendler 1984). We observed one such incidence of predation when a brittlestar was accidentally dropped on the sand and was immediately attacked by a Trunkfish. Our observation of a pale brittlestar leaving maroon sponges would therefore suggest that the risk of predation created by moving away is less than the risk of remaining on a mismatched sponge.

Our observation that pale brittlestars were more difficult to place on maroon sponges than on lavender sponges led to laboratory trials examining clinging and abandonment behavior of dark and pale brittlestars. Presumably brittlestars placed on mismatched sponges would be more likely to abandon it than brittlestars on matched sponges. Our results showed no difference in dark brittlestars preferentially clinging to either lavender or maroon sponges. On the other hand, pale brittlestars did react differentially upon their placement on either sponge. All but one held onto lavender sponges while those on maroon sponges demonstrated an equal probability of clinging and dropping. This is consistent with our field observations of pale brittlestars having left maroon sponges and again suggests that, in this case, the risk of leaving is lower than the risk of staying.

Predation is prevalent at Columbus Park – we witnessed several incidences of attacks on brittlestars while setting up our experiments. The predation data gathered supports the laboratory site fidelity experiments and our field observations. Since dark brittlestars were found to experience equal predation on either sponge, there would be no pressure for them to remain on either one or the other color sponge (as indicated in the lab trials). Light brittlestars, however, experience more predation on maroon sponges and therefore should presumably abandon these sponges more readily, as was observed in the lab trials and field observations. This trend could also explain the observed field distribution of pale brittlestars found mostly on lavender sponges. Since pale brittlestars leave maroon sponges more often and those that do no leave face a high predation risk, one would expect to find few pale brittlestars on maroon sponges as was observed in the field.

However, our data do not explain the observed field distributions of dark brittlestars. Other mechanisms should be explored to understand their differential distributions. Perhaps the brittlestars can change color to match their substrate. This is unlikely, however, since high predation rates would not seem to allow sufficient time for a brittlestar to change color. Our brittlestars had not changed colors within 24 hours and experienced at least 60% predation while on unmatched sponges. Brittlestars may also move along the sponge to avoid predators, a variable eliminated in our experiment since we tied the brittlestars to the sponges.

Improvements on methods. Due to the time constraints inherent in a diving project and to the dynamics of diving with three people (and thus being unable to split up and divide work) our field experiments were spaced at greater intervals than was ideal. We were unable to check site fidelity experiments at intervals less than 24 hours. Evidence for site fidelity may have been obscured by high predation rates during this time. Perhaps a reduction in trial length would yield more significant results and eliminate much of the influence of predation.

We were also unable to run all predation trials at the same time of day; one set of trials was exposed during the morning and afternoon while the second was exposed overnight. We do not believe our data to be biased since total hours of exposure was almost equal for both sets of trials (8hr and 6hr), and it is known that predation on brittlestars is drastically reduced at night (Hendler 1984). However, running both sets of trials at the same time of day, perhaps comparing between day and overnight predation, would eliminate this possible source of inaccuracy.

Future studies. Further studies are necessary to better understand the brittlestar-sponge color associations. Genetic studies should be done to determine whether differential coloration is a genotypic or purely phenotypic characteristic. If it is not genotypic, the brittlestars may change colors, depending on the color of their substrate. The mechanism of this possible change should also be explored. For example, are the brittlestars absorbing a chemical from the sponge?

More replicates of the predation trials could prove useful in revealing differential predation on dark brittlestars. Perhaps the difference is a result of the varied palatability of the two color morphs. Future researchers may wish to tether the two types of brittlestars on buoys, where neither has the advantage of crypsis, to determine if predators actually prefer one over the other.

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Appendix A. Data collected for field site fidelity, lab sponge fidelity and field predation trials.

Brittlestar on sponge combinations	Field site fidelity		Lab sponge fidelity		Field predation trials	
	remaining	absent	clinging	dropped	depredated	survived
dark on maroon	11	22	17	8	8	5
light on maroon	2	12	15	11	13	0
dark on lavender	5	12	19	5	6	4
pale on lavender	2	7	26	1	6	4

Appendix B. Data collected for field predation trials by Gorman, et al (1991).

Brittlestar on sponge combinations	depredated	survived
dark on maroon	4	2
pale on maroon	8	0
dark on lavender	6	2
pale on lavender	4	2

Appendix C. Combined data for field predation trials collected by Gorman, et al. (1991) and Burnaford, et al. (1992).

Brittlestar on sponge combinations	depredated	survived
dark on maroon	12	7
pale on maroon	21	0
dark on lavender	12	6
light on lavender	10	6