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RESEARCH ARTICLE

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Habitat use by sponge-dwelling brittlestars

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Abstract Cryptic organisms often associate with sessile invertebrates for refuge in space-limited environments. To examine interspecific habitat associations on coral reefs, tube- and vase-shaped sponges were surveyed for associated brittlestars at six sites on the coral reefs off Key Largo, Florida. Of 179 sponges encountered, *Callyspongia vaginalis* was the most abundant (43.0%), followed by *Niphates digitalis* (39.7%), and *Callyspongia plicifera* (4.5%). Three of eight sponge species surveyed did not differ from *C. vaginalis* in two physical refuge characteristics: oscular diameter and inner tube surface area. Brittlestars (416 total), all of the genus *Ophiothrix*, were only found in *C. vaginalis*, *N. digitalis*, and *C. plicifera*. The most abundant brittlestar, *O. lineata* (326), occurred on *C. vaginalis* (99.0%) and *N. digitalis* (1.0%), while *O. suensonii* (67) occurred on *C. vaginalis* (79.1%), *N. digitalis* (19.4%), and *C. plicifera* (1.5%). There was no pattern of co-occurrence of *O. lineata* and *O. suensonii* on *C. vaginalis*. The abundance of *O. lineata* increased with surface area of *C. vaginalis*. Differential habitat use was observed in *O. lineata*, with small individuals (< 5 mm disk diameter) located inside and on the surface of sponge tubes and large individuals (≥5 mm) solely inside tubes. The number of large *O. lineata* in *C. vaginalis* never exceeded the number of tubes per sponge, and tagged *O. lineata* remained in the same sponge for at least 3 weeks. In density manipulations, no pattern of intraspecific competition among large *O. lineata* was observed; however, there was evidence for interaction between size-classes. Brittlestars selected live sponge habitat over a non-living refuge, suggesting a mechanism for sponge habitat recognition. Sponge-dwelling brittle stars prefer some tube- and vase-shaped sponge species despite similar oscular diameters and surface areas. Surprisingly, these preferred sponge species are known from previous studies to be chemically undefended against generalist fish predators; therefore, brittlestars that inhabit these sponges do not gain an associational chemical defense. Sponge habitat use by *O. lineata* may be governed by intraspecific interactions to maintain habitat and access to food. While past studies have suggested that *O. lineata* is an obligate sponge commensal, the present study suggests that *O. lineata* has a species-specific association with the tube-sponge *C. vaginalis*.

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Introduction

Habitat use is of primary importance in understanding the abundance and distribution of organisms. Habitat structure in a community, which can mediate predation (e.g. Gause 1934; Huffaker 1958; Heck and Wetstone 1977) and competition (e.g. Sale 1975; Holbrook 1979; Edgar 1983), has been examined in both terrestrial (e.g. MacArthur 1958; Holmes et al. 1979; Stinson and Brown 1983) and marine systems (e.g. Randall 1963; Hacker and Steneck 1990; Beck 1995). On coral reefs, where predation is intense and space is limited, numerous cryptic species are found in reef interstices as well as associated with sessile benthic invertebrates. Investigations of coral reef ecology require an understanding of the relationship between cryptic fauna and their living and non-living habitat.

Sponges are a dominant component of coral reef benthic invertebrate fauna, often rivaling scleractinian corals in diversity and abundance (Targett and Schmahl 1984). Sponges are also host to a wide variety of infauna (Pearse 1950; Tyler and Böhlke 1972; Rützler 1976; Westinga and Hoetjes 1981; Pawlik 1983; Duffy 1992). Brittlestars (Echinodermata: Ophiuroidea), which are often described as living in association with other invertebrates, are a predominant member of the sponge infauna (Clark 1933; Devaney 1974; Sloan 1982; Schoppe 1996). The sponge *Zygomycale parishii* contained eleven phyla of infauna, of which 64% of the individuals collected were the brittlestar *Ophiactis saviginyi* (Duarte and Nalesso 1996). Another numerically dominant brittlestar, *Ophiactis quinqueradia*, can crowd the osculae of *Agelas sparus* (Kissling and Taylor 1977). Given the frequency of sponge–brittlestar associations, this relationship provides an ideal system for examining the association of cryptic fauna with sessile invertebrates.

Recent studies suggest that predation pressure limits the mobility of cryptic fauna and leads to specialization of habitat that provides defense from predation and access to food. Herbivorous amphipods, for example, associate with algae that provide a chemical refuge from fish predation and that serve as a food source (Hay et al. 1987; Hay 1991; Duffy and Hay 1994). The nudibranch *Tritonia hamnerorum* specializes on the sea fan *Gorgonia ventalina* and sequesters compounds that protect it from predation (Cronin et al. 1995). The snapping shrimp *Synalpheus gambarelloides* lives inside sponges and consumes sponge tissue (Rützler 1976; Duffy 1992).

Predation on brittlestars is often intense (Hendler 1984; Aronson 1988), and association with sponges may provide brittlestars with a refuge from fish predation (Hendler 1984). In addition, many sponges produce secondary metabolites that deter predation by reef fishes (Pawlik et al. 1995), and may serve as a chemical as well as a physical barrier from predation. Sponges also provide greater access to food particles for suspension-feeding brittlestars (Fedra et al. 1976) and a feeding surface for deposit feeding (Hendler 1984). Thus, brittlestars may select sponge habitat because it provides both predation refuge and access to food.

While previous studies have addressed sponge habitat use by brittlestars, few studies have experimentally examined the association (Hendler 1984; Turon et al. 2000). In considering sponge–brittlestar associations, we asked the following questions: What is the distribution of brittlestars in tube and vase sponges? Do brittlestars actively select and prefer sponge habitat and, if so, what factors affect habitat selection? For example, do ophiuroids preferentially select chemically defended sponges? If brittlestars do select sponge habitat and exhibit species preferences, is habitat limiting, based on availability of unoccupied habitat? If habitat is limiting, do brittlestars compete for space?

To address these questions we first examined the distribution of brittlestars living in tube and vase sponges in the Florida Keys. This morphological group of sponges is comprised of both chemically defended and undefended species (Pawlik et al. 1995). We then conducted multiple field manipulations using the sponge-dwelling brittlestar *Ophiothrix lineata* to examine the last three questions. A non-selective deposit-feeder, *O. lineata* is frequently observed living in tubes of the sponge *Callyspongia vaginalis* (Hendler 1984) and has been suggested to be an obligate sponge-dweller, limited by the presence of suitable sponge habitat (Kissling and Taylor 1977).

Materials and methods

Brittlestar survey

Experiments were conducted on coral reefs off Key Largo, Fla., from 8 May to 20 July 2000. The distribution of sponge-dwelling brittlestars was surveyed on three shallow reefs at 10 m depth [North Dry Rocks (NDR, 25°07.850 N; 80°17.521 W), Shallow Pickles Reef (SPR, 24°59.286 N; 80°24.6 W), Crocker Reef (CR, 24°54.24 N; 80°31.49 W)] and three deep reefs at 20 m depth [Dixie Shoals (DS, 25°04.66 N; 80°18.74 W), Deep Pickles Reef (DPR, 24°59.07 N; 80°24.97 W), and Conch Wall One (CWO, 24°57.01 N; 80°27.25 W)]. At each site, three parallel 10-m transect surveys were conducted, each ≥4 m apart at a constant depth. Because we were interested in studying sponge-dwelling brittlestars, transects were conducted on reefs with sponge coverage. All tube and vase sponges within 1 m on either side of the transect line were counted and identified to species, for a total survey area of 20 m^2 per transect. Number of tubes per sponge and oscular diameter were measured for each individual sponge. Sponge tubes were rolled opened by partially slicing the base of the tube and then cutting longitudinally. This permitted individual counts per tube for multi-tubed sponges. Resident brittlestars were removed from the sponges and identified to species. Disk diameter was measured for each brittlestar using a ruler, and brittlestars were returned to sponges or brought to the laboratory for accurate identification. Because sponge tube surface area is later calculated as a function of tube height and diameter and does not incorporate interstices, only brittlestars visible on the surface and interior of sponge tubes were used in analyses. Brittlestars were returned to the sponge host, and examination of the sponge 1 month later revealed complete healing along the incision and no apparent harm to sponges. Other habitat types (e.g. reef pavement, gorgonians, fire coral, and algae) were carefully examined along transects for brittlestars.

Two physical refuge characteristics were measured for each sponge tube: oscular diameter and inner sponge tube surface area. Inner sponge tube surface area (SA) was calculated as: $\mathrm{SA} = 2\pi \times$oscular radius (cm)×tube height (cm).

An analysis of variance on log-transformed data was used to compare interspecific differences in physical refuge characteristics of sponge species that were counted at least five times in transects. Multiple comparisons between species were conducted using the Tukey–Kramer honestly significant difference (HSD) test (Sokal and Rohlf 1981). A chi-square contingency test was conducted to determine if brittlestars were randomly distributed among available sponge species. To examine the distribution of *O. lineata*, abundances of this brittlestar were standardized to total *C. vaginalis* surface area per 20 m^2 transect and compared across all sites using analysis of variance on arcsine-transformed data (Sokal and Rohlf 1981). All statistics presented herein were conducted using JMP IN 3.2.1 software.

Sponge habitat selection

To determine whether brittlestars prefer sponge habitat to structurally similar non-living habitat, we compared the emigration from and immigration to paired live sponge tubes and skeleton tubes. Skeleton tubes were made from the sponges *Callyspongia vaginalis* and *Niphates digitalis* by rinsing sponges in fresh water and placing them in a mild bleach solution, approximately 0.15% sodium hypochlorite, for 20 min, to remove all cellular material from the refractory spongin skeleton. Sponge skeletons were deployed in the field for 2 days prior to the start of experiments to remove any trace of bleach. Paired skeleton tube and living sponge tube of the same species and similar size were cable-tied upright to a brick, approximately 7 cm apart, with the base of both tubes resting on the brick. Bricks were placed haphazardly on the reef, at least 2 m apart at 15 m depth. To examine emigration, one brittlestar ($\geq$5 mm disk diameter) was placed into each live and skeleton tube. Based on data from the transect surveys, *O. lineata* was placed into *C. vaginalis* and *O. suensonii* into *N. digitalis*. In a preliminary study, brittlestars were found to leave non-sponge habitat within a 24-h period; therefore, all experiments were checked after 24 h for the presence of brittlestars. The experiment was conducted once at Conch Reef and twice at Deep Pickles Reef. For each experiment, the difference in brittlestar presence between paired live sponge and sponge skeleton was assessed using McNemar's test (Zar 1984).

To further investigate preferences for sponge habitat versus structurally similar refuge habitat, the presence of immigrating brittlestars was compared between paired live and skeleton tube sponges. As above, paired live and skeleton tubes of *C. vaginalis* and *N. digitalis* were cleared of all infauna, cable-tied upright to a brick, and placed haphazardly on the reef. Sponges were examined for immigrant brittlestars after 24 h and then weekly for 3 weeks. After the third week, sponge skeletons began to decompose and lose initial physical characteristics. All immigrant brittlestars were identified to species, and disk diameter was measured. Differences in the abundance of immigrant brittlestars at the end of 3 weeks were compared between live and skeleton tubes using the Wilcoxon signed-rank test (Sokal and Rohlf 1981). Differences in immigration were examined by comparing the distribution of brittlestar species between live *C. vaginalis* and *N. digitalis* using a chi-square contingency test (Sokal and Rohlf 1981).

Susceptibility to predation

Predation pressure on *O. lineata* and *O. suensonii* by resident reef fishes was examined by removing brittlestars from sponges and dropping them from a distance of 5 m above the reef. A second observer, stationed on the reef surface below the release site, monitored time to first bite, predators present, and lethality of attack. The experiment was conducted at DPR (20 m) during midday with 10 individual *O. lineata* and 12 individuals of *O. suensonii*, all >5 mm disk diameter. Lethal attacks were predefined as any attack in which the disk was completely consumed. Each brittlestar was monitored until it was either consumed, evaded predation by crawling into reef crevices, or was not attacked after 3 min. Number of attacks on each brittlestar species was compared using a Pearson chi-square coefficient (Sokal and Rohlf 1981).

Sponge species and oscular diameter

To further decouple the importance of physical refuge characteristics and individual sponge species on habitat selection, we compared emigration of *O. lineata* from *C. vaginalis*, *N. digitalis*, and *N. digitalis* with restricted osculae. For this last treatment, the osculae of *N. digitalis* were cinched to 1.5 cm diameter using monofilament line, causing no apparent harm to the sponge and producing the same mean oscular diameter as found for *C. vaginalis*. Paired sponges of similar size were cable-tied upright to a brick as described earlier, and placed on the reef at 15 m depth. Fifteen bricks were used and the experiment was conducted once for each paired treatment: *C. vaginalis* and *N. digitalis*, *C. vaginalis* and cinched *N. digitalis*, and *N. digitalis* and cinched *N. digitalis*. The same *C. vaginalis* tubes were used in both paired experiments. Brittlestars were collected from *C. vaginalis* at the same site for each experiment. One large *O. lineata* ($\geq$5 mm disk diameter) was placed into each sponge tube, and tubes were examined after 24 h for the presence of brittlestars. For each of the three experiments, the presence of *O. lineata* in the paired sponge tubes was compared using McNemar's test (Zar 1984). This experiment was conducted in May 2001 at Conch Reef, Key Largo, Florida.

Habitat fidelity

We examined the movement of tagged *O. lineata* from their habitat sponge, *C. vaginalis*. At site SPR (10 m), sponges with three to four tubes were cleared of all brittlestars. Large *O. lineata* were collected from surrounding sponges. Brittlestars were brought to the surface and tagged with two dots of the vital dye congo red on the oral side of three arms. This tagging technique has been used successfully to track brittlestars (McGovern 2002), and laboratory experiments proved the dye to be non-lethal to *O. lineata* and to remain on the brittlestars for up to 3 months. Thirteen replicate sponges were cleared, and one tagged brittlestar was placed into each sponge, with replicate sponges >5 m apart. Because sponges previously contained individual *O. lineata*, it was assumed that each sponge was habitable. Sponges were re-examined after 24 h to ensure the presence of a tagged brittlestar. Sponges without a brittlestar after 24 h were not included in subsequent analysis. Each sponge was examined weekly by looking inside sponge tubes to confirm the presence of a brittlestar. After 3 weeks, sponges were sliced longitudinally to check for tagged brittlestars. A one-tailed binomial test was used to determine if *O. lineata* remained in a sponge more often than leaving a sponge (Zar 1984).

Intraspecific competition for habitat

In field surveys, the number of large *O. lineata* in individual *C. vaginalis* never exceeded the number of sponge tubes. Intraspecific competition was examined by varying the density of *O. lineata* in a single sponge tube. Brittlestars were collected from surrounding sponges and tagged as described above to distinguish experimental brittlestars from possible immigrants. Live tubes of *C. vaginalis* of similar size were collected, cleared of all infauna and cable-tied upright to bricks. Tagged, large *O. lineata* were placed into each replicate sponge tube at initial densities of four and six individuals per tube ($n=20$ and $n=18$, respectively). If intraspecific competition was intense, then we would expect brittlestars to leave a sponge tube at similar rates at a high (4 ind. per tube) and maximum density (6 ind. per tube). In order to reduce the likelihood that brittlestars would remain in a lower quality habitat due to a lack of available refuge, an additional commensal-free *C. vaginalis* tube was cable-tied 7–10 cm away from the experimental sponge. Sponges were left on the reef at 12 m depth for 5 days, after which time the density of the remaining brittlestars was recorded. The procedure was also used to examine intraspecific interactions between size-classes of *O. lineata*. Initial densities of two large size-class brittlestars ($\geq$5 mm disk diameter) and four small size-class brittlestars (<5 mm disk diameter) were used for this experiment. Thirteen replicates were established as above and examined after 5 days for changes in brittlestar density.

Results

Distribution of sponge-dwelling brittlestars

Of the tube- and vase-sponges counted in transects, *Callyspongia vaginalis* and *Niphates digitalis* were the most abundant (Fig. 1). In total, eight sponge species were encountered at least five times; however, brittlestars were found only in the osculae of *C. vaginalis*, *C. plicifera*, and *N. digitalis*. Sponges differed in both oscular diameter (ANOVA, $F_{7,387}=36.12$, $P<0.0001$)

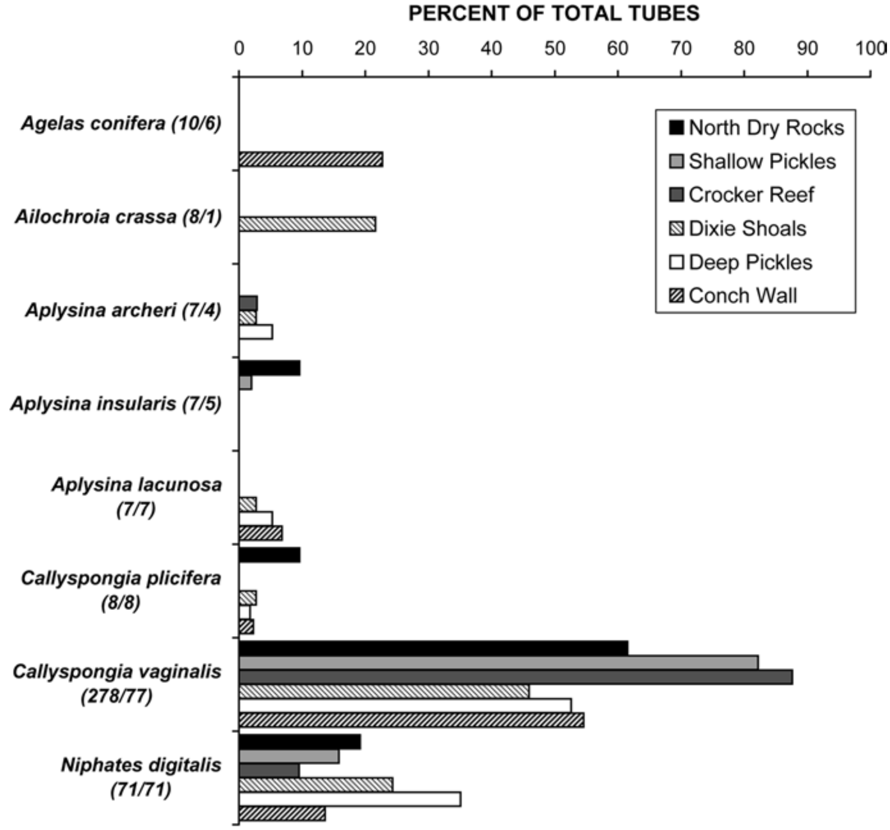


Fig. 1 Frequency of tube and vase sponge tubes at each study site with at least a total of five tubes surveyed. Total number of tubes and total number of individual sponges are shown *in parentheses* for each species

and inner tube surface area (ANOVA, $F_{7,386} = 24.22$, $P < 0.0001$); however, three species were not significantly different from *C. vaginalis* in both oscular diameter and inner tube surface area (Fig. 2).

Four species of the genus *Ophiothrix* were found in or on *C. vaginalis*: *O. lineata*, *O. suensonii*, *O. angulata*, and *O. orstedii*. Of these, *O. lineata* was the most abundant, followed by *O. suensonii*. While *O. suensonii* and *O. lineata* frequently co-occurred on *C. vaginalis*, the abundance of *O. suensonii* on *C. vaginalis* did not vary with abundances of *O. lineata* standardized to sponge surface area ($y = -0.0349x + 0.0034$, $R^2 = 0.0059$, $P = 0.507$). Unlike *O. suensonii*, which was also commonly observed inside *N. digitalis*, *O. lineata* preferentially occupied *C. vaginalis* (Fig. 3, $\chi^2 = 132.86$, $P < 0.0001$). Of all individuals of *C. vaginalis* surveyed (77), 14% did not contain *O. lineata*.

The abundance of *O. lineata* standardized to surface area of *C. vaginalis* did not differ between sites (ANOVA, $F_{1,10} = 0.6680$, $P = 0.657$) and increased with the surface area of *C. vaginalis* per 20 m^2 (Fig. 4). With only one exception, no *O. lineata* ≥5 mm disk diameter was observed on the outer surface of *C. vaginalis*. Large *O. lineata* occurred singly inside a tube 77% of the time, and only co-occurred with other large individuals 4% of the time. While no pattern between abundance of small individuals and sponge size was detected, the number of large brittlestars in a particular sponge never exceeded the number of tubes per sponge and increased with increasing surface area per sponge (Fig. 5).

Habitat selection

The brittlestars *O. lineata* and *O. suensonii* were put into live and skeleton tubes of *C. vaginalis* and *N. digitalis*, respectively. After 24 h, the number of brittlestars was greater in live tubes than in skeleton tubes for both brittlestar species (Fig. 6). The results were consistent over all trials. All live tubes of *C. vaginalis* contained at least one *O. lineata* after 24 h.

Over the 3-week period, no brittlestar was ever observed to immigrate to a sponge skeleton tube. Brittlestar presence was significantly different between live and skeleton tubes for both *C. vaginalis* and *N. digitalis*. All immigrant brittlestars were ≤ 5 mm disk diameter. The sponges *C. vaginalis* and *N. digitalis* hosted different species of brittlestars, with *O. lineata* being predominant in *C. vaginalis* and *O. suensonii* and *O. orstedii* in *N. digitalis* (Fig. 7). The presence of *O. lineata* and *O. suensonii* were associated with *C. vaginalis* and *N. digitalis*, respectively ($\chi^2_{1,14} = 12.44$, $P < 0.001$).

Susceptibility to predation

Both *O. suensonii* and *O. lineata* were attacked by reef fishes, primarily the parrotfish *Sparisoma aurofrenatum*, the grunts *Haemulon* sp., and the sharpnose puffer *Canthigaster rostrata*. Brittlestars differed in the number of individuals attacked. Nine *O. lineata* (90%) were attacked by reef fishes, while only six *O. suensonii* (50%) were attacked ($\chi^2_{1,20} = 4.023$, $P = 0.045$). Both brittlestar species suffered lethal attacks in 25% of assays.

Sponge species and oscular diameter

A single large *O. lineata* was placed into paired sponge tubes, *C. vaginalis* and *N. digitalis*, *C. vaginalis* and cinched *N. digitalis*, and *N. digitalis* and cinched *N. digitalis*. After 24 h, brittlestars remained in

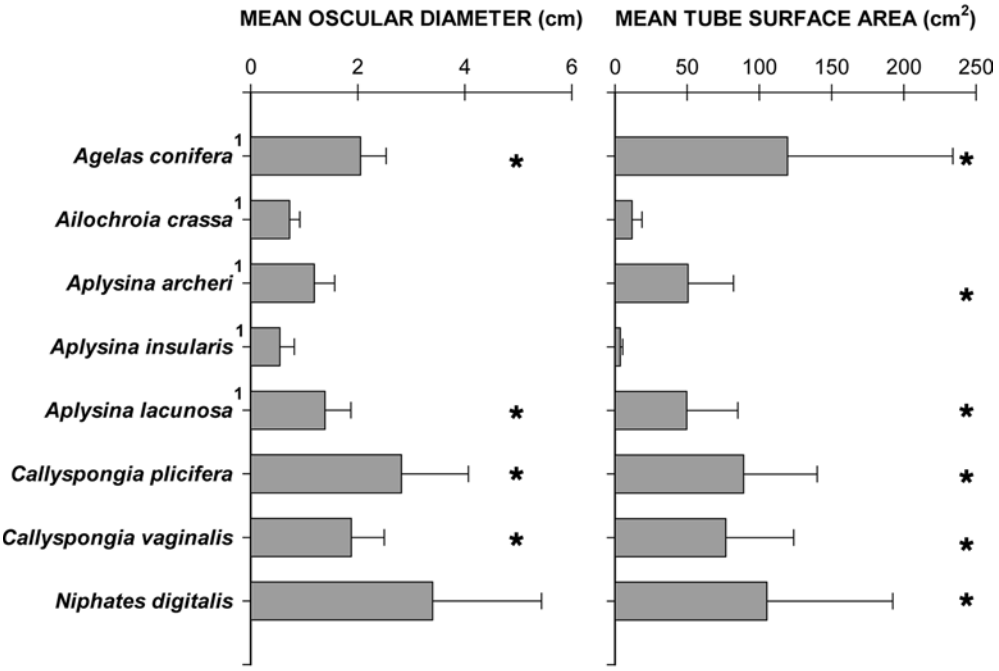


Fig. 2a, b Comparison of physical refuge characteristics. Mean osculum diameter (**a**) and calculated surface area (**b**) for tube and vase sponges surveyed. *Asterisks* represent sponge species that are not statistically different from *Callyspongia vaginalis* (Tukey–Kramer HSD on log-transformed data). *Superscript 1* denotes sponges that are chemically defended against generalist fish predators (Pawlik et al. 1995)

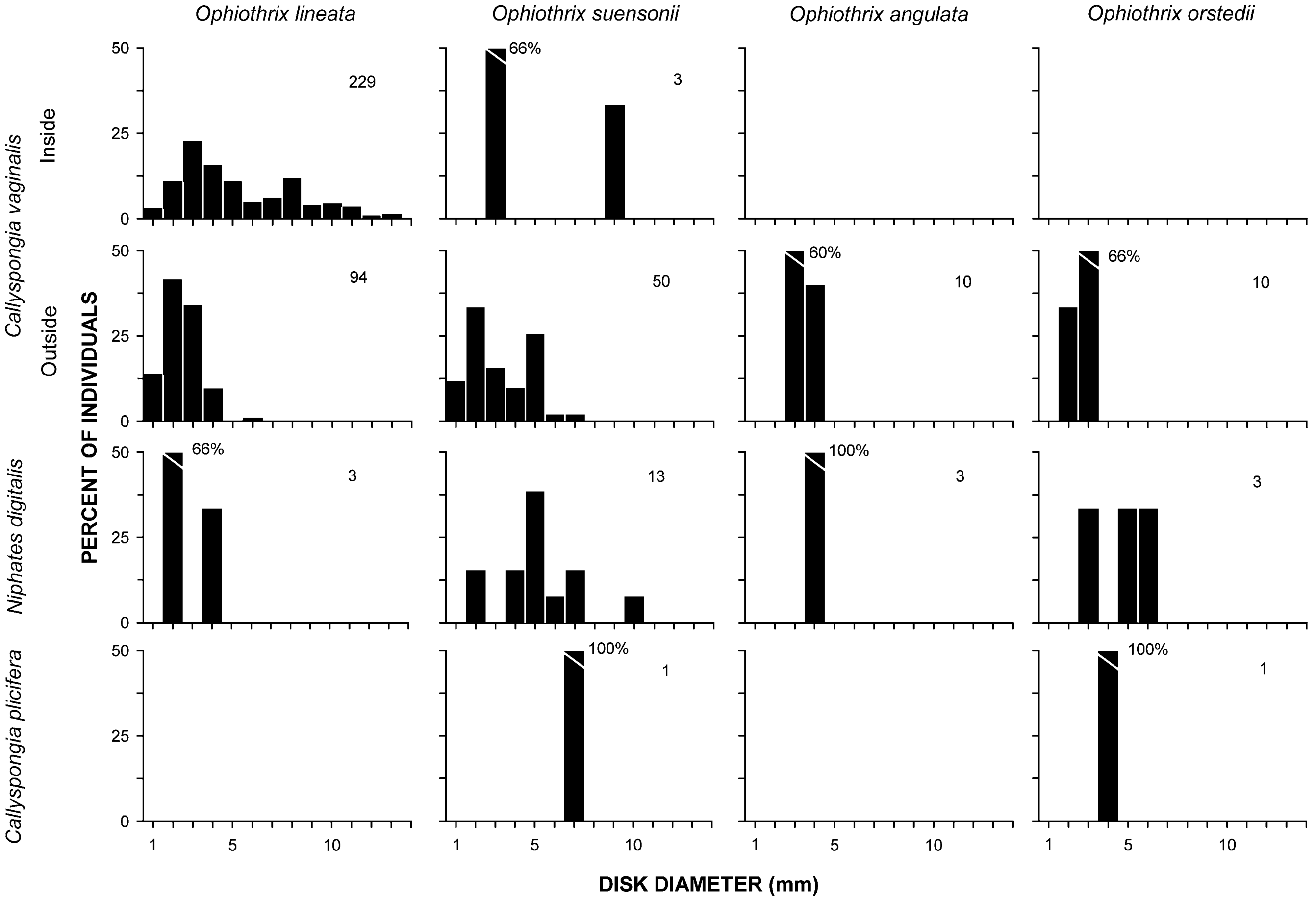


Fig. 3 Size-frequency distribution of sponge-dwelling brittlestars from surveyed tube and vase sponges. Brittlestars were only found inside or on the surface of tubes from *Callyspongia vaginalis* ($n=77$), *C. plicifera* ($n=8$), and *Niphates digitalis* ($n=71$). Total number of brittlestars is indicated for each sample

C. vaginalis more than the *N. digitalis* with which they were paired ($\chi^2_1=11.08$, $P<0.001$). There was no difference in the number of brittlestars remaining in paired *C. vaginalis* and cinched *N. digitalis*, or in *N. digitalis* and cinched *N. digitalis* (Fig. 8).

Habitat fidelity

After 3 weeks, 10 of the 13 individuals of *O. lineata* were still found in the sponges in which they were

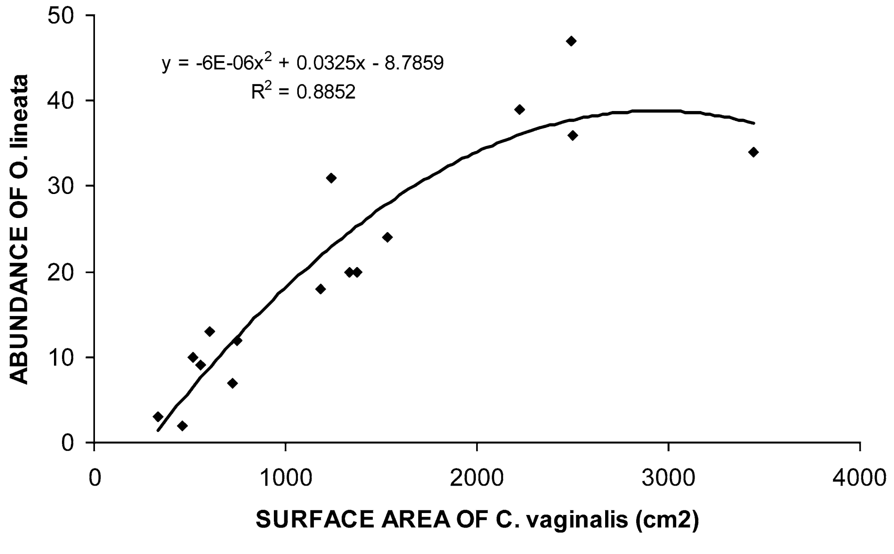


Fig. 4 Abundance of *Ophiothrix lineata* compared to total surface area of *Callyspongia vaginalis* per 20 m^2 transect

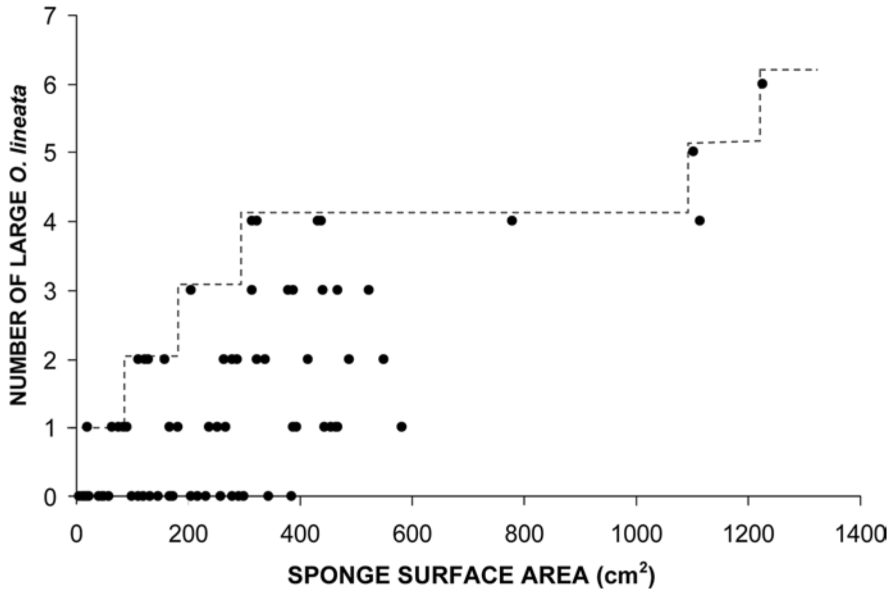


Fig. 5 Abundance of large *Ophiothrix lineata* (≥5 mm disk diameter) living inside individual *Callyspongia vaginalis*. *Dashed line* represents the maximum number of individuals for a given sponge surface area

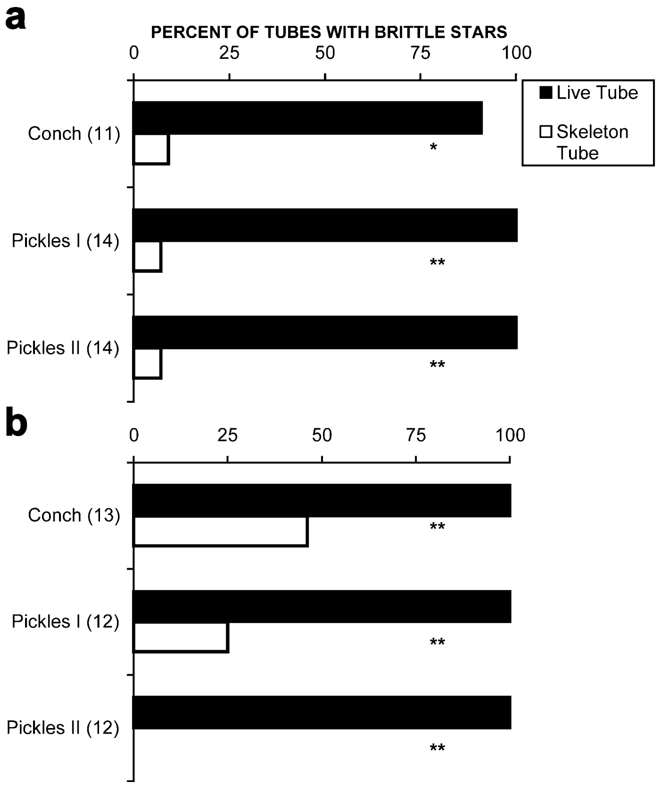


Fig. 6a, b Number of brittlestars remaining in live and skeleton sponge tubes after 24 h at 3 locations. The presence of individual brittlestars was significantly greater in live tubes than in skeleton tubes for both *Ophiothrix lineata* in *Callyspongia vaginalis* (**a**) and *Ophiothrix suensonii* in *Niphates digitalis* (**b**) in all trials. Number of paired blocks for each trial shown *in parentheses*; McNemar's test $^{*}P<0.05$, $^{**}P<0.01$

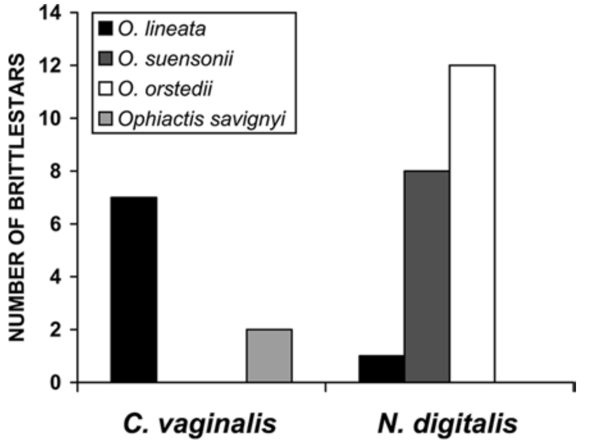


Fig. 7 Immigration of brittlestars to live *Callyspongia vaginalis* ($n=14$) and *Niphates digitalis* ($n=15$) tubes. No brittlestar was observed in skeleton tubes

originally placed. Site fidelity was exhibited by *O. lineata* in *C. vaginalis* ($P=0.046$, one-tail binomial test).

Intraspecific competition

After 5 days in the field, sponge tubes into which four large *O. lineata* had been placed were re-examined. Of the 20 tubes established, 2 were at the initial density of 4 brittlestars per tube and 12 (60%) of the tubes had 2 or fewer brittlestars (Fig. 9a). When the experiment was repeated with initial densities of 6 individuals per tube, only 3 sponge tubes (22%) had 2 or fewer brittlestars, while the remaining 15 had 3–6 brittlestars per tube (Fig. 9b). No brittlestars were observed in the second empty sponge tube during all experiments.

The abundance of large and small *O. lineata* per tube also varied after 5 days in the field. There were no tubes found at the initial density of two large brittlestars and four small individuals. The majority of tubes, 61%, contained densities of one to two large brittlestars with one or no small individuals (Fig. 10).

Fig. 8 Number of sponge tubes with *Ophiothrix lineata* after 24 h in the field ($n = 15$ pairs for each trial); $^{***}P < 0.001$

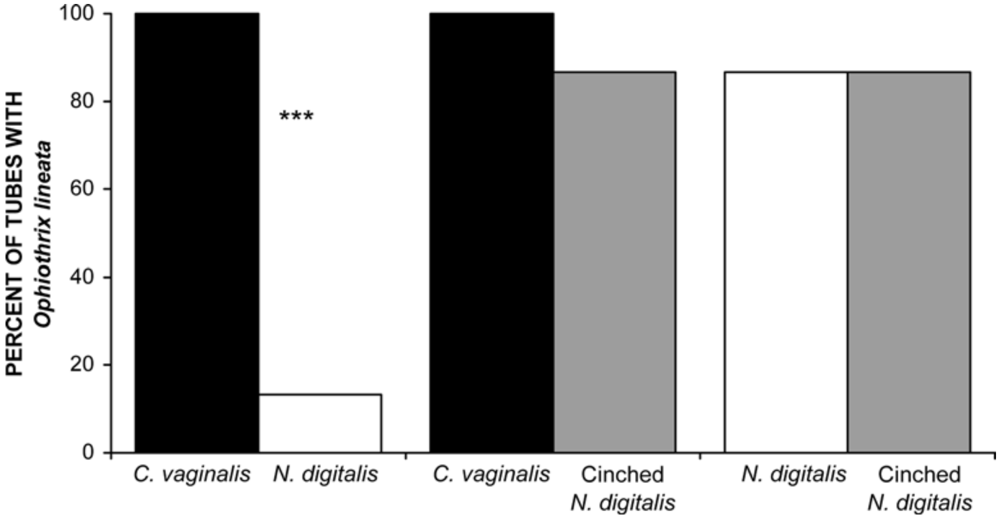
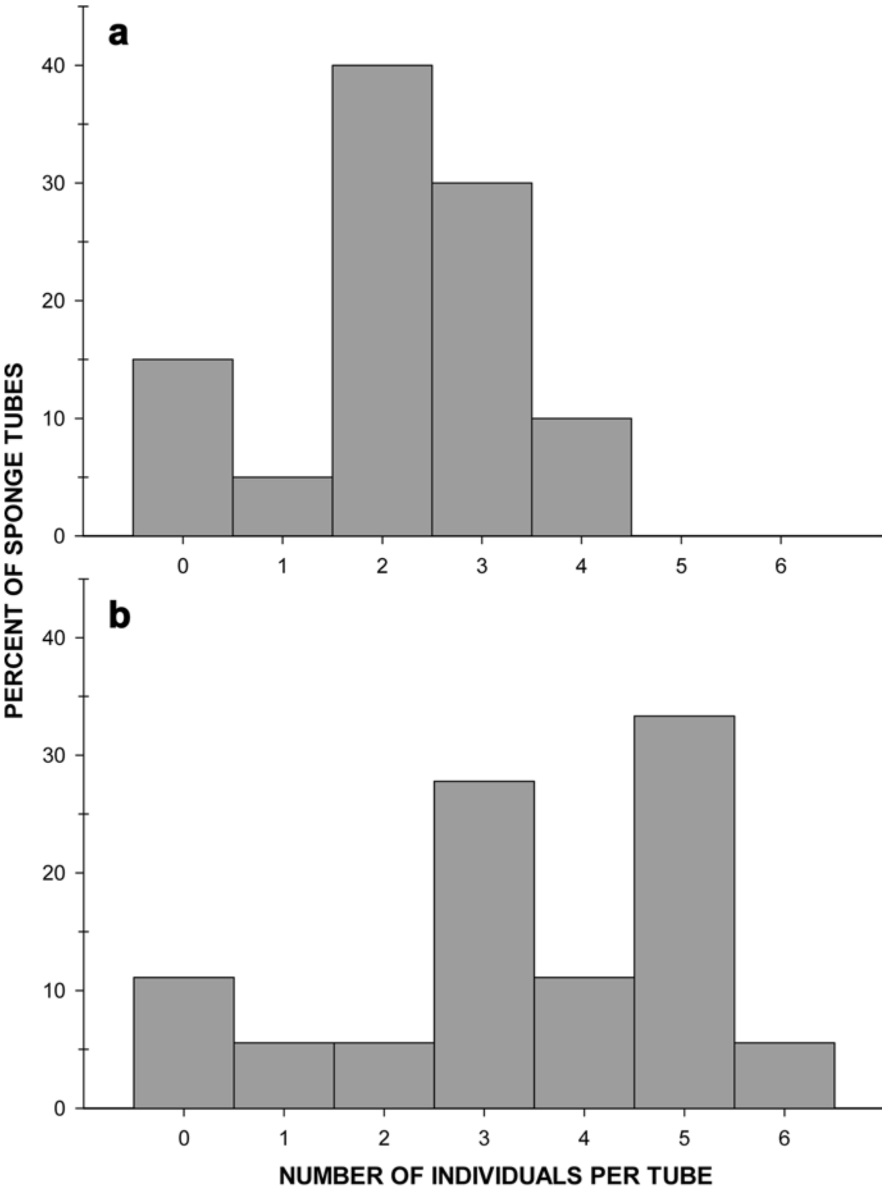


Fig. 9a, b Density frequencies of large *Ophiothrix lineata* after 5 days in the field. Original densities were four individuals per sponge tube (**a**) and six individuals per sponge tube (**b**)



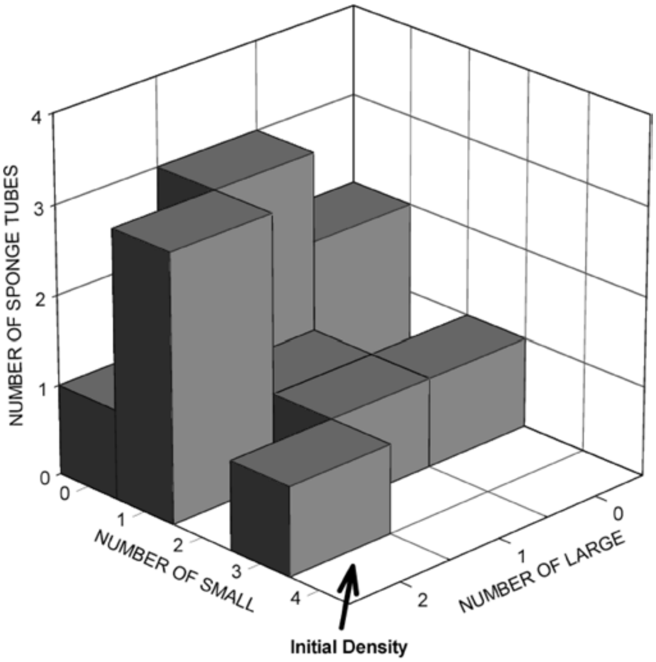


Fig. 10 Size-class density frequency of *Ophiothrix lineata* after 5 days in the field. Initial density was four small individuals (≤ 5 mm disk diameter) and two large individuals (≥5 mm disk diameter)

Discussion

Brittlestars and sponge habitat

All of the brittlestars observed in transects were species of the genus *Ophiothrix*. Species in this genus have been described as living in association with not only sponges, but gorgonians, fire coral, sea grasses, and coral rubble (Clark 1933; Clark 1939; Devaney 1974). Kissling and Taylor (1977) described *O. orstedii* in greatest abundance in back-reef grass beds and *O. angulata* as also living in coral rubble. These alternative habitats were carefully examined as they occurred along each transect; however, no brittlestar species found in sponges was also observed on other substrata. In past studies, Clark (1933) observed *O. suensonii* solely on gorgonians, while Devaney (1974) only observed *O. suensonii* as an inhabitant of sponges. This study corroborates the observations of the latter author, finding *O. suensonii* entirely on sponges; however, we have on occasion observed *O. suensonii* living on fire coral at different locations in the Florida Keys. While *O. suensonii* is not an obligate sponge-dweller, sponges appear to serve as a primary habitat for the species. The most abundant sponge-dweller, *O. lineata*, was only found living on sponges, occurring on *Callyspongia vaginalis* 99% of the time. Single *O. lineata* have been reported living in the tube sponge *Aplysina* (*Verongula*) *lacunosa* (Kissling and Taylor 1977). Only seven *A. lacunosa* were encountered in our surveys, with no *O. lineata* found on them, and only three small *O. lineata* were found on the vase sponge *Niphates digitalis*.

Based on emigration and immigration patterns, sponge-dwelling brittlestars actively detect and select live sponge habitat over a similar, non-living predation refuge. This suggests that these brittlestars not only prefer sponge habitat, but must have a mechanism for recognizing live sponge. When placed in sponge skeletons, both *O. lineata* and *O. suensonii* emigrated within a 24-h period, while individuals inside living tubes remained. Immigrating brittlestars also favored live sponge tubes over skeleton tubes. Both *O. lineata* and *O. suensonii* immigrated preferentially to *C. vaginalis* and *N. digitalis*, respectively, mirroring observations from transects. The importance of chemical cues in the settlement of marine invertebrate larvae is well recognized (Pawlik 1997), and the Mediterranean brittlestar, *O. fragilis*, exhibits recruitment and post-settlement preferences for sponge habitat (Turon et al. 2000). Sponge-dwelling shrimps also recognize and select specific sponge species as habitat (Duffy 1992, 1996).

Sponge habitat: simply a predation refuge?

Living inside a sponge tube provides an obvious barrier from predation, and sponges have been demonstrated to provide brittlestars with a physical refuge from fish predation (Hendler 1984). The physical dimensions of a refuge habitat will determine the ability of that refuge to provide protection from a suite of predators (Eggleston et al. 1990). We measured two physical characteristics that affect the ability of a sponge to provide refuge: the diameter of the osculum and the amount of living space. Oscular diameter will limit the size of potential predators that are able to enter the refuge, and surface area provides a measure of available habitat that is comparable between sponge species. The sponges *C. vaginalis* and *N. digitalis* were the most abundant sponges surveyed and contained 99% of all brittlestars. Of the remaining six common sponge species surveyed, three had comparable physical dimensions to *C. vaginalis* (Fig. 2). Given the identical physical refuge characteristics between sponge species, brittlestars are not limited to specific sponge species based on oscular diameter or living space. Predation may, however, limit the distribution of some brittlestars from sponges with large oscular diameters, such as *N. digitalis.*

Attempts to decouple the importance of oscular diameter and sponge species on habitat selection provided interesting results. After 24 h, *O. lineata* emigrated from unmanipulated *N. digitalis* and remained in *C. vaginalis* (Fig. 8). We observed a Spanish hogfish, *Bodianus rufus*, consume brittlestars from inside *N. digitalis* shortly after establishing the experiment, and found multiple brittlestars in *C. vaginalis* tubes at the end of the experiment, having most likely emigrated from the paired *N. digitalis*. When the osculum of *N. digitalis* was experimentally manipulated to duplicate that of *C. vaginalis*, brittlestars remained in both sponges. In the absence of the preferred sponge habitat (*C. vaginalis*), there was no difference in the presence of *O. lineata* between *N. digitalis* with both opened and manipulated osculum.

The interaction between oscular diameter and sponge species appears to be complex. One possible interpretation is that the manipulated *N. digitalis* provided identical physical refuge characteristics as *C. vaginalis*, and therefore *O. lineata* remained in *N. digitalis*. In the absence of *C. vaginalis*, *O. lineata* did not detect a more suitable habitat nearby and therefore remained in *N. digitalis*. This would be expected as predation is more likely when even a suboptimal refuge is abandoned to search for another. While additional experiments are required to decouple the importance of oscular diameter and sponge species in habitat selection, refuge characteristics appear important in determining habitat selection.

Many sponges are known to produce secondary metabolites that deter fish predation, and sponge-dwelling brittlestars may gain a chemical defense by association with chemically defended sponges. Two of the three sponge species that had similar refuge characteristics as *C. vaginalis* are chemically defended (Pawlik et al. 1995). However, both *C. vaginalis* and *N. digitalis* are not chemically defended from fish predation and are commonly preyed upon by spongivorous reef fishes, primarily angelfishes (Randall and Hartman 1968; Pawlik 1997). Therefore, habitat selection by brittlestars is not a function of chemical refuge. Hendler (1984) used an arm regeneration index as a proxy for predation rates on brittlestars found on *C. vaginalis* and the chemically defended *Neofibularia nolitangere* (which is rare on Florida reefs), and found no difference in regeneration between brittlestars found on either sponge. Brittlestars do not appear to select sponge habitat for any associational chemical defense.

While *C. vaginalis* is chemically undefended and preyed upon, the sponge is not a preferred food and survives grazing by sponge-eating fishes (Pawlik 1997). Further, while brittlestars, including *Ophiothrix*, make up $>10\%$ of the stomach contents of ten coral reef fish species, only one fish, the filefish *Cantherhines pullus*, has been found to ingest both sponges and *Ophiothrix* species (Randall 1967; Randall and Hartman 1968). Therefore, while *C. vaginalis* and *N. digitalis* both lack chemical defenses, these sponges nevertheless provide a physical barrier from fish predation. The lack of chemical defenses in these sponges may also make them a more favorable feeding source for deposit-feeders such as *O. lineata* that ingest mucus from the sponge surface. Despite being chemically undefended, association with sponges may result in a decreased probability of being encountered by generalist invertebrate predators, and additional mechanisms, such as the cryptic coloration of *O. lineata*, may further decrease detection by visual predators (Hendler 1984).

Sharing habitat

Ophiothrix species frequently co-occurred on *C. vaginalis*, with *O. lineata* and *O. suensonii* being the most abundant. The two species do not appear to positively or negatively associate together on sponges, suggesting that interspecific interactions have minimal effect on the presence of brittlestars on *C. vaginalis*. While the presence of *O. suensonii* and *O. lineata* is not precluded by the other, the sponge-dwellers appear partitioned on sponge habitat, with *O. lineata* primarily occupying the inside of sponge tubes and *O. suensonii* occurring on the outside of sponges.

The partitioning of habitat between *O. lineata* and *O. suensonii* may be a function of both mode of feeding and the presence of possible physical defenses. The deposit-feeder *O. lineata* feeds by sweeping its arms over the surface of sponge tubes (Hendler 1984). Unlike its congener, *O. suensonii* is a passive suspension-feeder that lives conspicuously on the outside of sponge tubes with a more elevated feeding posture at night (Hendler et al. 1995). The physical characteristics of *O. lineata* and *O. suensonii* are also distinctly different. The dorsal arm spines of *O. suensonii* are thin, sharply pointed, and several times longer than the width of the arm. Conversely, the dorsal arm spines of *O. lineata* are relatively shorter, with a rounded tip, and dorsoventrally flattened. Relative predation rates of *O. lineata* and *O. suensonii* removed from sponges suggest that *O. suensonii* is less susceptible to predation by reef fishes than *O. lineata*. Although individuals are still consumed by fishes (Randall 1967), the physical characteristics of *O. suensonii* may provide adequate defenses to allow individuals to live on the surface of *C. vaginalis* as well as on other substrata. The differences in feeding strategy and physical protection from predation may permit cohabitation of these two brittlestar species on *C. vaginalis*.

Differential habitat use by *O. lineata*

Size-classes of *O. lineata* use sponge habitat differently, with small individuals living on both the outside and inside of sponge tubes and large individuals only occurring inside tubes. This pattern of segregation of size-classes was also observed in Belize by Hendler (1984). In the present study, however, small individuals were more frequently observed inside sponge tubes than on the sponge surface. The difference might reflect the larger sample size in the present study, as well as differences in size-class abundances and available habitat between the two locations. Differential habitat use may reflect a response to predators, with larger brittlestars requiring refuge inside of tubes, while smaller individuals may evade detection by visual predators in crevices on the sponge surface (Hendler 1984).

Differential habitat use between size-classes may also be a response to allocation of food resources. Because *O. lineata* is a deposit-feeder and mobility is restricted because of predation, the amount of food available to each individual is a function of the surface area of the sponge it inhabits. Thus, sponge habitat directly correlates to food availability. While both size-classes were found living inside sponge tubes, large specimens of *O. lineata* rarely occurred in a sponge tube with other brittlestars and were observed singly 77% of the time. The number of large brittlestars in a sponge appears to be limited by the surface area available per sponge (Fig. 5). Sponges exhibit a carrying capacity for large individuals, with a maximum of four individuals in sponges between 200 and 600 cm^2. Also, sponges $>400\ \text{cm}^2$ always contained at least one large individual, and the number of large *O. lineata* never exceeded the number of tubes per sponge. These trends were not observed for small *O. lineata*, as abundances of small individuals varied sporadically with differing surface areas of *C. vaginalis*. Large brittlestars will have a greater food requirement than small individuals and are restricted to the interior of *C. vaginalis* by predation. As a result, large brittlestars may out-compete smaller individuals for the inside of sponge tubes.

Large *O. lineata* also exhibited site fidelity, remaining in an individual sponge for at least 3 weeks. On a subsequent research trip to the study area, 3 months after the original experiment was established, we located three sponges from this experiment, and found three tagged brittlestars in the original sponges, providing additional evidence for the long-term site fidelity of *O. lineata*. If a sponge is necessary for both predation refuge and feeding, then it should be beneficial to remain in the habitat for as long as the habitat remains viable.

Does competition control size-class structure in *O. lineata*?

Differential habitat use by *O. lineata* of different sizes could be maintained through intraspecific interactions either within a size-class or between size-classes. Densities of up to 15 small individuals per sponge were observed in transect surveys, with no correlation of brittlestar abundance and sponge size. Large *O. lineata*, however, rarely exceeded four per sponge, and never exceeded one per sponge tube. Interactions among small individuals are less likely to form the observed size structure, because small *O. lineata* are able to use both the surface and interstices of *C. vaginalis*, and are therefore less limited by habitat availability. Interactions among large *O. lineata* or between the two size-classes are more likely to create the observed size-class structure.

Observations of more than one large individual in a single tube were very rare, comprising only 4% of all large brittlestar observations. When initial densities were four large *O. lineata* per tube, approximately 60% of replicates decreased to two or less per tube after 5 days. If intraspecific competition was occurring between large individuals, similar final densities would be expected when the initial number of individuals per tube is increased. However, at initial densities of six large individuals per sponge tube, 50% of the replicates had four or more brittlestars after 5 days (Fig. 9). The decrease in surface available for each individual to deposit feed does not appear to affect large *O. lineata* densities in a given sponge tube over the short timeframe of the experiment. The risk of predation is one possible factor that may cause large brittlestars to remain in refuge habitat despite the apparent decrease in food availability and habitat quality. Nevertheless, competitive interactions between large individuals do not directly account for the observed segregation of large individuals between available sponge habitat.

Interactions between size-classes may be responsible for the differential use of *C. vaginalis* by *O. lineata*. Of the 13 sponge tubes established with 2 large brittlestars and 4 small individuals, 62% (8 tubes) had at least 1 large individual and 1 or no small individuals (Fig. 10). While movement patterns of small *O. lineata* are unclear, the disappearance of small individuals from the presence of large individuals suggests that some intraspecific interaction may explain the observed habitat patterns.

Habitat use by *O. lineata*

Based on the observations presented in this paper, we propose the following hypothesis for habitat use by *O. lineata*. Large individuals require the inside of a sponge tube for refuge from predation and for food, while small individuals are able to evade predation on outer surfaces of the sponge, and have a smaller food demand. As small individuals grow, they require refuge inside of a tube and an increase in available surface area to feed. Small brittlestars do not select tubes inhabited by large individuals due to some interaction between the two size-classes. Once a suitable habitat is encountered, individuals remain in that habitat and remain in it for as long as the habitat is viable.

If the foregoing is true, large *O. lineata* are more likely to be limited by available habitat. Demographic bottlenecks due to size-specific shelter requirements have been demonstrated to limit crustacean populations through mortality, emigration, or stunting of the affected size-class (Caddy 1986; Caddy and Stamatopoulas 1990; Beck 1995). If large *O. lineata* require a specific amount of surface area for refuge and access to food, then is the current habitat creating a demographic bottleneck? While 85% of all *C. vaginalis* surveyed contained *O. lineata*, only 58% (45/77) contained large individuals. Of the 42% without large *O. lineata*, the majority are large, multi-tube sponges that appear to be viable habitat. Additionally, the majority of sponges with large *O. lineata* do not appear to contain the maximum number of brittlestars per surface area (Fig. 5). Thus, it appears that the large *O. lineata* are not restricted by available habitat.

Density-dependent habitat selection also predicts that, as local abundances increase beyond a certain point, fitness begins to decrease, leading to a spillover into other habitat types (Fretwell and Lucas 1970). As sponge habitat reaches carrying capacity, intraspecific population pressure should cause *O. lineata* to use other habitat species. Given that *O. lineata* occurred on *C. vaginalis* in 99% of all observations, it does not appear that local abundances are above habitat carrying capacity.

O. lineata: an obligate sponge-dweller?

The literature contains only a few references to the ecology of *O. lineata* (Clark 1933; Devaney 1974; Kissling and Taylor 1977; Hendler 1984). Previous studies have suggested that *O. lineata* is an obligate sponge commensal based on the consistent observation of the brittlestar on sponge habitat. While these few observations of *O. lineata* do not always identify the sponges on which *O. lineata* was found, those that report habitat of the brittlestar contain references to *Callyspongia*-like sponges. Kissling and Taylor (1977) reported that *O. lineata* occurred in gray tube sponges (most likely *C. vaginalis*) as well as in *Aplysina lacunosa* and suggested that the distribution of the brittlestar might be limited by the presence of habitable cavities provided by large sponges. In the present study, small *O. lineata* were found to immigrate to *C. vaginalis*, demonstrating that the brittlestar is not confined to *C. vaginalis* and does move about the reef. Therefore, it would be expected that *O. lineata* may be observed occasionally in other habitats, as noted by Kissling and Taylor (1977). The present study provides the first quantitative survey of brittlestars in tube and vase sponges, and provides evidence that *O. lineata* is not only an obligate sponge commensal, but may be a species-specific commensal.

Roughgarden (1975) outlined three factors that must occur in order for such a symbiosis to evolve: (1) the host should be easy to find, (2) the host should survive well with the symbiont, and (3) the host should provide substantial benefit to the guest. The regular association of *O. lineata* with *C. vaginalis* fits into this cost–benefit model. First, *C. vaginalis* was the most abundant and regular tube sponge surveyed. Second, the brittlestar deposit feeds off the surface of the sponge tube, clearing detrital material from the outer surface faster than ambient water movement, possibly reducing the energy expenditure of the sponge (Hendler 1984). While any true benefit to the sponge is unclear, the relationship is commensalistic, if not mutualistic. Finally, *O. lineata* derives both predation refuge and access to food from *C. vaginalis* (Hendler 1984).

If *O. lineata* is an obligate of *C. vaginalis* then we would expect numerous adaptations that would facilitate the association. Larval dispersal, recruitment, and post-settlement activities are likely to be key factors in the distribution of this sponge-obligate. While future work should focus on selective adaptations of this obligate sponge-dweller, this paper provides further support for the role of interspecific associations in mediating species distribution and abundance on coral reefs.

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