Factors affecting distribution of brittlestars (Echinodermata: Ophiuroidea)

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Abstract: Brittlestars (Ophiuroidea) are common in shallow coral reefs. We hypothesized that observed natural aggregations are a result of species-specific preference for association with other brittlestars of the same or different species. We predicted that niche partitioning of feeding times and methods allow these associations to occur. The species composition of natural brittlestar aggregations was found to be non-random; *Ophiocoma echinata* preferentially associated with conspecifics, while *Ophioderma appressum* preferentially associated with other species. In laboratory experiments, interference appeared to occur between pairs of brittlestars entering a single refuge. Additionally, the activity patterns and feeding methods of *O. echinata* and *O. appressum* differed over the course of the night. This differentiation in feeding patterns may be one mechanism facilitating the coexistence of multiple brittlestar species on a single coral reef, and under a single refuge.

Key Words: aggregation, competition, coral reef, niche differentiation

INTRODUCTION

Brittlestars (Ophiuroidea) are a diverse class of echinoderms in shallow coral reef environments. Sides (1981) found 14 species coexisting under rubble at Discovery Bay, Jamaica. The mechanisms that allow the coexistence of these species are a subject of debate. Previous studies have focussed on predation (Aronson and Harms 1985) and hurricane disturbance (Aronson 1993) as controlling factors on populations of brittlestars. Sides and Woodley (1985) analyzed niche separation in several brittlestars in terms of refuge size and feeding behavior. In that observational study, they found clear niche differentiation between *Ophiocoma wendtii*, *O. echinata*, and *O. pumila*. *O. wendtii* occupied the larger crevices beneath rubble, and extended its arms further at night than the other species. *O. pumila* occupied the smallest crevices and was least exposed at night.

In this study, we examined several factors that may permit coexistence of many brittlestar species in the backreef at Discovery Bay, Jamaica, as they are often found in the same refuge. Studies focussed on the two most common species found in transects, *O. echinata*, and *O. appressum*, but refuge seeking trials were also conducted with *O. pumila*, *O. wenditii*, *O. cinerum*, and *O. angulata*. We first hypothesized that natural distributions of all species would be non-random with some brittlestar species showing preference for which species they associated with. In laboratory trials, we tested the factors causing these species specific associations. We predicted that some species would exclude others from refuges when refuge space was limited. Additionally, we predicted that when given a choice of refuges, species would differ in the degree to which they choose to associate with conspecifics or other species under a single refuge. We examined these behaviors during both day and night as we predicted that time of day would affect the perceived importance of refuge space. Finally, we predicted that species would differ in the times and methods by which they fed during the night, thus partitioning resources temporally and spatially to provide a possible mechanism for coexistence.

METHODS

The brittlestar population of the west backreef at Discovery Bay, Jamaica was studied from 6 to 11 March, 1999. Initial surveys of the natural population were conducted by overturning coral rubble along eight, 5 m transects and recording the number of individuals and species present. Species were identified using Hendler et al. 1995. The

number of rocks with no individuals underneath was recorded. To test the degree to which refuge availability limits the distribution of brittlestars, four marked pieces of rubble were placed on the backreef and checked for occupancy every 24 h for three days.

In all laboratory experiments naive brittlestars (of the species noted in Table 1) were collected each morning, allowed to acclimatize for two hours, and then used for the trials of that day/night. Individuals were released the following day. We examined the refuge-seeking behavior of *O. echinata*, *O. appressum* *O. pumila*, *O. wenditii*, *O. cinerum*, and *O. angulata*, in a 2 x 5 x 1 m outdoor tank with running seawater. In the tank, we submerged an arena (a clear plastic 6 L bucket) with a single coral rubble refuge, and placed either one or two brittlestars in it. The refuge was large enough to shelter the largest brittlestars in our trials. No brittlestars were used in more than three trials, and all were given at least a 10 minute recovery period between trials. In each trial two times were recorded; the time until the disk of the brittlestar was under the refuge and also the time until 80% (four out of five legs) of the brittlestar was under the refuge. Trials were stopped at five minutes if the brittlestar did not enter the refuge. We used several brittlestar species of different sizes in both day and night to see which brittlestar characteristics effected refuge-seeking behavior.

Using the same 6 species, we also examined whether two brittlestars would associate under a single refuge, or go to separate ones when presented with two separate refuges. We set up a 10 x 40 cm glass aquarium with similar sized refuges at the two ends, submerged within the outdoor tank. Two brittlestars were placed in the middle of the aquarium, between the two refuges, and as before, the time until the disk of the brittlestar was under the refuge and also the time until 80% of the brittlestar was under the refuge were recorded.

Feeding patterns of brittlestars were examined over the course of four nights for *O. appressum* and *O. echinata*. Arenas contained one brittlestar and one refuge. On the final two nights, arenas were provided with a sandy substrate. All night time observations were conducted using flashlights with red lenses as brittlestars do not react as quickly to red light (Sides 1985). Feeding activity was monitored every 30 min for 2 hours at dusk (17:00-19:00), midnight (23:00-1:00), and dawn (5:00-7:00) for a total of 15 observations per night. At these times, the number of arms exposed was noted, and feeding activity was characterized as resting (not moving, or in refuge), suspension feeding (tips of arms elevated) or deposit feeding (actively crawling over substrate). The difference between the two species in the nightly pattern of arm exposure was analyzed with a Kolmogorov- Smirnov test for goodness of fit (Sokal and Rohlf 1969). The proportion of individuals with 4 or 5 arms exposed, out of all trials across 4 nights was used in the analysis. Species-specific differences in feeding method were analyzed with a X^2 test. A regression was performed to determine the effect of a brittlestar's size on its time to get under a refuge.

RESULTS

Ten different species of brittlestars from five families were found under rubble in the west backreef of Discovery Bay, Jamaica (Table 1).

Table 1. Brittlestar species found on eight five m transects in the west backreef at Discovery Bay, Jamaica (** indicates species used in refuge seeking trials).

Species	Family
Ophiocoma echinata **	Ophiocomidae
Ophiocoma pumila **	Ophiocomidae
Ophiocoma wendtii **	Ophiocomidae
Ophioderma appressum **	Ophiodermatidae
Ophioderma brevicaudum	Ophiodermatidae
Ophioderma cinerum **	Ophiodermatidae
Ophiomyxa flaccida	Ophiomyxidae
Ophionereis reticulata	Ophionereididae
Ophionereis squamulosa	Ophionereididae
Ophiothrix angulata **	Ophiotrichidae

Only those individuals found more than once were included in the analysis. *O. echinata* was found less frequently with other species than expected in a random distribution, while *O. appressum* was found more frequently with other species than expected in a random distribution. Along our transects, 20% of rubble was not occupied by brittlestars. As well, no colonization occurred within 72 hours under the substrates that we placed in areas of known brittlestar aggregations.

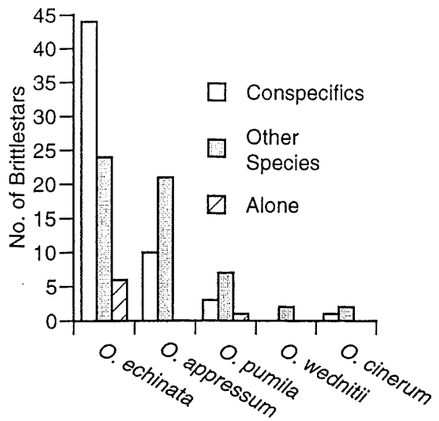

Figure 1. Associations found naturally among 5 brittlestar species found more than once in the west backreef at Discovery Bay, Jamaica. Bars are totals from eight, 5 m transects *O. echinata* was significantly more likely to be found with conspecifics than expected, while *O. appressum* was more likely to be found with other species than expected (X^2 = 14.08, df = 4,110, P = 0.007).

In refuge-seeking trials, brittlestars in paired trials took 80 sec to enter a refuge, almost twice as long as when they were alone (Wilcoxon, X^2= 4.6, df = 1, P = 0.03). This was consistent for both day and night trials. There were no differences between the six species in the time they took to enter a refuge (Wilcoxon, X^2 = 4.1, df = 4, P = 0.39). During the day, the overall percentage of individuals going to a refuge was significantly greater than at night (Wilcoxon, X^2= 21.5, df = 1, P < 0.001; Fig 2).

Of all factors measured, the individual's size was the only accurate predictor of the time it took to enter a refuge. As arm length increased, brittlestars entered refuge more quickly at night (r^2 = 0.22, df = 1,16, P = 0.04). There was no relationship between individual size and time to enter a refuge during daytime trials.

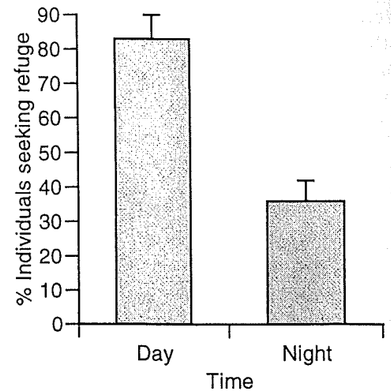

Figure 2. Percentage of individuals of all species seeking refuge in day and night laboratory experiments (Wilcoxon, X^2=21.5, df=1, P<0.0001). The six species indicated in Table 1 are included.

In trials with two individuals in an arena with two refuges, none of the six species showed a preference for associating with conspecifics, individuals of other species, or not going to a refuge at all (X^2= 3.0, df = 6, P = 0.80). As well, there was no difference across different times of day (X^2 = 1.4, df = 1, P = 0.24).

Nightly activity patterns were different in *O. echinata* and *O. appressum*. *O. appressum* was more likely to be fully exposed in the midnight observation period, while *O. echinata* was more likely to be fully exposed in the dawn period (Kolmogorov-Smirnov test, D = 0.107, P < 0.05; Fig. 3). The methods of feeding employed by each species were also significantly different. *O. appressum* was deposit feeding twice as frequently as suspension feeding, while *O. echinata* was never observed deposit feeding (X^2 = 42.3, df = 3, P < 0.001).

DISCUSSION

Brittlestars are found in aggregations under rocks in the backreef of Discovery Bay. These aggregations are not likely to be caused by space limitation because there is uninhabited reef space open for colonization, and also the vacant substrates we put in the field were not colonized after 72 hours. These aggregations are not random either, as *O. echinata*, and *O. appressum* show a preference in which species

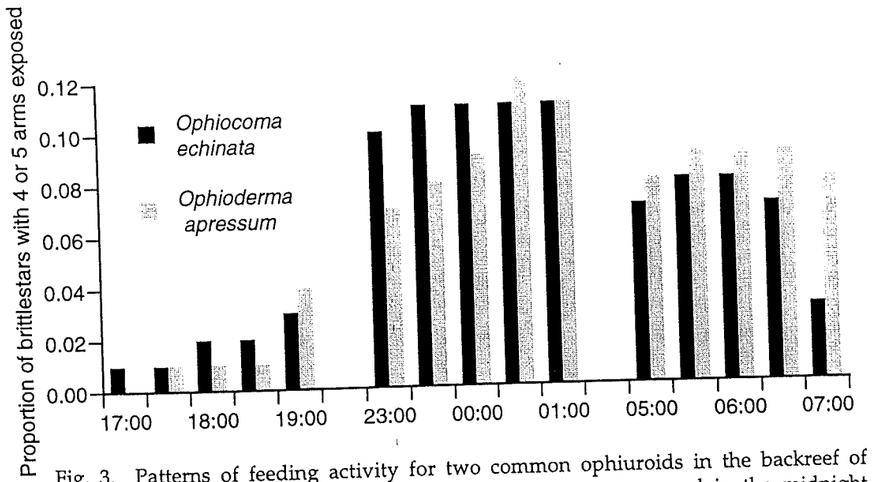

Fig. 3. Patterns of feeding activity for two common ophiuroids in the backreef of Discovery Bay, Jamaica. *O. echinata* is significantly more exposed in the midnight observation period, while *O. apressum* is more exposed during the dawn period (Kolmogorov-Smirnov test, P < 0.05).

they associate with. There must be some mechanism to generate these patterns. In an attempt to uncover these mechanisms, we looked at brittlestars in controlled conditions. Some interaction appeared to be occurring between the brittlestars in our trials, because when individuals are alone they enter refuge more quickly than when they are paired. This suggests that interference or some assessment of competitive ability may occur between individuals.

The fact that larger individuals enter refuges more quickly at night is probably related to the relative ease with which larger individuals can find an object in a small enclosure. At night, even without distal cues such as shading, individuals with longer arms can detect more distant refuges. Though there are night-active predators, e. g. crabs, refuges are probably more important for predator avoidance during daylight hours due to the greater abundance of visual predators at that time. In night trials, many brittlestars were observed to locate a refuge then extend several arms and begin to feed.

Though there was no difference between species for preference of sharing a refuge with others, this does not seem to be the case in natural conditions where species specific associations were seen. Perhaps the five minute duration of the trials was too short to see the eventual distribution of individuals under the same refuge, which may more closely resemble that observed in the backreef.

Neither competition for refuge space nor competition for food appears to occur in the brittlestar species examined in our study. We found no evidence of competition for refuge space, as different species showed no preference for associating with conspecifics or individuals of different species. As well, in both field and laboratory experiments, brittlestars were observed resting on top of one another. Competition for food between the two most common brittlestar species, *O. echinata* and *O. appressum* probably does not influence their distribution, as they differ in the time of night and the method in which they feed. Strong competition for refuges and food do not seem to be important for brittlestars, which may facilitate the continued coexistence of the many species found naturally beneath coral rubble. In addition, the lack of evidence for the occurrence of competition suggests that predation or abiotic factors may be more

important determinants of brittlestar community structure.

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