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

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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,

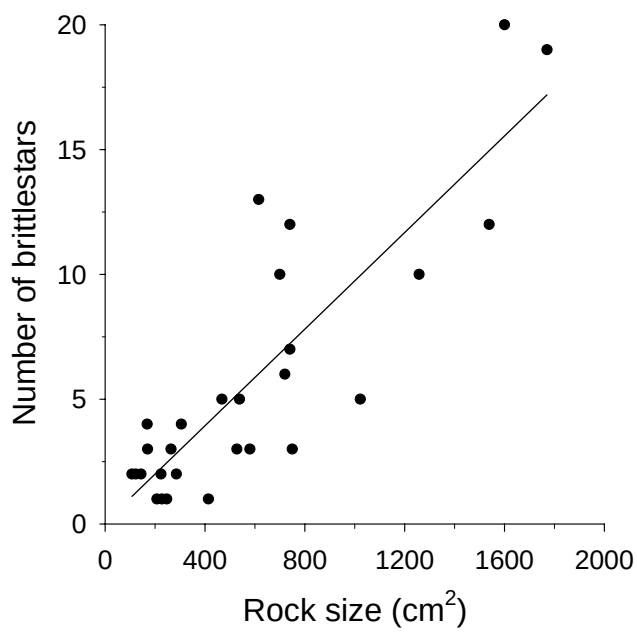

Figure 1. The number of brittle-stars under rocks increased with rock size (n = 28).

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).

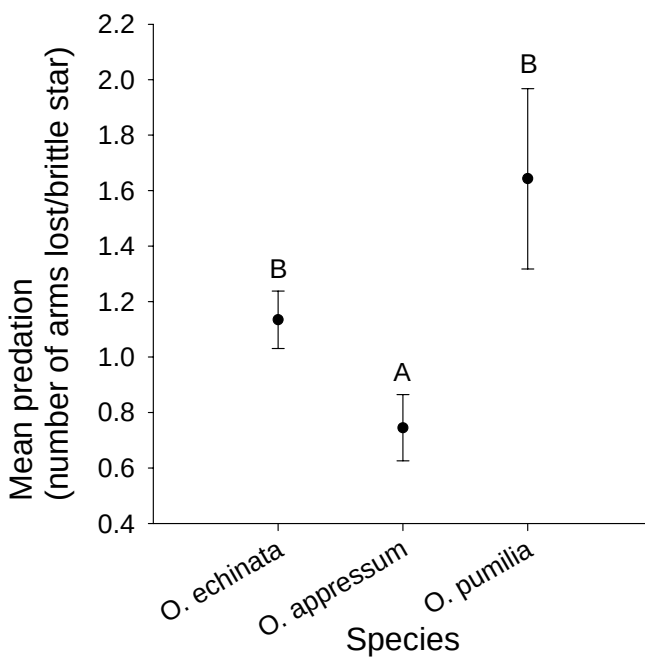

Figure 2. Mean number of arms damaged per brittle-star for *Ophiocoma echinata*, *Ophioderma appressum*, and *Ophiocoma pumilia*. Letters indicate significant differences in predation level. Values are mean ± 1 SE (n = 143).

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

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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.

We chose three species of fish com-