INTERSPECIFIC INTERACTIONS BETWEEN *MONTASTREA ANNULARIS* AND OTHER CARIBBEAN REEF CORALS

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Abstract, The importance of aggressive interactions among corals to their community structure may increase with coral density and diversity. We examined factors affecting the importance of these interactions at two sites by conducting field surveys of interactions between *M. annularis* and other coral species. We hypothesized that frequency of interspecific interactions would vary with distance and species of recipient coral. We further hypothesized that interactions between corals on *M. annularis* mounds would increase with overall site coral density (% cover) and abundance (# coral heads per mound). Alternatively, increased site structural complexity may reduce frequency of interactions by providing alternative substrate and reducing coral density and abundance. We predicted that if interspecific interactions were affecting coral distribution, then there should be low variation in nearest neighbor distances. We found that frequency of interspecific interactions is related to neighbor species and distance, coral density, coral abundance, and species diversity. Our site comparisons suggest that coral density at both sites is too low for interspecific interactions to regulate coral spatial distribution.

Key Words: aggressive interactions, community structure, coral density, mesentary filaments, spatial distribution, sweeper tentacles

INTRODUCTION

Aggressive interactions between scleractinian corals by means of mesentery filaments and sweeper tentacles have been examined in a number of studies (Lang 1973, Sheppard 1981, Chornesky 1983, Chornesky 1989, Lang and Chornesky 1990). The frequency of these interactions may increase with coral density and diversity (Van Veghel 1996), although their importance in affecting coral community structure is not clear (Chadwick 1991). In areas where high disturbance coral density and abundance may be reduced to levels below which competitive interactions play a major role in determining community structure (Chadwick 1991).

M. annularis is a common Caribbean reef building coral near Discovery Bay, Jamaica. It grows in mounds that divide and die as they grow, leaving many separated live coral heads per mound. This growth pattern provides substrate for other corals on the mounds (Humann 1993). *M. annularis* is considered a competitively dominant coral (*sensu* Lang 1973) because of its ability to attack and kill the tissues of neighboring coral species using mesenterial filaments (Lang 1973, Van Veghel 1996). Sheppard (1981) found that the reach of aggressive interactions by a *Montastrea* species was ~3.5 cm, regardless of the recipient species. We assumed that *M. annularis* would exhibit similar behavior. However, our initial observations of coral interactions on forereefs near Discovery Bay Marine Laboratory (at M1 and Pear Tree Bottom) suggest that Sheppard's findings do not hold true at these sites. Corals seemed to be growing much closer than 3.5 cm to *M. annularis*, and distances seemed to vary with neighboring species. Of these two sites, Pear Tree Bottom is more structurally complex due to many canyons and overhangs, and has higher coral density and abundance. M1 is characterized by more sparse coral cover, and nearly all structural complexity is created by the *M. annularis* mounds (Berg et al., pers. obs.). We wondered if these two coral communities differed in density, spatial arrangement, and potential interactions of corals on *M. annularis* mounds.

We hypothesized that interactions between corals on *M. annularis* mounds would vary between our two study sites. The higher overall density and abundance of corals at Pear Tree may lead to higher density and abundance on *M. annularis* mounds, and therefore more interactions. Alternatively, the greater structural complexity of the reef at Pear Tree may provide alternative substrates and reduce species packing on *M. annularis* mounds. If this were the case, coral density and abundance, and therefore

number of interspecific interactions, on *M. annularis* mounds would be lower at Pear Tree. A third possibility is that neither coral density, abundance nor frequency of interactions differ between these sites. In 1981 and again in 1988, coral communities all along the fringing reef of Jamaica's north coast were decimated by direct hit hurricanes. Coral density and abundance at both sites may now be so low that interspecific interactions are dependent upon other factors such as the random settlement and distribution of coral colonies.

We also wanted to determine if the interspecific aggressive interactions via mesenterial filaments and sweeper tentacles affected the coral community structure in the two reefs. If interspecific interactions are regulating community structure, then higher coral density and abundance should lead to colonies being more evenly distributed. Interspecific interactions should keep neighboring corals at regular, evenly-spaced distances from each other. If corals are distributed randomly at higher density and abundance then we could conclude that (1) aggressive interactions do not affect community structure, or (2) the coral density and abundance is not high enough for these interactions to have an impact on community structure.

METHODS

From 6 - 10 March 1998, we conducted two types of field surveys on the fore reefs at Discovery Bay (M1) and Pear Tree Bottom, Jamaica: (1) a survey of interspecific coral interactions between *M. annularis* and other Caribbean corals and (2) a survey of *M. annularis* mound community structure.

For the survey of interspecific interactions at M1, we recorded (1) the distance between a *M. annularis* coral head and its nearest heterospecific neighbor within a 3.5 cm (the aggressive 'reach' of a *Montastrea* species studied by Sheppard (1981)) and (2) the number of interactions between the two neighbors. We recorded the data along 5 swim transects of ~ 50 - 60 minutes parallel to the reef crest at depths of 5 - 8 m. We scored interactions by assessing necrosis, discoloration, or overgrowth on the heterospecific neighbor.

For the survey of *M. annularis* mounds at M1 and Pear Tree, we used a 1 x 1 m^2 randomly placed grid overlay to measure (1) species richness, (2) percent coral cover, (3) number of coral heads, (4) frequency of interspecific interactions between any species of coral (#/m^2), and (5) distance between each *M. annularis* head and its nearest interspecific neighbor. We recorded the data along 6 swim transects of ~ 50 - 60 minutes parallel to the reef crests at depths of 5 - 8 m. We estimated percent coral cover by subdividing the grid and visually estimating percent substrate occupied by live coral, and we scored interactions as before.

We used a one-way ANOVA to test the effect of species on nearest neighbor distance between *M. annularis* and 7 other Caribbean corals. We tested multiple pair-wise comparisons by a Tukey-test (Tukey, $\alpha = 0.05$). We also used a one-way ANOVA to test the effect of interspecific interactions (as a fixed effect, either present or absent) on nearest neighbor distance between *M. annularis* and other corals. We used a Chi-Square analysis to test differences in the frequencies of interactions between these corals. Expected values were generated based upon the null model that there was equal probibility of *M. annularis* agression for each neighbor species. We used one-way ANOVAs to analyze effect of site on species richness, frequency of interactions, percent coral cover, and number of coral heads between sites. Three correlation analyses tested the relationships of species richness, percent coral cover, and number of coral heads on the frequency of interspecific interactions. We also calculated coefficients of variation for the distances to nearest neighbors at M1 and Pear tree using arcsine transformed data, and used a one-way ANOVA to compare the variances.

RESULTS

Those corals that showed signs of interactions were closer to *M. annularis* than those with no interactions (0.58 ± .084 cm vs.1.19 ± 0.10 cm, interactions vs. no interactions respectively; $F_{1,128} = 4.34$, $P = 0.039$). Mean distances from *M. annularis* differed with coral species ($F_{6,123} = 3.81$, $P = 0.002$; Table 1). Proportions of colonies within 3.5 cm of *M. annularis* showing signs of interactions varied significantly with species (Table 1).

Although Pear Tree had higher coral abundance (Berg et. al, pers. obs.), the number of species and number of interspecific interactions per *M. annularis* mound were higher at M1 than at Pear Tree. Percent coral cover and number of coral heads per mound did not differ significantly between sites (Table 2).

TABLE 1. Minimum distance from *M. annularis* to its nearest neighbor, mean distance ± SE from *M. annularis* to its nearest neighbor, and the frequency of interspecific interactions for 7 Caribbean corals.

Coral Species	Minimum Distance to Nearest Neighbor (cm)	Mean Distance to Nearest Neighbor (cm)	Site	
			Proportion	Partial Chi-Squares
brain	0.81	1.4 ± 0.44 [a,c]	0/3	0.90
finger	0.10	10.0 ± 0.14 [a]	9/22	3.94
fire	0.03	0.77 ± 0.12 [a]	0/51	15.30
lettuce	0.25	1.74 ± 0.27 [b,c]	4/16	0.032
mustard	0.15	1.70 ± 0.43 [b,c]	2/11	0.15
sea whip	0.05	0.84 ± 0.18 [a]	14/22	20.39
staghorn	0.4	1.23 ± 0.42 [a,c]	1/5	0.027
total	-	1.05 ± 0.084	30/130	40.74 *

- mean distances followed by the same letter are *not* significantly different (Tukey, $\alpha = 0.05$).
* $P < 0.0001$

TABLE 2. Species richness, frequency of interspecific interactions, percent coral cover, and number of coral heads on *M. annularis* mounds at M1 and Pear Tree (Mean ± SE).

Characteristic	Site		$F_{1,52}$	P
	M1 (mean ± SE; n=29)	Pear Tree (mean ± SE; n=25)		
# spp.	5.97 ± 0.32	4.92 ± 0.35	4.93	0.03
# interactions	2.72 ± 0.62	1.12 ± 0.29	5.01	0.03
% coral cover	21.60 ± 2.57	26.08 ± 2.46	1.56	0.22
# of coral heads	3.26 ± 0.25	3.63 ± 0.28	0.98	0.33

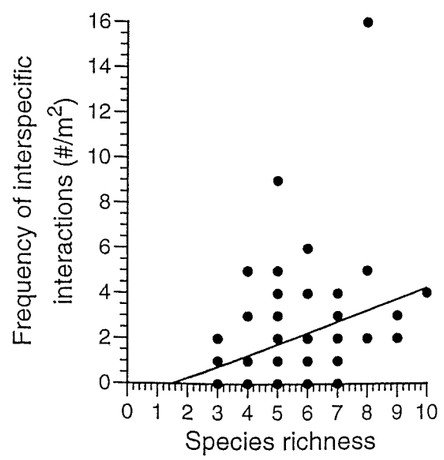

FIG. 1. Frequency of interspecific interactions between *M. annularis* and other Caribbean corals as a function of species richness.

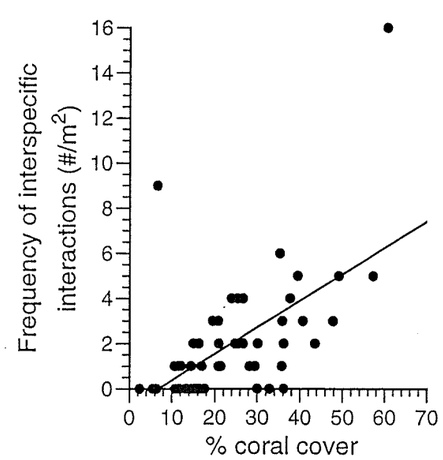

FIG. 2. Frequency of interspecific interactions between *M. annularis* and other Caribbean corals as a function of percent coral cover.

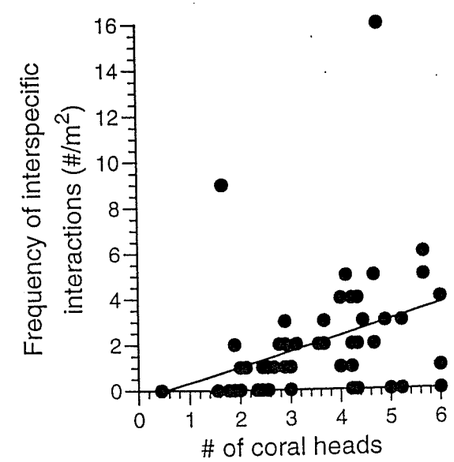

FIG. 3. Frequency of interspecific interactions between *M. annularis* and other Caribbean corals as a function of number of coral heads.

The number of interspecific interactions increased with species richness ($r = 0.33$, $P = 0.016$), percent coral cover ($r = 0.57$, $P < 0.0001$), and number of coral heads ($r = 0.34$, $P = 0.011$) per mound (Figs. 1, 2, and 3).

The distribution of coral heads within *M. annularis* mounds was more random at M1 than at Pear Tree (Mean coefficient of variance = 0.111 ± 0.009 and 0.082 ± 0.010 for M1 and Pear Tree respectively; $F_{1,51} = 4.10$, $P = 0.05$) although the percent cover and number of corals on mounds did not differ between site.

DISCUSSION

Our field study of *M. annularis* interspecific interactions revealed that *M. annularis* appears to interact differently with different species of corals. The mean distance between *M. annularis* heads and their nearest neighbor varied depending upon the species of the neighbor. This could be the result of different distribution patterns of the neighboring corals, but as we only measured distances within the reported reach of *M. annularis* (Sheppard 1981), it is reasonable to believe that interspecific interactions plays some role in this spacing. Overall *M. annularis* was found to interact more often with some species then others, and those corals that were nearest to *M. annularis* were most likely to be attacked. However, both distance and neighbor species seem to be important, as fire coral which had the lowest mean distance from *M. annularis* was never attacked while finger coral had a high frequency of interactions despite being found farther from *M. annularis* .

The results show that interspecific interactions between corals are occurring in Discovery Bay, but they were evident in only 30 of 130 corals (23%) which were positioned within the reach of *M. annularis*. The species and distance dependence of these interactions suggests that at high enough coral densities, these interactions could affect the interspecific spatial distribution on *M. annularis* mounds.

Although not tested, our personal obervations indicated that the Pear Tree site had higher overall coral density and abundance than the M1 site. This greater coral density did not correspond to a higher coral density on *M. annularis* mounds (as measured by percent coral cover and number of coral heads per quadrat), or to more frequent interspecific interactions. Our observations suggest that this could be due to the greater structural complexity of the reef at Pear Tree, such that there would be more substrate for corals, lessening the competition for space on *M. annularis* mounds. These mounds, with little additional relief, provide the only structure at the M1 site.

We found that the number of interspecific interactions was positively correlated with coral density (% cover, # of heads) and number of species on a mound. This result suggests that interspecific interactions are more likely to affect coral distribution on mounds that have many small colonies of different species. On mounds with low coral densities or made up exclusively of *M. annularis*, these interactions should play less of a role in coral spacing.

We found that corals were less evenly spaced at M1 than at Pear Tree, despite the greater number of interactions and species present on mounds at that site. This trend has two possible explanations: (1) coral interactions have more of an effect on spatial distribution at M1 and the larger variation is due to the greater number of species present, all of which *M. annularis* appears to interact with at different distances, or (2) coral densities are too low at either site for interspecific interactions to significantly affect coral spacing, and the difference in variation between sites is due to some other factor of coral settlement or distribution. We can not determine which of these best explains the trends we saw, but given the low frequency of interspecific interactions, the second appears more likely. Future studies could examine this question by

manipulating coral densities and species composition through transplants and removals to determine the long term effects of these factors on interspecific interactions.

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