

Competition among small colonies of *Agaricia*: the importance of size asymmetry in determining competitive outcome

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ABSTRACT: Scleractinian corals may experience competition at early life history stages, particularly where aggregated settlement decreases the space available for growth. The outcome of such interactions can affect post recruitment success and the relative abundance of coral species. The purpose of this study was to determine the importance of competition among small colonies (≤ 4 cm diameter) of *Agaricia* on shallow (≤ 10 m depth) reefs in St. John (US Virgin Islands) and Jamaica. The association between the density of small *Agaricia* and the frequency of congeneric encounters was examined, together with the relationship between density of *Agaricia* and reef rugosity (topographic complexity). Rugosity was analyzed because it indirectly affects competitive interactions by providing cryptic habitats that promote aggregated settlement and coral-coral interactions. To test one possible mechanism determining the outcome of such interactions, the relationship between size asymmetry of competing colonies and competitive outcome was assessed. The results demonstrate that competition among small *Agaricia* is common, particularly where aggregated settlement is favored by high topographic complexity. In other words, competitive interactions among small *Agaricia* are affected by both physical (e.g. topographic complexity) and biological (e.g., settlement patterns) factors. The outcome of such interactions is influenced by the difference in size of competing colonies, with dominant colonies generally being larger than subordinate colonies. Further research is required to identify the mechanistic basis of dominance, but currently the most likely hypotheses are that large colonies are dominant because they have greater energy resources than small colonies, or intrinsically faster growth rates. The high frequency of competition among *Agaricia* colonies in St. John and Jamaica suggests that further studies of congeneric competition within the Scleractinia may prove valuable in understanding the population biology of this taxon.

KEY WORDS: Competition · Size asymmetry · Scleractinians · Small · *Agaricia*

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INTRODUCTION

Space often is a limiting resource for sessile marine invertebrates in hard-substratum, benthic communities (Jackson & Buss 1975, Sebens 1982). In the absence of major disturbances or predation, competition for this resource (i.e., space) may play an important role in shaping community structure (Jackson & Buss 1975, Connell 1978). This is particularly important for sessile, clonal taxa that often encounter other

organisms when they spread laterally through asexual proliferation (Sebens 1982, Buss 1986). Coral reefs provide a particularly good example of an ecosystem dominated by sessile, clonal taxa (scleractinians), and where spatial competition has a strong effect on organism distribution (Sheppard 1979, 1980). Thus, the competitive ability of corals likely influences their population dynamics and individual fitness (Lang 1973, Connell 1978, Sheppard 1980).

Given the role of competition in determining coral community structure (Lang 1973, Sheppard 1979, 1980), mechanisms of interspecific aggression among scleractinians have been studied extensively (Lang &

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Chornesky 1990). Interspecific dominance patterns are a result of a variety of agonistic mechanisms, where dominance typically is genetically determined, based on the type, relative abundance and/or delivery mode of the agonistic structures or agents (Chornesky 1983, Lang & Chornesky 1990). In contrast, intraspecific competitors cannot rely on species-level differences in agonistic structures to determine competitive outcome (Hidaka & Yamazato 1984). Instead, the outcome of intraspecific encounters depends on the vagaries of chance events (i.e., storms, Connell 1978, Hughes 1989), or other factors such as the genotypic identity of individual colonies (Ayre & Grosberg 1995), water flow (Genin et al. 1994), or size asymmetry of competing colonies (Rinkevich & Loya 1983). Colonies of some species attain dominance in intraspecific interactions by growing large (Rinkevich & Loya 1983). For example, the overgrowth of small colonies by large colonies may reflect the energetic cost of competition (Padilla et al. 1996), and the greater ability of large colonies to meet this cost (Rinkevich & Loya 1983, Padilla et al. 1996). The reduction in growth rates of competing colonies further suggests that competition is energetically costly (Rinkevich & Loya 1983, Padilla et al. 1996). Thus, assuming excess energy can be translocated across coral colonies, and used for competition (Oren et al. 1997), large colonies should win competitive encounters with smaller colonies (Rinkevich & Loya 1983, Padilla et al. 1996).

Most studies of coral competition have focused on adult colonies (>10 cm diameter; Lang 1973, Chornesky 1983, Rinkevich & Loya 1983) that, by definition, are sexually mature (Harrison & Wallace 1990). This is because adult corals typically are conspicuous members of the reef community, and fulfill a diversity of ecologically important functions (Buss & Jackson 1979). Few studies however, have focused on competitive interactions among small corals (most of which also are young; Bak & Engel 1979), despite strong evidence for aggregated settlement favoring competitive encounters in this size class (Morse et al. 1988, Smith 1997). Because small corals have important effects on coral demographics (Hughes & Jackson 1985, Bak & Meesters 1999), the paucity of information about competition among them makes it difficult to fully understand the biological processes affecting the population biology of corals (Hughes & Jackson 1985, Dunstan & Johnson 1998).

The ecological importance of competition (if any) among small corals will be accentuated under conditions favoring such encounters. One such scenario may occur on reefs with high coral cover and high recruitment, as in the tropical west Pacific (Sheppard 1980, Wallace 1985, Connell et al. 1997). Similar conditions could also occur when coral larvae settle adjacent to

one another in confined locations, such as cracks and crevices (Bak & Engel 1979, Morse et al. 1988, Smith 1997). Aggregated larval settlement (Lewis 1974, Goreau et al. 1981, Smith 1997) will further accentuate intraspecific encounters in such locations. The importance of aggregated settlement in promoting competition should increase in topographically complex communities (Carleton & Sammarco 1987), where spatial refuges and cryptic habitats are common (Menge 1976). Aggregated settlement is particularly common in corals with a brooding life history strategy, which often produce larvae with limited dispersal and a tendency for philopatric settlement (Carlson & Olson 1993). Once newly settled conspecifics encounter one another, two or more colonies will fuse (Hidaka 1985), or competition will result in a distinct winner and loser emerging (Lang & Chornesky 1990).

The brooding Caribbean coral *Agaricia* provides a tractable system to study competition among small corals. This is because *Agaricia* is one of the most common genera encountered during surveys of coral recruitment (Bak & Engel 1979, Hughes 1985, Smith 1997, Edmunds 2000, Hughes & Tanner 2000), and typically is aggregated in cryptic locations (Lewis 1974, Rogers et al. 1984, Smith 1997) where congeneric interactions are common. As a result, competition among *Agaricia* may have an important effect on the density and distribution of colonies, as well as possibly the genetic structure of adult populations. For example, competition among *Agaricia* at early life history stages could result in selection for competitively superior genotypes (Snell 1979, Yund 1991).

The purpose of this study was to determine the importance of competition among small (young) *Agaricia*, and to test one possible determinant of competitive outcome. *Agaricia* were not separated into *A. agaricites* and *A. humilis*, both of which are common in shallow water (Hughes 1985, Van Moorsel 1985, Hughes & Tanner 2000), because they have similar morphologies (especially when small) that cannot be distinguished reliably in the field (Van Moorsel 1983, 1985). An analysis at the genus level is unlikely to affect the outcome of this study, since only 2 species are involved, and both have comparable 'weedy' life history strategies (Hughes 1985, Hughes & Tanner 2000). Moreover, both species have similar mechanisms of interspecific aggression (i.e., sweeper tentacles), at least as adult colonies (Chornesky 1983, C. Zilberberg pers. obs.). To address the importance of competition among *Agaricia*, first we quantified the frequency of congeneric encounters as well as encounters with other taxa (benthic algae, scleractinians [other than *Agaricia*], and other invertebrates). Using the relative frequencies of encounters as a measure of importance, we determined whether competition among *Agaricia* was equally im-

portant for large and small colonies, and whether it was affected by the physical structure of the reef (i.e. topographic complexity). Second, to gain insights into possible mechanisms determining competitive outcome among *Agaricia*, we tested whether the outcome was related to the size asymmetry of competing colonies (i.e., the relative difference in sizes).

MATERIALS AND METHODS

Study sites. Competition among small *Agaricia* was studied on the south-facing, shallow (6 to 10 m depth) reefs of Great Lameshur Bay, St. John (US Virgin Islands), and at Dairy Bull reef on the north coast of Jamaica (2 km east of Discovery Bay). Maps of the study sites are provided in Edmunds (2000) and Edmunds & Carpenter (2001). All research was completed during 1998 and 1999, and surveys were carried out on 2 islands in order to strengthen the conclusions and their application to a larger spatial scale. The study reefs in St. John were located at Yawzi Point and Tektite cliffs (at 6 to 7 m depth), and had a high percentage cover of algal turf and macroalgae, and a low cover of scleractinian corals (Table 1). At the study location on Dairy Bull reef (8 to 10 m depth), the percent cover of algal turf and macroalgae also was high, but the scleractinian cover was 5-fold greater than in St. John (Table 1). Near-by reefs had <5% coral cover and, therefore, Dairy Bull was not typical of Jamaican reefs (Edmunds & Bruno 1996, Edmunds 2000, Edmunds & Carpenter 2001).

Frequency of congeneric interactions. The relative importance of competition among *Agaricia* was determined using transects ($N = 4$ to 6 site^{-1}) placed at random locations, parallel to the shore on reefs in St. John and Jamaica. All colonies (regardless of size) of *Agaricia* within 1 m of either side of the transect were scored for competitive interactions. Competing organisms were categorized as algae (including both macroalgae [>5 mm high] and algal turf [<5 mm high], sensu Steneck & Watling 1982), *Agaricia*, scleractinians (other than *Agaricia*), or other sessile invertebrates

(e.g., sponges, tunicates and bryozoans). Scleractinians and invertebrates were quantified as broad taxonomic groups to underscore differences between coral-coral and other types of competitive encounters. Interactions were defined as physical contact between the margins of *Agaricia* colonies and other taxa (sensu Lang & Chornesky 1990).

Interactions between *Agaricia* and algae only were scored when algae were the single source of contacts. When other taxa (i.e., not algae) also were in contact with *Agaricia*, then the other interaction was quantified. Although this approach has the potential to underestimate the frequency of interactions with algae, this bias was minimized by the occurrence of most *Agaricia* colonies within cracks and crevices where turf and macroalgal cover were minimal. Multiple contacts between *Agaricia* and taxa other than algae were infrequent in both St. John and Jamaica (C. Zilberberg pers. obs.) but, when observed, only the interaction with the longest perimeter of contact was scored.

To test the hypothesis that the frequency of congeneric competition in *Agaricia* varied with colony size, the number of congeneric interactions was compared among size classes. Sizes were assessed from the average of the maximum and minimum colony diameters, as determined with calipers (± 0.1 mm), and were pooled into 3 classes (≤ 4 cm, 4.1–10 cm and >10 cm diameter). These classes also separated young (≤ 4 cm) and adult (>10 cm, sexually mature) colonies (Van Moorsel 1983, 1985); the medium size class (4.1–10 cm) contained colonies of ambiguous sexual maturity (Van Moorsel 1983, 1985). Although size and age in corals are poorly related due to partial mortality and fission (Hughes & Jackson 1980), these factors rarely affect small corals that typically experience whole, rather than partial, mortality (Hughes & Jackson 1985). Fusion between colonies is another potential factor contributing to the poor relationship between size and age, although it is most likely to occur immediately after settlement and becomes less common as colonies increase in size (Frank et al. 1997). Assuming that partial mortality and fusion are uncommon for *Agaricia* colonies ≤ 4 cm diameter, then corals in this

size class are young (~ 2 to 3 yr old; Bak & Engel 1979, Van Moorsel 1983, Hughes & Jackson 1985), and of sexual origin. Small colonies with the fractured surfaces that are characteristic of asexual reproduction (Highsmith 1982, Edmunds 2000) were not found.

Preliminary surveys revealed that the frequency of competitive interactions among small *Agaricia* was highest in cracks and crevices, where small colonies of this genus were most abun-

Table 1. Percent cover (means \pm SE) of macroalgae, algal turf and scleractinians in St. John and Jamaica (at 6 to 10 m depth). Sample sizes in parentheses with quadrats as replicates, except for algal turf in St. John, where sites are replicates; algal turf and vacant hard substratum were combined in St. John. Data from published sources as follows: ^a = Edmunds & Bruno 1996, ^b = Edmunds 2000, ^c = Edmunds & Carpenter 2001

Sites	Macroalgae	Algal turf	Scleractinians
St. John	17.0 \pm 3.0 (17) ^b	69.9 \pm 4.9 (18) ^b	5.0 \pm 1.5 (17) ^b
Jamaica	40.0 \pm 15.0 (36) ^a	52.6 \pm 5.4 (20) ^c	23.0 \pm 20.0 (36) ^a

dant (C. Zilberberg pers. obs.). To address the possibility that increase in availability of cryptic habitats would enhance opportunities for competitive encounters, surveys were expanded at Dairy Bull (which has areas of high and low relief) to examine the relationships among cryptic habitats, the density of *Agaricia*, and the frequency of congeneric interactions.

To determine whether the frequency of competitive encounters was related to *Agaricia* density, 22 quadrats (0.25 m²) were placed randomly along 2 transects at Dairy Bull (10 m depth), and used to quantify small (≤ 4 cm) *Agaricia* and the number involved in congeneric competition. To determine whether the density of small *Agaricia* was related to availability of cryptic habitats, the topographic complexity (TC; Rogers et al. 1984) of the reef was measured. TC is a measure of rugosity, and here we assume that rugosity is positively correlated with the availability of cryptic microhabitats. TC was calculated by conforming a fine chain (with 15 mm links) to the reef within each quadrat, and dividing the length of the conformed chain by the width of the quadrat to provide a dimensionless index with a minimal value of 1 for a flat reef.

Relationship between colony size and competitive outcome. To determine whether the competitive outcome was associated with the relative size of the competing colonies, transects were placed parallel to shore at 6 to 10 m depth, and competing pairs of *Agaricia* were sampled for size and outcome (dominant or subordinate). The surveys were completed in Jamaica (4 transects) and St. John (6 transects), and the results pooled for statistical analysis. All pairs of colonies within 1 m of either side of the transects were surveyed, and only colonies ≤ 4 cm diameter were considered. Dominance was defined by overgrowth of the adjacent colony (the subordinate; Buss 1980) and the colony pair was excluded from the analysis if dominance could not be established by visual detection of colony overgrowth; a mean of $32 \pm 8\%$ (\pm SD, N = 2 islands) of the colony pairs were excluded for this reason. Colony size was calculated as the average of the maximum and minimum diameters as measured with calipers (± 0.1 mm). Thus, each pair of colonies generated 2 dependent measures of size and outcome. To obtain independent measurements, competitive outcome and size asymmetry was expressed relative to 1 colony of each pair that was selected at random. Size asymmetry was calculated by subtracting the size of the rejected colony from the size of the selected colony.

Statistics. A *G*-test of independence was used to determine whether the frequency of interactions with 4 categories of competing organisms (algae, *Agaricia*, other scleractinians, and invertebrates) was dependent on site. Where the frequency of interactions differed between sites, unplanned tests with selected subsets

of data were used to determine where the significant differences occurred (Sokal & Rohlf 1995). A *G*-test of independence was also used to compare frequencies of congeneric interactions among size classes and between sites.

Pearson correlations were used to examine the relationships between density of *Agaricia* and both frequency of competition and TC. A logistic regression (independent variable = size asymmetry; dependent variable = outcome [dominant or subordinate]) was used to test the null hypothesis that the outcome of congeneric competition was independent of size asymmetry.

All statistical analyses were completed using Systat 5.2 (SPSS corp., Chicago, IL) except for the logistic regression, that was completed using JMP 3.2.2 (SAS corp., Cary, NC), and unplanned comparisons of the significant *G*-tests of independence that were carried out using BIOM-pc (Exeter corp., Setauket, NY).

RESULTS

Frequency of congeneric interactions

Agaricia were conspicuous members of the shallow coral reefs in St. John and Jamaica, although densities differed markedly between sites. In St. John, the mean density of *Agaricia* colonies was 0.8 ± 1.2 m⁻² (\pm SE, N = 40, P. J. Edmunds unpubl. data), and in Jamaica it was 67.7 ± 6.1 m⁻² (\pm SE; N = 21; C. Zilberberg unpubl. data). However, the majority (>90%) were interacting with other taxa at both sites, and therefore large num-

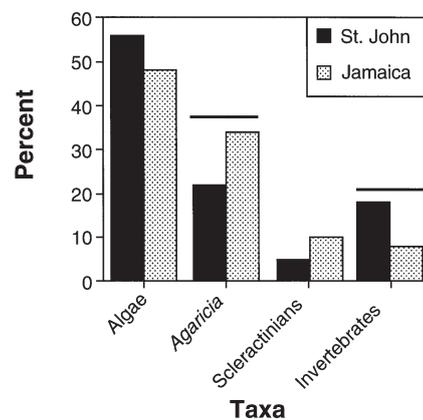


Fig. 1. Competitive interactions by taxon involving *Agaricia* in St. John (N = 360) and Jamaica (N = 402). Interactions are shown by taxon of competitor, and the values shown are the percentage of the total number of interactions. Horizontal bars indicate where unplanned comparisons demonstrated that significant differences occur (*G*-test, unplanned comparisons; $p \leq 0.05$)

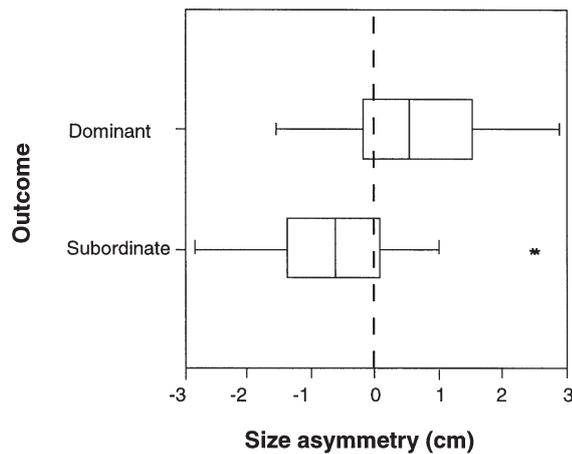


Fig. 5. Relationship between size asymmetry and the outcome of congeneric competition for small (≤ 4 cm) *Agaricia*, pooled between sites (St. John and Jamaica; $N = 36$). There was a significant (Logistic Regression; $\chi^2 = 12.46$, $df = 1$, $p \leq 0.001$) and positive relationship between size asymmetry and outcome, so that dominant colonies generally were larger than subordinate colonies. Box plot shows medians (middle vertical lines inside the interquartile range boxes), interquartile ranges (length of the boxes), the horizontal lines outside the interquartile boxes are observations within 1.5 interquartile ranges. * = observations that are more than $1.5 \times$ (interquartile range) from the median. Refer to text for further details

DISCUSSION

This study was carried out to determine the relative importance of competition among small *Agaricia*, and to document the role of colony size asymmetry in determining the outcome of congeneric competition. Colonies of *Agaricia*, regardless of size, were engaged in competition with congeners more often than any kind of interaction, other than with algae (macroalgae and algal turf combined). This relationship was found in St. John and Jamaica, suggesting that it is common in at least 2 locations in the Caribbean which differ in densities of *Agaricia*. In addition, congeneric competition was more common among the smallest (≤ 4 cm diameter) size class of *Agaricia*, particularly in areas of high topographic complexity where algal turf was minimal and small *Agaricia* were abundant. Although, the density of *Agaricia* was almost 84-fold higher in Jamaica than in St. John, the frequency of congeneric interactions among small *Agaricia* was similar in both places, probably because small *Agaricia* were aggregated in cryptic microhabitats regardless of location. These results underscore the potentially important synergism between biological events (e.g., aggregated settlement; Goreau et al. 1981, Carlon & Olson 1993) and physical factors (e.g., topographic complexity;

Carleton & Sammarco 1987) in intensifying competition among young *Agaricia*. The positive relationship between size asymmetry and competitive outcome for small *Agaricia* agrees with previous studies with bryozoans (Buss 1980, Padilla et al. 1996) and at least one other scleractinian (*Stylophora pistillata*, Rinkevich & Loya 1983). It is likely that this result (that large size is associated with competitive dominance) has general application to other sessile, colonial taxa in the marine environment.

Competitive interactions among colonies of *Agaricia* were relatively more frequent in small compared to large colonies. Although this effect was large (Fig. 2), it was not significant in the G -test of independence because an intrinsic hypothesis was used to generate expected values (sensu Sokal & Rohlf 1995) that were similar between sites and among size classes. One reason for the high frequency of congeneric encounters among small (≤ 4 cm diameter) compared to large (> 4 cm diameter) *Agaricia*, may be a change in the biological factors affecting colonies as they grow. For instance, congeneric competition might be replaced by interspecific competition (Lang & Chornesky 1990) as colonies become larger and grow out of the cryptic habitats where the larvae prefer to settle (Carlon & Olson 1993). In such cryptic locations, the densities of small *Agaricia* can be very high (Lewis 1974, Smith 1997, this study), and the resulting acute space limitation promotes congeneric encounters. Topographically complex reefs have more spatial refuges for *Agaricia* larvae to settle in (Carleton & Sammarco 1987), and this, in turn, facilitates congeneric interactions. Not all scleractinians display aggregated settlement, but there are other conspicuous examples of this strategy, including *Favia fragum* and *Porites porites*, in the Caribbean (Goreau et al. 1981, Carlon & Olson 1993), and *Goniastrea aspera* and *Pocillopora damicornis* in the Pacific (Birkeland et al. 1981, Babcock 1984). For these, and other scleractinians that display aggregated settlement, intraspecific competition at early life history stages may be an important factor affecting population structure (Sammarco 1980, Hughes 1985). There is growing recognition of the importance to coral demographics of understanding the sources of mortality among newly recruiting corals (Hughes & Tanner 2000), and here we show that congeneric competition at early life history stages may be one such factor.

The density of small *Agaricia* increases with topographic complexity on a reef at Dairy Bull, Jamaica, and this increases the number of encounters among small colonies. Such encounters likely develop into competitive interactions, since overgrowth (a common outcome of competition, Buss 1980) was widespread, and fusion was rare ($< 0.5\%$ of such encounters).

Fusion among conspecifics occurs in many colonial organisms, including corals (Hidaka 1985), hydroids (Shenk & Buss 1991) and colonial ascidians (Sabbadin & Astorri 1988). However, the ability to fuse can vary with age in hydroids (Shenk & Buss 1991) and scleractinians (Hidaka 1985, Frank et al. 1997), with the highest potential for fusion occurring immediately after settlement (Shenk & Buss 1991, Frank et al. 1997). Newly settled *Agaricia* (i.e., spat) were not included in the present analysis as it is impossible to resolve such small objects (ca <2 mm diameter) by eye in the field. Thus, it is possible that fusion occurs among *Agaricia* spat, but further research will be required to evaluate the likelihood of such events. Based on the low rates of fusion we observed among *Agaricia*, together with the lack of evidence of fusion among *A. humilis* (Raimondi & Morse 2000), it is likely that fusion does not result in a biologically significant loss of colonies in this genus. Regardless of the possibilities for fusion, the present results demonstrate that congeneric competition has a strong potential to affect the density of small *Agaricia*.

To understand how (if at all) congeneric competition influences the population structure of *Agaricia*, it is important to know how a colony becomes dominant (as opposed to subordinate). This is because subordination can lead to partial mortality (Buss 1986) and increased susceptibility to further injuries and death (Hughes 1984). This, in turn, can affect population structure by decreasing the number of colonies attaining size-dependent sexual maturity (Hughes & Jackson 1985). Two possible factors determining competitive outcome may be: (1) the availability of energy and the ability to allocate it towards competition (Oren et al. 1997), and (2) limited regenerative capabilities in colonies with large lesions relative to their small size (Rinkevich 1996). The energy hypothesis assumes that the mechanisms of competition (e.g., sweeper tentacles and nematocysts) are energetically costly to produce, that energy is a limiting resource, and that energy resources can be translocated across a competing colony. The limited regeneration hypothesis assumes that stem cells, which play a role in tissue regeneration, can be a limited resource in anthozoans (Rinkevich 1996). If correct, then the importance of stem cell limitation will be inversely related to colony size, because small colonies have less tissue to support the repair of lesions. The assumptions of the energy hypothesis hold true for several organisms (Miles et al. 1995, Oren et al. 1997), but they have yet to be addressed for *Agaricia*. Conversely, there are no experimental tests of stem cell limitation of regeneration in anthozoans. Before further research is completed to determine which hypothesis best accounts for the present results (i.e.,

Fig. 5), manipulative experiments first are required to establish a cause-and-effect relationship between colony size and competitive outcome. The mensurative experiments employed in the present study cannot be used to infer a cause-and-effect relationship (sensu Buss 1990) and, indeed, several alternative hypotheses could account for our results. For example, colony size may be a consequence of congeneric competition (rather than a determinant of outcome), with larger size occurring after dominance is achieved. Dominance itself might be determined by factors other than size at first encounter, including angle of contact between competing colonies (Buss 1981, Romano 1990), ambient flow conditions (Genin et al. 1994), or random factors (e.g., storms or predation; Connell 1978, Hughes 1989) coincident with the contact between colonies.

Although further research is required, we believe that disparities in growth rate—interpreted broadly to include mass deposition, linear extension and skeletal morphology—provide the most parsimonious explanation for competitive outcomes between *Agaricia* colonies. All aspects of coral growth show a high degree of intraspecific variation (Harrison & Wallace 1990, Hall & Hughes 1996, Bruno & Edmunds 1997), and rapid growth and directional change can provide powerful mechanisms of competitive dominance, at least in adult corals (Romano 1990). Thus, it is likely that small colonies of *Agaricia* that have intrinsically fast growth, or enhanced ability to change morphology, may be able to overgrow (i.e., out compete) colonies with slower growth and/or reduced ability for morphological change. Preliminary experiments support the role of rapid linear growth in determining competitive dominance among small *Agaricia* (Zilberberg 2001).

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