

Interactions in the canopy among Caribbean reef octocorals

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ABSTRACT: The incidence of octocoral–octocoral interactions and the physical effects of the interactions were determined in surveys of 29 branching octocoral species at 2 sites in St. John, U.S. Virgin Islands. Close proximity, defined as the bases or branches of octocorals being within 5 cm of each other, creates the potential for direct competitive interactions. Cases of close proximity were common (63 and 34% of the colonies at the 2 sites), and were more abundant at the site with higher colony density and proportionately more colonies with tall, highly branched morphologies. Damaged branches associated with neighboring colonies were found in 19% of the colonies in close proximity. *Eunicea flexuosa* colonies exhibited less damage than the 5 most common species it interacted with (*Antillogorgia americana*, *Eunicea mammosa*, *Gorgonia ventalina*, *Pseudoplexaura crucis*, and *Pseudoplexaura wagneri*). Of the colonies in close proximity, 23% featured asymmetric colony forms, representing the effects of competition through the preemption of canopy space. *G. ventalina* had the highest incidence of asymmetry. Nearest-neighbor analyses detected a weak but significant signal of competition in the combined sizes of neighboring colonies. Competition among octocorals in the canopy probably has limited effects on their spatial distribution, but tissue damage and altered colony form could affect growth and fitness.

KEY WORDS: Gorgonian · Preemption · Coral reef · Interference competition · Canopy · Animal forest · Colony morphology

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INTRODUCTION

The role of competition on coral reefs has been one of the central themes in reef ecology over the past 50 yr (Chadwick & Morrow 2011, and references therein), and competition for space is well documented for scleractinian corals (Lang 1973, Romano 1990, Rinkevich & Sakai 2001) and among cryptic encrusting species (Jackson & Buss 1975, Buss & Jackson 1979). Similarly, the competitive interactions of scleractinian corals with macroalgae and sponges have been, and continue to be, the focus of many studies (cf. Tanner 1995, Aerts 1998, Vermeij 2006, Box & Mumby 2007). However, the processes and extent of competition among other macrobenthos are less

often studied. The paucity of research on other taxa reflects the difficulties in species level identifications and in characterizing abundances among arborescent species, where most of the 'space' used by colonies is in the canopy and not on the substratum. Competition in these 'animal forests' (sensu Rossi et al. 2012) can occur through competition for space on the substratum at the time of settlement, and then among colonies that form the canopy. Competition in the canopy can take the form of exploitative competition for resources in the water column (cf. Kim & Lasker 1997), direct interference through the abrasion of branches, the use of sweeper tentacles (Sebens & Miles 1988), allelochemicals (Sammarco et al. 1983, Griffith 1997), exploitation of the physical

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space, i.e. preemption, or more dramatically as occurs when structural parasites such as *Millepora* spp. (Wahle 1980) and sponges (McLean & Yoshioka 2007, McLean et al. 2015) overgrow octocoral colonies.

A better understanding of competition among reef macroinvertebrates, such as octocorals, is especially important, as anthropogenic effects in concert with natural events such as hurricanes have led to marked declines in Caribbean scleractinian abundance (Gardner et al. 2003, Jackson et al. 2014) and have opened up space for colonization by other taxa (Hughes 1994). Thus, benthic organisms, such as macroalgae, octocorals, ascidians, zoanthids and corallimorpharians may benefit from the loss of scleractinians by increasing in abundance on coral reefs (Norstrom et al. 2009, Chadwick & Morrow 2011). Octocorals appear to be better equipped to tolerate aspects of climate change and human disturbances than scleractinians (Lasker et al. 1984, Lang et al. 1992, Lasker 2003, Inoue et al. 2013, Gabay et al. 2014, Torres et al. 2001), and 2 studies have reported an increased abundance of octocorals on Caribbean reefs in Florida and the U.S. Virgin Islands (Ruzicka et al. 2013, Lenz et al. 2015).

If octocorals increase in abundance on coral reefs, competition for space among octocorals will presumably also increase, and differences in the competitive abilities of different species may be important in structuring reef communities dominated by octocorals. Competition for space plays an important role in determining species abundance, individual size, distribution patterns and biodiversity on coral reefs (Bak & Engel 1979, Aerts 1998, Vermeij 2006, Box & Mumby 2007). The potential importance of direct competitive interactions among Caribbean octocorals is suggested by the surveys of Wahle (1985), in which he found a high incidence of damage to colonies, some of which was likely due to abrasion with adjacent octocorals. Tissue damage results from physical contact between branches of adjacent colonies, causing erosion of tissue in areas of contact. Injury from contact between octocorals can be the direct effect of the mechanical contact and may also be generated by nematocysts or allelochemicals. Sweeper tentacles have been observed in one species in the Caribbean (Sebens & Miles 1988). Allelochemical interactions have not been reported among Caribbean octocorals but are known from Indo-Pacific species (Sammarco et al. 1983, Griffith 1997). Tissue damage can reduce fitness by removing reproductive polyps (Wahle 1985), by causing colonies to reallocate energy to healing, thus reducing the

energy available for processes such as growth (Bak 1983, Meesters et al. 1994, Lirman 2000) and reproduction (Van Veghel & Bak 1994, Zakai et al. 2000, Page & Lasker 2012, Tsounis et al. 2012), and by promoting overgrowth by competitors (Wahle 1980, 1985, McLean & Yoshioka 2007). The presence of adjacent colonies may also alter patterns of colony growth, a process analogous to that observed in forest canopies (Schröter et al. 2012). An adjacent colony that has preempted space in the canopy may prevent the development of a typical, symmetric form, generating colonies that are smaller than symmetric colonies of similar age, presumably reducing productivity, growth and reproduction.

The objective of this study was to investigate the incidence and effects of competitive interactions among all octocoral species in the canopy at sites on St. John, U.S. Virgin Islands. The amount of space in the canopy occupied by an octocoral colony and the potential for interaction with neighboring colonies is directly related to population density and to colony size, morphology and flexibility. The incidence of colonies in close proximity to each other was determined as a measure of potential colony–colony interaction, and species-specific physical effects of competition, i.e. tissue damage and the development of asymmetric colony forms, were explored by examining their incidence in the field and from more detailed surveys of interactions involving *Eunicea flexuosa* for studies of tissue damage and *Gorgonia ventalina* for studies of colony asymmetry. Nearest-neighbor analyses were applied to characterize the spatial distribution of colonies, since nonrandom spacing may indicate the presence of interference competition.

MATERIALS AND METHODS

We looked for interactions among colonies in the canopy in surveys of branching octocorals on the south shore of St. John, U.S. Virgin Islands, within the Virgin Islands National Park. Observations were made in July and August 2014 and February and March 2015 at Europa Bay (18° 19.003' N, 064° 43.796' W) and East Cabritte (18° 18.551' N, 064° 43.129' W). Both sites were between 7 and 10 m deep. The reefs in this area have been monitored for >25 yr and have experienced an increase in abundance of some octocorals (Colvard & Edmunds 2011, Lenz et al. 2015), while scleractinian corals have decreased in coral cover in some habitats (Edmunds 2002, Rogers & Muller 2012).

Colony–colony interactions

Octocoral colonies at East Cabritte and Europa Bay were surveyed to assess the spatial distribution and, in particular, the incidence of colonies in close proximity to each other. At each site, five 10 m × 1 m parallel belt transects were set up perpendicular to shore at 10 m intervals starting at an arbitrarily selected point. *Erythropodium caribaeorum* and the encrusting form of *Briareum asbestinum* were not included in the surveys because they are not branching and, therefore, do not compete for space in the canopy. Each octocoral ≥5 cm in height was identified to species level in the field when possible; otherwise a small, 3 cm long sample was collected from colonies ≥15 cm tall for sclerite examination under a microscope. Images of the colony and a close-up image of the collected branch were also obtained. Identifications were based on Bayer (1961) and Sánchez (2009).

Colonies were divided into 2 classes, those in close proximity to a neighbor, cases in which a colony's branches or base were within 5 cm of another octocoral colony, and those more distantly spaced. When the branches of 2 colonies are <5 cm apart, branch movement driven by currents and wave action often leads to contacts between the branches. Large colonies whose bases are within 5 cm of each other almost always have branches within 5 cm of each other, and small colonies with bases <5 cm apart at the time of settlement will almost inevitably come into contact with each other as they grow in the canopy. We recorded all instances of interactions. We did not distinguish between inter-specific and intra-specific interactions since our goal was to first determine the overall incidence of competition among branching octocorals at the 2 sites.

At East Cabritte, which had a greater density of octocorals than Europa Bay, 4 randomly selected 1 × 1 m² quadrats on each transect were surveyed while all 10 quadrats on each transect were surveyed at Europa Bay. The height of each colony was measured to the nearest centimeter. Each colony was assessed for proximity to adjacent colonies and for effects of proximity, tissue damage to branches in close proximity to an adjacent colony and/or an asymmetric colony form. Only the octocorals with an asymmetric colony form attributable to the presence of another octocoral were scored as asymmetric in this study. Colonies that were asymmetric as a result of growing adjacent to a physical obstruction were not included as our focus was on the incidence of competition among octocorals. Examples of the different effects are shown in Fig. 1.

The data from the surveys were analyzed using hierarchical log-linear tests in SPSS (Version 22) to investigate the relationship of colony proximity with colony height (height classes of 5–19 cm, 20–29 cm, 30–39 cm and ≥40 cm), octocoral genus and site. The proximity data were analyzed with respect to octocoral genus instead of species due to the low numbers of colonies in any one species. The 4-way analysis could not be undertaken due to a large number of expected values below 5, and the data were analyzed using three 3-way log-linear analyses. (The 4-way analysis yielded similar results, Table S1 in the Supplement at www.int-res.com/articles/suppl/m546p085_supp.pdf).

Nearest-neighbor analyses

To further examine the spatial distribution of colonies and potential competition among them, nearest-neighbor data were collected along the belt transects from each site. Each transect had 20 sampling points arranged at the corners of every 1 m² quadrat along the first 9 m of each transect. The octocoral colony closest to each sampling point was selected, identified, and the distance between its base and the base of its nearest branching octocoral neighbor was measured to the nearest centimeter (Fig. S1 in the Supplement). The height, width and length of each colony was measured to the nearest centimeter to calculate cross sectional area (height × length) and volume (height × width × length), and the proximity of the colony's branches to nearby octocorals was also noted. Due to the water flow and the resulting oscillation of colony branches, measurements were made when the branches were vertical in the water column to optimize the precision of our measurements. To increase sample sizes, an additional 9 m transect parallel to the other 5 was sampled at each site.

The nature of the spatial distribution of octocorals at each site was determined from the nearest-neighbor data following Clark & Evans (1954). Observed and expected mean distances between the octocoral neighbors were calculated using the total distance between neighbors, sample size (120 pairs of octocorals per site) and the density of octocorals at each site (calculated from the belt transect data). The ratio (R) of the observed and expected (given a randomly distributed octocoral community) mean distances between octocoral neighbors describes the octocoral distribution at each site, where $R = 1$ denotes a random distribution, $R < 1$, an aggregated distribution,

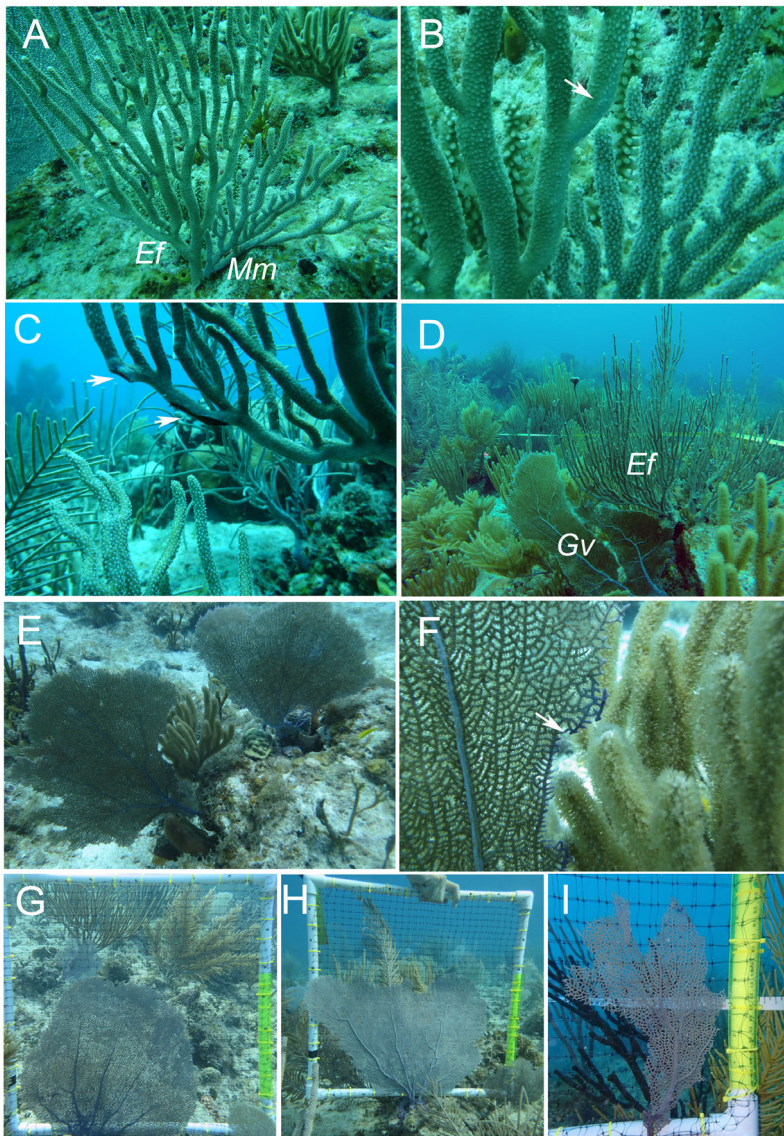


Fig. 1. Octocoral colony interactions. (A) *Muricea muricata* (*Mm*) exhibiting asymmetric growth around an *Eunicea flexuosa* (*Ef*) colony. (B) Close-up of Panel A showing first-degree damage to the *E. flexuosa* colony (arrow). (C) Second-degree damage (arrows) to *Eunicea flexuosa* in close proximity to *Muricea* sp. (D) Asymmetric growth of *Gorgonia ventalina* (*Gv*) around an *E. flexuosa* colony. (E) Asymmetric colony of *G. ventalina* adjacent to an unidentified plexaurid. Note symmetric *G. ventalina* in the background. (F) Close up of Panel E showing that the asymmetric form of the *G. ventalina* colony was caused by damage and loss of *G. ventalina* branches. Arrow points to one instance in which anastomosing branches appear to have been lost. (G) Symmetric colony. (H, I) *G. ventalina* colonies exhibiting increasing levels of asymmetry

and $R > 1$, a uniform distribution (Clark & Evans 1954). The significance of R was determined by analyzing the standard variate of the normal curve (c), since the measured distances between neighbors in a randomly dispersed community are expected to follow a normal distribution.

The effects of colony–colony proximity on colony size were assessed by correlating the distance between neighbors at the base with the sum of their sizes (Pielou 1962). If competition affects growth, then the closer the organisms are, the smaller their expected sizes will be (Pielou 1962). Implicit in these analyses is the notion that size is both an indicator of resource use and of success in acquiring resources.

The relationships among the distance between octocoral neighbors at the base (divided into 3 distance groups to make the data categorical: 5–14 cm, 15–24 cm and 25–34 cm), branch proximity and site were analyzed using a hierarchical log-linear test in SPSS. The relationship between the distance between neighbors and branch proximity was further analyzed in a separate log-linear test in SPSS.

Eunicea flexuosa interactions

Since physical effects of octocoral–octocoral proximity were common, we examined the physical effects on different species by comparing their interspecific interactions with 75 colonies of *E. flexuosa*. The choice of *E. flexuosa* was based on its abundance and on the reliability of identifying *E. flexuosa* colonies in the field. We sampled at East Cabritte, as the high octocoral density there led to a high incidence of interactions. We searched for *E. flexuosa* within the same 500 m² area as the belt transects and selected colonies based on the presence of interspecific interactions. Tissue damage due to proximity between octocorals was categorized into first- and second-degree damage. First-degree damage was defined as slight signs of abrasion including fewer polyps or retracted polyps in contact areas and lightly eroded calyces, whereas second-degree damage involved the erosion of the soft tissue past the surface layer, sometimes down to the proteinaceous skeleton. If an octocoral had branches exhibiting both first- and second-degree damage, it was scored as having the

more severe, second-degree damage. Colonies in close proximity were identified to species and were assessed for damage and asymmetry. Fisher's exact tests of independence were used in R to test for the effect of the species pairing on damage type and the presence or absence of colony asymmetry.

Gorgonia ventalina asymmetry

While colony asymmetry was observed in many species, the planar form of *G. ventalina* was particularly conducive to quantifying colony size and asymmetry. The surface areas of both symmetric and asymmetric *G. ventalina* colonies were measured to evaluate the extent of asymmetry. We did not distinguish between intra- and inter-specific competitive interactions with asymmetric *G. ventalina* since our goal was to compare the sizes of asymmetric and symmetric colonies.

We sampled at Europa Bay, where similar numbers of symmetric and asymmetric *G. ventalina* colonies were found. We searched for *G. ventalina* within the same 500 m² area as the belt transects, and we selected colonies based on their health (colonies overgrown with algae or hydrocorals were excluded from the study), size class (15–24 cm, 25–34 cm and 35–44 cm tall) and the presence or absence of asymmetry, since we wanted similar numbers of colonies in each category. A total of 142 *G. ventalina* colonies (78 symmetric and 64 asymmetric) were photographed. Each image included a 1 m² quadrat and a ruler. The Perspective Tool in the program GIMP (Version 2.8) was used to correct parallax in the images, and ImageJ (Version 1.48, NIH) was then used to measure the height and surface area of the colonies. The surface areas of symmetric and asymmetric colonies were tested for normality using a Shapiro-Wilk normality test and for equal variances using a Levene Test (analyses were performed using R software). Areas were square root transformed to meet the assumptions of the analysis of covariance (ANCOVA) to test if the linear regressions of the surface areas and heights of symmetric and asymmetric colonies were different.

RESULTS

Colony–colony interactions

A total of 29 species were identified on the belt transects in St. John (Table S2 in the Supplement). The most common species at East Cabritte were

Antillogorgia americana, *Eunicea flexuosa* and *Plexaura homomalla* forma *kükenthali*, and at Europa Bay they were *A. americana*, *E. flexuosa*, *Muriceopsis flavida* and *Plexaurella dichotoma*. The mean density \pm SE of octocorals at East Cabritte was 17.0 ± 0.9 octocorals m⁻², and the mean density at Europa Bay was 8.3 ± 0.6 octocorals m⁻². A total of 326 of the 856 octocoral colonies present on the belt transects at East Cabritte and all 423 colonies at Europa Bay were assessed for close proximity to any other octocoral, abrasive damage and asymmetry. At East Cabritte, 40% of the octocorals had branches within 5 cm of another octocoral and 23% had bases within 5 cm of another octocoral. At Europa Bay, 14% of the octocorals had branches within 5 cm of another octocoral and 20% had bases within 5 cm of another octocoral. Of the octocorals in close proximity at East Cabritte, 24% exhibited asymmetric colony form and 24% exhibited tissue damage from contact. At Europa Bay, 21% were asymmetric and 10% had tissue damage from contact. In combination, 41% of the colonies in close proximity to another octocoral and 19% of all of the colonies exhibited octocoral-induced damage and/or colony growth asymmetry.

The log-linear analysis testing the relationships between site, genus and height class indicated significant relationships between each pair of factors (see details below). The composition of the octocoral communities at East Cabritte and Europa Bay (Fig. 2) was significantly different (site by genus; partial chi-squared = 208.404, df = 8, $p < 0.001$). Parameter estimates in the log-linear analysis (Table S3 in the Supplement) indicated that *Antillogorgia*, *Eunicea*, *Plexaura* and *Pseudoplexaura* colonies had significantly higher relative abundances at East Cabritte than at Europa Bay, while Europa Bay contained significantly higher relative abundances of *Muriceopsis*

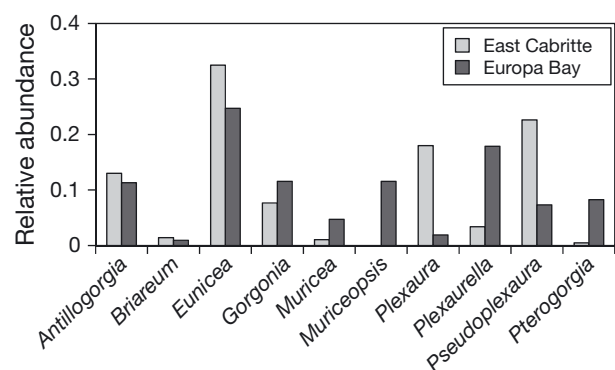


Fig. 2. The relative abundance of octocoral genera at East Cabritte and Europa Bay. A total of 862 colonies were surveyed at East Cabritte, and 425 at Europa Bay

and *Plexaurella* colonies. *Gorgonia*, *Muricea* and *Pterogorgia* colonies were not different in relative abundance between the 2 sites. The 3-way interaction was not significant (likelihood ratio chi-squared = 17.441, df = 24, p = 0.829).

Colony heights differed between genera (genus by height class; partial chi-squared = 122.305, df = 24, p < 0.001) and between sites (site by height class; partial chi-squared = 41.269, df = 3, p < 0.001). *Antillogorgia* and *Pseudoplexaura* colonies were rarely in the 5–19 cm and 20–29 cm height class, respectively, and *Pterogorgia* colonies were often in the 20–29 cm height class (Table S3). *Antillogorgia*, *Pseudoplexaura*, *Eunicea* and *Gorgonia* colonies were in the ≥40 cm height class more frequently than the other genera. East Cabritte had fewer colonies in the 5–19 cm height class and more colonies in the ≥40 cm height class than Europa Bay (Table S3).

The analyses examining the relationship between the potential for colony–colony interaction, i.e. proximity, with genus and height class, and between proximity, genus and site identified significant relationships between each pair of factors. Interactions in the 2 analyses were not significant (likelihood ratio chi-squared = 28.860, df = 24, p = 0.225; likelihood ratio chi-squared = 5.576, df = 8, p = 0.695). However, the 2-way partial associations in the analyses indicate that the likelihood of colonies being in close proximity varied with colony height, genus and between sites. Octocoral proximity was related to the site (proximity by site; partial chi-squared = 45.307, df = 1, p < 0.001), height (proximity by height class; partial chi-squared = 17.985, df = 3, p < 0.001) and genus (proximity by genus; partial chi-squared = 55.772, df = 8, p < 0.001). East Cabritte had significantly greater proportions of octocorals in close proximity than did Europa Bay (Table S4 in the Supplement). Height also affected proximity, and colonies in the 5–19 cm height class were rarely within 5 cm of another colony compared to the other height classes (Table S5 in the Supplement). The genus also played a role, since *Plexaurella* colonies rarely were in close proximity, while *Pseudoplexaura* colonies frequently were (Table S5).

The analysis of the number of colonies in close proximity for each genus was different when the sites were analyzed separately, even though there was no significant 3-way interaction between proximity, genus and site (likelihood ratio chi-squared = 5.576, df = 8, p = 0.695). Most of the genera at East Cabritte had many cases of close proximity (Fig. 3A). *Plexaurella* spp. had a significantly lower incidence of being in close proximity than did the other genera (Table S6

in the Supplement). At Europa Bay, octocorals were less commonly in close proximity (Fig. 3B). *Muriceopsis* colonies were in close proximity more frequently than were the other genera, while *Muricea* and *Plexaurella* colonies had fewer cases of close proximity (Table S7 in the Supplement).

Nearest-neighbor analyses

The spatial distribution of octocorals at each site was characterized following the methodology of Clark & Evans (1954) to test the deviation from a random distribution. The octocorals at East Cabritte were randomly distributed ($R = 1.05$, $c = 1.14$), while those at Europa Bay were more uniformly distributed ($R = 1.25$, $c = 5.23$).

The influence of octocoral proximity on size was investigated since a positive correlation between them can provide evidence of competition (Pielou 1962). Height, area and volume were all used as measures of size. All 3 indices produced similar results with respect to significant correlations. Therefore, only the results of height are reported. The correlation between nearest-neighbor distance and total height, $r = 0.309$, was small but significant ($t = 5.01$,

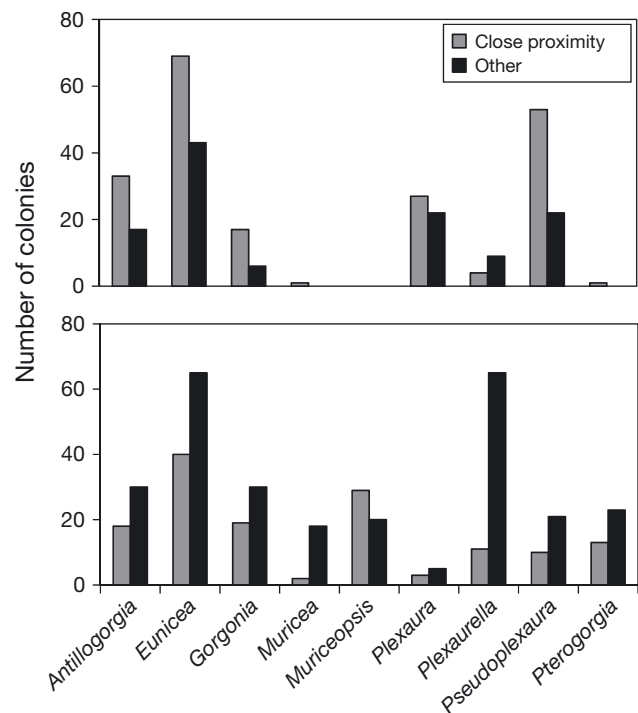


Fig. 3. Abundance of genera at East Cabritte (upper) and Europa Bay (lower), differentiating colonies in close proximity from more distantly spaced colonies

$p < 0.001$), indicating that octocorals closer together were smaller than those further apart (Fig. 4).

The log-linear analysis testing the presence of relationships among the site, distance between neighboring octocorals and incidence of close proximity between branches detected relationships between the site and branch proximity (partial chi-squared = 35.318, $df = 1$, $p < 0.001$) and between the site and the distance between octocoral neighbors (partial chi-squared = 12.833, $df = 2$, $p = 0.002$). The analysis did not find a significant relationship between the distance between colonies and the incidence of branches in close proximity (partial chi-squared = 1.410, $df = 2$, $p = 0.494$) or a 3-way relationship between the site, distance between octocorals and proximity between branches (likelihood ratio chi-squared = 3.775, $df = 4$, $p = 0.437$). However, the distance between neighboring octocorals did have a significant effect on the potential for interaction between their branches when analyzed separately (likelihood ratio chi-squared = 9.673, $df = 2$, $p = 0.008$), indicating that octocorals whose bases were in the 5–14 cm distance group had more instances of close proximity between branches than did those in the 25–34 cm distance group (Fig. 5, Table S8 in the Supplement).

Eunicea flexuosa interactions

The outcome of interactions for space in the canopy between *E. flexuosa* and other species were asymmetric. *E. flexuosa* had significantly less tissue damage than the species it interacted with (Fig. 6; Fisher's exact test, $p = 0.008$), and there was no significant difference in the degree of damage received among the 5 most common species (*Antillologorgia*

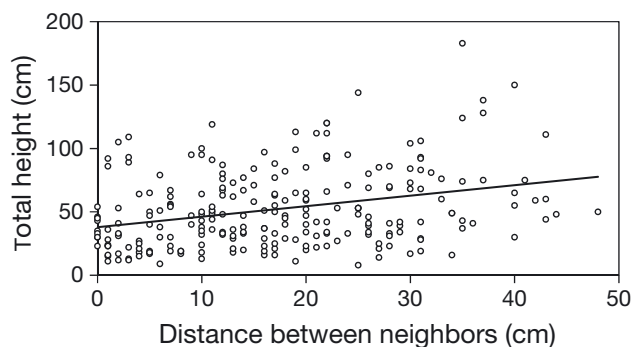


Fig. 4. Summed colony heights as a function of nearest-neighbor distance for octocorals at East Cabritte and Europa Bay. Line represents the significant linear regression ($R^2 = 0.095$, $t = 5.01$, $p < 0.001$)

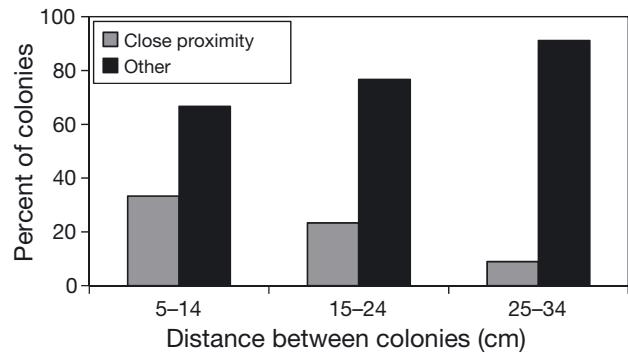


Fig. 5. The percentage of octocorals with canopies in close proximity or ≥ 5 cm apart as a function of distance between colony bases. Sample sizes for the 3 size classes were 63, 60 and 45, in order of increasing distance between colony bases

americana, *Eunicea mammosa*, *Gorgonia ventalina*, *Pseudoplexaura crucis* and *Pseudoplexaura wageanaari*) found interacting with *E. flexuosa* (Fisher's exact test, $p = 0.141$). *E. flexuosa* colonies were also asymmetric less frequently than the species they interacted with (Fig. 7; Fisher's exact test, $p < 0.001$), and *G. ventalina* colonies were more frequently asymmetric than the other 4 most common species (Fisher's exact test, $p = 0.004$).

Gorgonia ventalina asymmetry

The surface areas of symmetric and asymmetric *G. ventalina* colonies were compared to evaluate the effects of asymmetry caused by interactions. The square-root-transformed areas of symmetric and asymmetric *G. ventalina* colonies were normally dis-

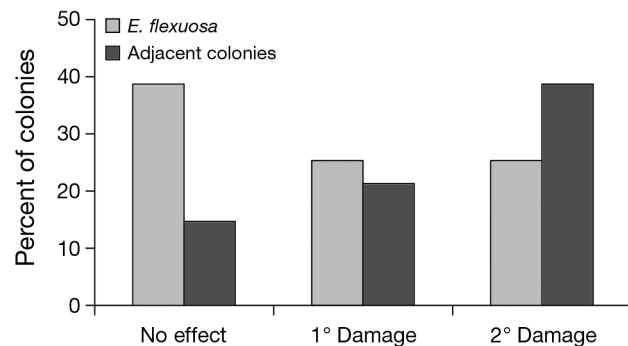


Fig. 6. Prevalence of tissue damage among *Eunicea flexuosa* ($n = 67$) and adjacent colonies ($n = 56$) that were within 5 cm of each other. Adjacent colonies represent a mix of 17 species. 1° and 2° = first and second degree damage, respectively (see 'Materials and methods — *Eunicea flexuosa* interactions')

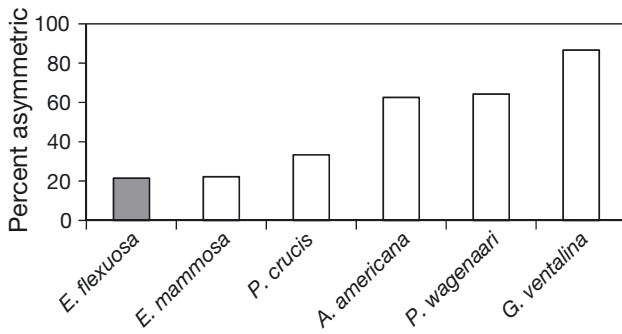


Fig. 7. Percentages of colonies in close proximity to *Eunicea flexuosa* that exhibited asymmetric form at East Cabritte. Sample sizes: *E. flexuosa*, 75; *Eunicea mammosa*, 9; *Pseudoplexaura crucis*, 6; *Antillogorgia americana*, 8; *Pseudoplexaura wagenara*, 14; *Gorgonia ventalina*, 15. Open bars: the most common colonies interacting with *E. flexuosa*

tributed (Shapiro-Wilk normality test, $p = 0.066$, $p = 0.075$, respectively) and had equal variances (Levene's test, $p = 0.751$). Since the residuals of the general linear model were not normally distributed (Shapiro-Wilk normality test, $p = 0.009$), the effect of asymmetry on surface area was analyzed using a nonparametric alternative to ANCOVA (analysis was performed using R software, vegan package, adonis command). Asymmetric *G. ventalina* colonies had smaller surface areas than symmetric colonies of similar height (Fig. 8), indicating *G. ventalina* surface area was significantly affected by the presence of asymmetry ($F = 35.490$, $p < 0.001$).

DISCUSSION

The high density of branching octocorals at many sites in the Caribbean (Ruzicka et al. 2013, Jackson et al. 2014, Lenz et al. 2015) offers ample opportunity

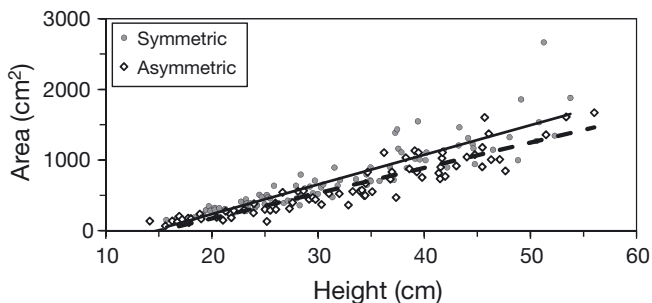


Fig. 8. Colony size (area) as a function of height among *G. ventalina* colonies with symmetric and asymmetric form. Linear regressions: solid line: symmetric colonies; dashed line: asymmetric colonies

for interactions between octocoral colonies that can affect colony size and mortality. This study has focused on the colony-level effects of direct interference and preemption of space in the canopy in octocoral–octocoral interactions.

Interactions between colonies were common at the 2 sites on St. John, but the incidence of interactions differed between sites. The density of colonies, colony size and colony form all affected the incidence of competitive interactions. The most notable difference between the 2 sites was the density of octocoral colonies. Not surprisingly, the denser community had smaller distances between neighboring colonies, resulting in more instances of close proximity and more cases of tissue damage (Fig. 5, Table S4 in the Supplement). This is similar to the patterns observed by Wahle (1985) in Jamaica where locations with denser octocoral communities had higher frequencies of damage. On St. John, community composition also influenced the incidence of colonies in close proximity due to species-specific differences in colony form, flexibility and height. The species that were common at East Cabritte, *Antillogorgia* and *Pseudoplexaura* spp., are tall with long, highly flexible branches and were frequently in close proximity to other octocorals. In contrast to East Cabritte, the species common at Europa Bay, *Plexaurella* and *Pterogorgia* spp. (Fig. 2, Tables S2, S4 & S6) have rigid branches, and the colonies are less profusely branched than species such as *Antillogorgia* spp. These species occupy a smaller amount of space in the canopy and are less likely to be in close proximity to other colonies regardless of the octocoral density (Fig. 3, Tables S6 & S7).

Tissue damage should affect octocoral fitness since it reduces the number of polyps available for gathering resources and reproducing (Wahle 1985). At the least, damaged colonies invest resources to replace lost tissues which would otherwise be available for growth and reproduction. Such effects have been reported for scleractinians in competitive interactions (Tanner 1997, Lapid & Chadwick 2006), as well as colonies recovering from other damage (Meesters et al. 1994, Oren et al. 1997, Lirman 2000). Severe damage may also increase the risk of infection by diseases (Bak & Criens 1981, Rogers et al. 1988) and the settlement of algae and invertebrate epibionts on the axial skeleton (Lang da Silveira & van't Hof 1977).

Asymmetry in the form of colonies can also reduce overall colony size, as apparent in the 2-dimensional form of *Gorgonia ventalina* (Figs. 1 & 7). In some cases, asymmetric colony form was also associated with tissue damage and, in extreme cases, appeared

to have been generated by tissue damage, but more commonly asymmetric growth had the effect of reducing contact between colonies and thus reducing direct damage, a pattern commonly observed in forests (Valladares & Niinemets 2007, Schröter et al. 2012, Longuetaud et al. 2013). Colony growth among branching octocorals can be viewed as the net effect of the extension of branches and the generation of new branches (Lasker & Sanchez 2002). Not all branches give rise to new branches; thus, growth of colonies is a function of the number of branches actively producing new branches (Lasker et al. 2003). Asymmetric growth can lead to fewer dividing branches, producing smaller colonies than would symmetric colonies of the same height. Even if there is no visible interaction between 2 colonies, asymmetric growth forms can be considered an effect of the preemption of space by one of the competitors or as an opportunity cost of growing next to a competitor.

The physical effects of inter-specific interference competition between *Eunicea flexuosa* and the other octocorals suggest that the competitive effects are not symmetric. *E. flexuosa* colonies were less commonly affected by tissue damage and were less likely to be asymmetric than were the other octocoral species (Figs. 6 & 7). The rough surface created by the dense surface rind of sclerites on *E. flexuosa* branches in combination with rigid branches probably helps protect *E. flexuosa* from abrasion while also damaging other octocorals. The 5 most common species interacting with *E. flexuosa* did not differ in the frequency of damage, but that result may reflect the small sample sizes for individual species. *G. ventalina* was more affected by asymmetry than the other species (Fig. 6), which may be the result of an unintentional bias since asymmetry was most noticeable in *G. ventalina* due to its 2-dimensional colony form. A much larger data set would be needed to determine if there is a competitive hierarchy among octocorals, as observed in scleractinians (Lang 1973, Abelson & Loya 1999, Rinkevich & Sakai 2001).

Effects to individual colonies might also generate community level effects in the abundance and spatial distribution of different species. In addition to the direct interactions reported here, resource competition between octocorals for particulates in the water column and for light may occur, and Kim & Lasker (1997) were able to detect reductions in growth of branches placed in close proximity. However, the nearest-neighbor and spatial distribution data suggest that when considered across colonies of different species and ages, the effects of competitive interactions are at best small. A weak signal of com-

petition was detected when correlating the distance between octocoral neighbors with their summed heights (Fig. 4). However, strong competition would be expected to generate uniform spatial distributions, and the presence of randomly distributed colonies at East Cabritte, the site with the greater incidence of interactions, suggests that competitive interactions were not a key factor driving a community's spatial structure. The apparent absence of competitive effects among naturally occurring colonies is consistent with the manipulative experiment of Birkeland (1974) in which an 83% reduction in density of *G. ventalina* at a site in Panama did not produce an increase in growth rates over the following 230 d; he concluded that mortality due to wave action had a far greater role in population dynamics at that site. Yoshioka & Yoshioka (1989) concluded that the availability of substratum that is suitable for recruitment and recruit survival, rather than the intensity of competition, has the greatest effect on octocoral distributions at sites in Puerto Rico.

In conclusion, octocoral–octocoral interactions and their physical effects should be common on many Caribbean coral reefs and will become more common and important if octocoral abundances increase. The potential for interactions was relatively high on shallow reefs in St. John, and, as also reported from Jamaica (Wahle 1985), was more frequently observed when octocorals were present in high density and among species whose colonies occupied large volumes in the canopy through their branching morphology, flexibility and height. At the colony level, competition for space in the canopy caused damage and/or restricted size, which likely reduces fitness. As these effects vary between species, it is likely that they play a role in determining local fitness and abundance. At the community level, nearest-neighbor analyses detected a weak but significant pattern consistent with the effects of competition, but the spatial pattern of colonies on the reef is likely to result from a combination of factors, and competition may play a smaller role than factors such as the distribution of suitable substrata for settlement.

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