

Interactions among Florida sponges. I. Reef habitats

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ABSTRACT: Spatial interference competition is well described for many sessile marine invertebrates, but few studies have addressed interactions between neighboring sponges. We conducted transect surveys to assess interspecific interactions among sponges in coral reef habitats in Key Largo, Florida, USA. In total, 15 transect sites were surveyed at 5 reef locations with mean densities ranging from 13.0 ± 3.6 to 33.3 ± 5.9 sponges m^{-2} . The most abundant of over 43 sponge species observed were *Amphimedon compressa*, *Aplysina cauliformis*, *Aplysina insularis*, and *Niphates erecta*, while the least abundant were *Hippospongia lachne*, *Ircinia campana*, and *Pseudaxinella lunaecharta*. A nearest-neighbor technique was used to determine the degree and frequency of interactions between randomly selected sponge pairs. Overall, 40.4% of sponges occurred alone, 31.0% in proximity to, and 28.6% in contact with other sponge species. Among sponges in contact interactions, 18.7% were epibionts, 19.4% were basibionts, and a relationship could not be resolved for the remainder. Statistical analyses of the frequencies of each interaction category revealed that the ability to overgrow or resist overgrowth varied among species. For example, *Aka coralliphagum*, *Ectyoplasia ferox*, and *Phorbis amaranthus* occurred alone in >60% of their interactions and were never overgrown by other species with which they came into contact. In contrast, *Agelas schmidtii*, *Ircinia felix*, *Dysidea janiae*, and *Scopalina ruetzleri* occurred alone in <30% of their interactions, with the first 2 species overgrown by, and the latter 2 overgrowing, most other species with which they came in contact. All contact interactions were further statistically examined, and 41 interspecific sponge pairs revealed significant overgrowth ability by 1 of the interacting species. While the overgrowth ability of a species is dependent on sponge morphology, the ability to resist overgrowth is associated with the production of allelochemicals.

KEY WORDS: Coral reef · Interspecific interactions · Nearest-neighbor · Overgrowth · Sponges · Allelopathy

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INTRODUCTION

Competitive interactions among sessile marine invertebrates have been studied extensively in many hard-substratum environments such as rocky shores (e.g. Connell 1961, Dayton 1971, Sebens 1986) and coral reefs (e.g. Jackson 1977, Suchanek et al. 1983). In these habitats, space is thought to be the most important limiting resource, and spatial interference competition often results in the overgrowth of one species by another (Stebbing 1973, Quinn 1982,

Rubin 1985). On coral reefs, sponges are commonly described as competitively dominant over other sessile invertebrates in their ability to overgrow or resist overgrowth by neighboring organisms including bryozoans and corals (Jackson & Buss 1975, Aerts 1998, Hill 1998). While competitive interactions among corals (Lang 1971, 1973, Sammarco et al. 1983, 1985, La Barre et al. 1986) and bryozoans (Buss 1979, Rubin 1985, Lopez Gappa 1989, Barnes & Dick 2000) are well documented, relatively few studies have addressed spatial interference interactions among

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sponges (Rützler 1970, Sará 1970, Pansini & Pronzato 1990, Wulff 1997).

Sponges are abundant and diverse members of benthic communities in coral reef habitats (Reiswig 1973, Rützler 1986, Diaz & Rützler 2001, Alcolado et al. 2004). Despite their sessile lifestyle and a soft, fleshy tissue that lacks physical protection from predation (Chanas & Pawlik 1995, 1996, Pawlik et al. 1995, Pawlik 1997), sponges are often found thriving on coral reefs that are characterized by high predation pressure (Huston 1985, Dunlap & Pawlik 1996, 1998) and intense spatial interference competition (Jackson & Buss 1975, Suchanek et al. 1983). While sponge–coral interactions are important to the community structure of Indo-Pacific reefs where coral cover is high (De Voogd et al. 2004), Caribbean reefs are dominated by sponges which attain much greater biomass per unit surface area than other sessile invertebrates (Reiswig 1973), and surpass corals in diversity and abundance (Suchanek et al. 1983, Targett & Schmahl 1984, Diaz & Rützler 2001, Alcolado et al. 2004). Further, studies have demonstrated that sponges are competitively dominant in interference interactions with corals (Suchanek et al. 1983, Porter & Targett 1988, Vicente 1991). In Guam, nearly 1 km of coral reef was covered by a species of the genus *Terpios* (Bryan 1973). A long-term study investigating the competitive abilities of organisms settling on artificial substrata revealed that sponges rank superior to most other marine invertebrates such as bryozoans, barnacles, polychaetes, tubicolous amphipods, and hydroids (Russ 1982). Considering the well-recognized dominance of sponges over other sessile marine organisms, it is surprising that only a handful of studies have examined interspecific overgrowth interactions among sponges (Rützler 1970, Sará 1970, Pansini & Pronzato 1990, Wulff 1997).

Interspecific sponge interactions are difficult to assess because it is often not clear whether interacting individuals are competing or mutualistic. Sponges have been described as competing for available substrata (Hartman 1957, Rützler 1965); however, tissue necrosis or mortality is rarely observed among overgrown individuals, suggesting mutualistic associations (Rützler 1970, Sará 1970). Further, some sponges can undergo specialized tissue adaptations to allow overgrowth by epibiotic species (Rützler 1970). Consequently, dense and diverse sponge populations are often vertically stratified and can remain stable over long periods of time (Sará 1970, Pansini & Pronzato 1990). Mutualistic relationships have also been described among branching sponges (Wulff 1997). While these studies focused on mutualistic sponge associations, little is known about the extent to which competitive interactions shape the community structure of sponges on coral reefs.

The purpose of this study was to investigate spatial interference interactions among sponge species in coral reef habitats of the Florida Keys, USA. Transect surveys were conducted to determine local sponge demographics and examine interspecific interactions. In addition, a nearest-neighbor technique was used to assess the degree of interaction among individual sponge species and their ability to overgrow or resist overgrowth by neighboring sponges. Frequencies of observed sponge interactions were analyzed statistically and comparisons made among overgrowth ability, sponge morphology, and the allelopathic effects of sponge extracts (Engel & Pawlik 2000).

MATERIALS AND METHODS

Study areas and sponge identification. Interspecific sponge interactions were examined on different coral reef habitats in Key Largo, Florida (Fig. 1a). Fifteen transect sites were established on the following 5 reefs, listed from north to south: 4 sites at North Dry Rocks (25° 07.85' N, 80° 17.52' W); 3 sites at Dixie Shoal

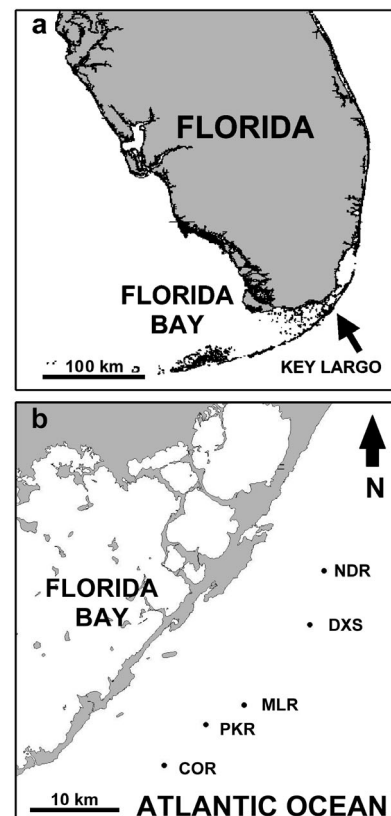


Fig. 1. Map of (a) Southern Florida indicating the location of Key Largo and (b) Key Largo indicating the location of the following 5 study locations: NDR = North Dry Rocks, DXS = Dixie Shoal, MLR = Molasses Reef, PKR = Pickles Reef, COR = Conch Reef

(25° 04.66' N, 80° 18.74' W); 3 sites at Molasses Reef (25° 01.02' N, 80° 22.53' W); 2 sites at Pickles Reef (24° 59.07' N, 80° 24.97' W); 3 sites at Conch Reef (24° 57.01' N, 80° 27.25' W) (Fig. 1b). Individual sites within a given reef location were variable with regard to water flow, temperature fluctuation, and light exposure. In addition to analyzing data for all reef sites, location-dependent factors were taken into consideration by analyzing data grouped by reef location.

The sponge communities at all reef locations are similar to those found throughout the Caribbean and contain most of the same species (Reiswig 1973, Alvarez et al. 1991, Diaz et al. 1991, Schmahl 1991, Van Soest 1994, Alcolado et al. 2004). All sponge individuals were identified by spicule and tissue preparations based on the available literature (DeLaubenfels 1936, Wiedenmayer 1977, Rützler 1986, Zea 1987, Hopper & Van Soest 2002). Conforming to most previous assessments of sponge communities (references above), this study quantified sponge number rather than biomass or substratum coverage. As defined by Hartman & Reiswig (1973), a sponge individual is contained within continuous tissue connected by an unbroken surface pinacoderm. Attached multiple lobes, tubes, or branches were considered part of the same individual.

Transects and nearest-neighbor analysis. Belt transects were conducted to determine the abundance and diversity of sponge species and examine interspecific interactions at different coral reef locations. Each transect was established by attaching a 10 m line, marked at 1 m intervals, to a randomly chosen point and stretching it parallel to the isobath of a chosen depth. A quadrat (1 m²) was placed directly over the transect line, with 2 opposing edges centered and perpendicular to the transect line. The quadrat was moved along the 1 m interval marks of the transect line 10 times, covering a total of 10 m². Three 10 m² transects were performed at each site, resulting in a total survey area of 30 m² of benthos at each transect site.

In each quadrat, the total number of sponge individuals was recorded and each identified to species level. These data were used to determine species abundance and diversity at each of the 5 reef locations. In addition, a nearest-neighbor technique was used to assess the degree of interactions between randomly chosen sponge pairs (Brower et al. 1997). Focal sponges were randomly selected by dropping 4 plastic markers into the quadrat, and choosing the closest sponge to each marker. The nearest-neighbor of each focal sponge was identified and the distance between the 2 individuals measured. Distance measurements were conducted along the shortest line connecting the proximal edges of 2 neighboring sponge individuals. This procedure was repeated 4 times, making certain that neither

the focal nor the nearest-neighbor sponges were selected twice for either category.

Observations of interacting sponge pairs were limited to those with a maximum distance of 5 cm between them. This limit was assigned under the assumption that the only interaction mechanism in non-contact encounters is the release of water-soluble allelochemicals with a maximum effective range of 5 cm. This assumption is supported by Turon et al. (1996), who found that a strong non-random pattern of negative sponge associations diminished with increasing distance and was absent beyond 5 cm from the edge of the interacting sponge species. In addition, studies investigating interactions among corals and between sponges and corals have indicated that non-contact interactions may have an interactive range of up to 5 cm (Richardson et al. 1979, Sheppard 1981, Aerts & Van Soest 1997, Aerts 1998). Given the above, we defined the following 3 categories of interactions:

Alone: includes encounters in which the focal sponge is found without a neighboring sponge growing within a 5 cm radial margin around its edge (distance to nearest-neighbor > 5 cm).

Proximate: includes encounters in which the focal sponge is found next to a neighboring sponge within its 5 cm radial margin but does not come in direct contact with it.

Contact: includes encounters in which the focal sponge is in direct contact with its neighboring sponge (distance to nearest-neighbor = 0 cm).

Statistical analyses were conducted on data for sponge species that occurred 5 or more times. A chi-square goodness of fit test ($\chi^2 \times 5.991$, $df = 2$, $p < 0.05$) was used to assess differences in frequencies between the above interaction categories for each sponge species. The null hypothesis (H_0) tested assumed equal distribution of individuals occurring alone, in proximate, and contact interactions. Rejecting the H_0 led to further investigations to examine species aggregation patterns (Zar 1996).

All contact interactions were subject to further analysis. In each case the sponge individuals encountered in a contact interaction were classified into 1 of 3 categories defined by the following 3 possible outcomes:

Over: includes encounters in which the focal sponge occurs as the epibiont, overgrowing an individual of another species.

Under: includes encounters in which the focal sponge occurs as the basibiont, being overgrown by an individual of another species.

Equal: includes contact interactions in which the degree of overgrowth is not sufficient to distinguish between epi- and basibionts. Both interacting sponge individuals are classified as equal.

Pairs of sponge species observed in 5 or more contact interactions were chosen for statistical analysis. The overgrowth ability of each sponge species was examined by calculating the average overgrowth rate from the observed frequencies of each contact category. This method was adapted from Russ (1982), who assigned points to interacting individuals to determine the competitive dominance of different marine invertebrates. For each observed contact interaction, 2 points were assigned to the overgrowing sponge and 0 points to the species being overgrown. For each observed 'equal' interaction, 1 point was given to both individuals. A chi-square goodness of fit test ($\chi^2 \times 3.841$, $df = 1$, $p < 0.05$) was conducted on the sums of these points as the observed values, and the total number of interactions (n) was used as the expected value for both species. The H_0 tested was that there was no difference in the overgrowth ability of the 2 interacting species. If the H_0 was rejected, the species with the higher overgrowth rate was regarded to be more likely to overgrow the other species and considered epibiotic.

The extent of the overgrowth of each sponge species observed in contact interactions was determined by calculating a species-specific overgrowth index using the results from the sponge pair analysis. The overgrowth index was calculated by subtracting the number of basibiotic interactions from the number of epibiotic interactions, and dividing by the total number of statistically tested pair interactions. This overgrowth index ranged from 1 to -1, indicating a species that is always overgrowing other sponges to a species that is always being overgrown by other sponges, respectively.

RESULTS

Sponge species abundance and diversity

Overall, 9984 sponge individuals comprising 43 species were recorded at all reef locations (Table 1). Species richness was highest at Molasses Reef (41 species),

Table 1. Sponge abundance and diversity indices for all reef locations. Species with less than 5 individuals were not included. S = species richness, n = total number of individuals, I_s = Simpson's dominance, D_s = Simpson's diversity, E_s = evenness, NDR = North Dry Rocks, Dixie Shoal, MLR = Molasses Reef, PKR = Pickles Reef, COR = Conch Reef

	Overall	NDR	DXS	MLR	PKR	CON
S	43	35	31	41	31	40
n	9984	3273	1144	2491	925	2085
I_s	0.057	0.079	0.062	0.056	0.092	0.055
D_s	0.943	0.922	0.939	0.944	0.908	0.945
E_s	0.966	0.948	0.969	0.967	0.938	0.969

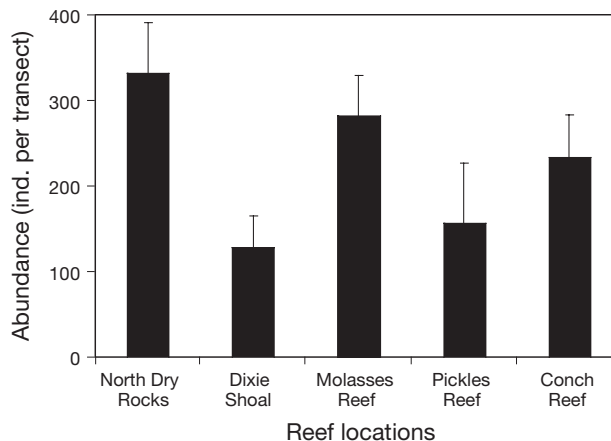


Fig. 2. Number of sponge individuals (mean + SD) per transect for each reef location

and lowest at Dixie Shoal and Pickles Reef (31 species) (Table 1). Sponge abundance was greatest at North Dry Rocks with a total of 3273 sponges averaging 332.9 ± 59.0 ind. transect⁻¹, followed by Molasses Reef ($2491; 283.8 \pm 46.8$), Conch Reef ($2085; 234.9 \pm 50.2$), Dixie Shoal ($1144; 129.8 \pm 36.3$), and Pickles Reef ($925; 158.2 \pm 70.6$) (Fig. 2, Table 1). Simpson's diversity indices indicated high species diversity at all reef locations, with the sponge community at Conch Reef being the most diverse and that of Pickles Reef the least diverse (Table 1). Morisita's indices revealed some differences in the sponge communities at each reef location, with the communities at Conch Reef and Molasses Reef being most similar, and those at Dixie Shoal and Pickles Reef most different (Table 2).

The most abundant sponge species were *Amphimedon compressa* and *Niphates erecta*, with over 1000 total individuals averaging over 200 individuals at each reef location (Fig. 3). The sponges *Aplysina cauliformis*, *Aplysina insularis*, and *Scopalina ruetzleri* were also relatively abundant, with over 500 total individuals averaging over 100 individuals at each reef location (Fig. 3). Third most abundant were *Agelas schmidtii*, *Callyspongia vaginalis*, *Ectyoplasia ferox*, *Iotrochota birotulata*, *Monanchora arbuscula*, and *Niphates digitalis*, with over 300 total individuals averag-

Table 2. Morisita's index of community similarity between each reef location based on Simpson's dominance (I_s) (Table 1); see Table 1 for reef abbreviations

Reef	NDR	DXS	MLR	PKR
COR	0.753	0.816	0.942	0.656
PKR	0.917	0.638	0.757	
MLR	0.891	0.769		
DXS	0.641			

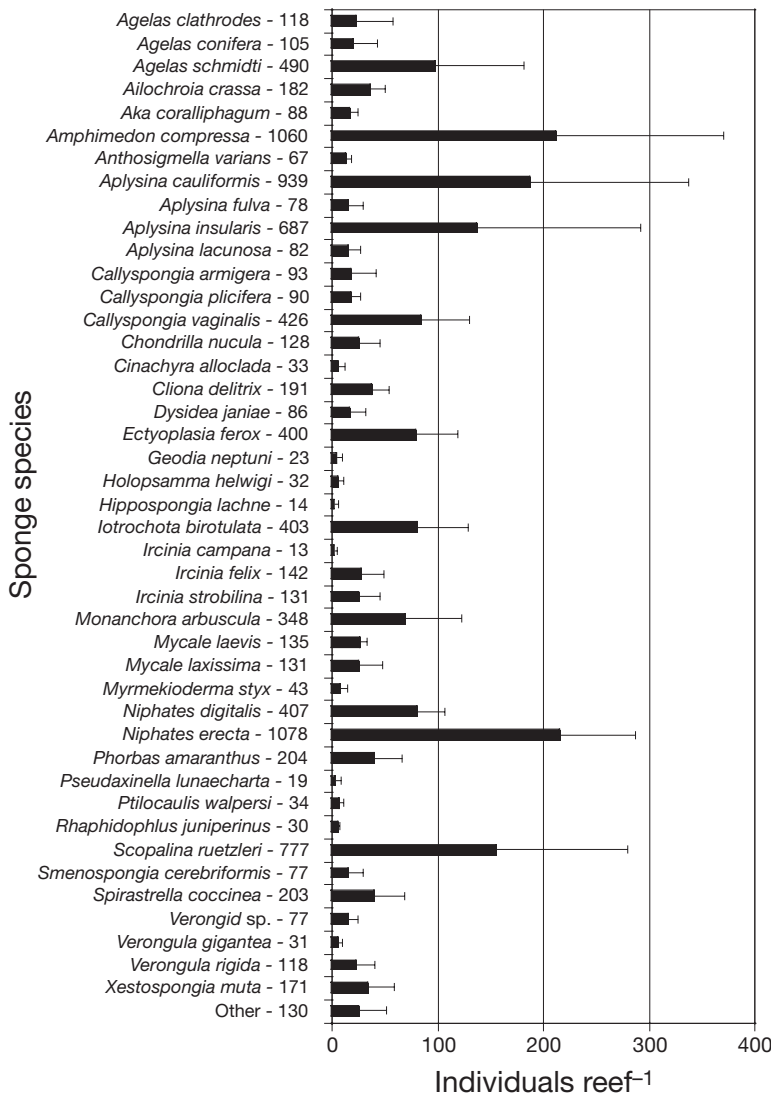


Fig. 3. Number of sponge individuals (mean + SD) per reef location for 43 most abundant species. Total number of individuals for each species is given next to the species name. 'Other' includes species with <5 ind.

ing over 50 individuals at each reef location (Fig. 3). The least abundant sponges were *Hippospongia lachne*, *Ircinia campana*, and *Pseudaxinella lunaecharta*, with less than 20 total individuals and only present at some but not all reef locations (Fig. 3).

Interactions among sponge species

Interspecific sponge interactions were examined with the nearest-neighbor data from a total of 5289 focal sponges recorded at all transect sites. Overall, 40.4% of focal sponges occurred alone, 31.0% in proximal, and 28.6% in contact interactions (Fig. 4a). The frequencies of these 3 interaction categories varied

considerably among sponge species. The following species occurred alone more frequently than in proximity to or in contact with other sponge species: *Aka coralliphagum*, *Anthosigmella varians*, *Aplysina insularis*, *Aplysina lacunosa*, *Cliona delitrix*, *Ectyoplasia ferox*, *Monanchora arbuscula*, *Mycale laevis*, *Phorbas amaranthus*, *Ptilocaulis walpersi*, *Rhaphidophylus juniperinus*, *Spirastrella coccinea*, and an unknown species of the genus *Verongula* (Fig. 4a). *Amphimedon compressa* and *Dysidea janiae* occurred most frequently in proximal interactions, and *Agelas schmidti*, *Callyspongia armigera*, *Iotrochota birotulata*, and *Scopalina ruetzleri* were observed more frequently in contact interactions than in proximal interactions or alone (Fig. 4a).

Among all 1512 sponge individuals observed in contact interactions, 61.9% occurred in 'equal' interactions, while only 18.7% were encountered as epibionts and 19.4% as basibionts to other sponge species (Fig. 4b). Overall, 86% of all species encountered in contact interactions occurred more frequently in 'equal' interactions than in those resulting in overgrowth (Fig. 4b). Because of the high frequency of 'equal' interactions between most sponges, the average overgrowth ability for each of the 29 species encountered in contact interactions was examined by conducting a chi-square goodness of fit test on assigned points ($\chi^2 \times 3.841$, $df = 1$, $p < 0.05$). While *Dysidea janiae* and *Scopalina ruetzleri* overgrew other species most frequently, *Agelas schmidti* and *Ircinia felix* were overgrown by other species most frequently (Fig. 4b).

Given that the percentages of each category are derived from the total number of observations, they can be regarded as the average frequencies for each interaction category. Most sponge species displayed frequencies close to the average frequencies of each category (Fig. 5). However, a few species displayed frequencies well above or below the average frequency of a given category. For example, *Aka coralliphagum*, *Cliona delitrix*, *Mycale laevis*, and *Ectyoplasia ferox* occurred alone in >65% and in contact in <10%, of all interactions (Figs. 4a & 5b). In contrast, *Agelas schmidti*, *Callyspongia armigera*, and *Iotrochota birotulata* occurred alone in <25% and in contact in >55% of all interactions (Figs. 4a & 5a). Among those species encountered in contact interactions,

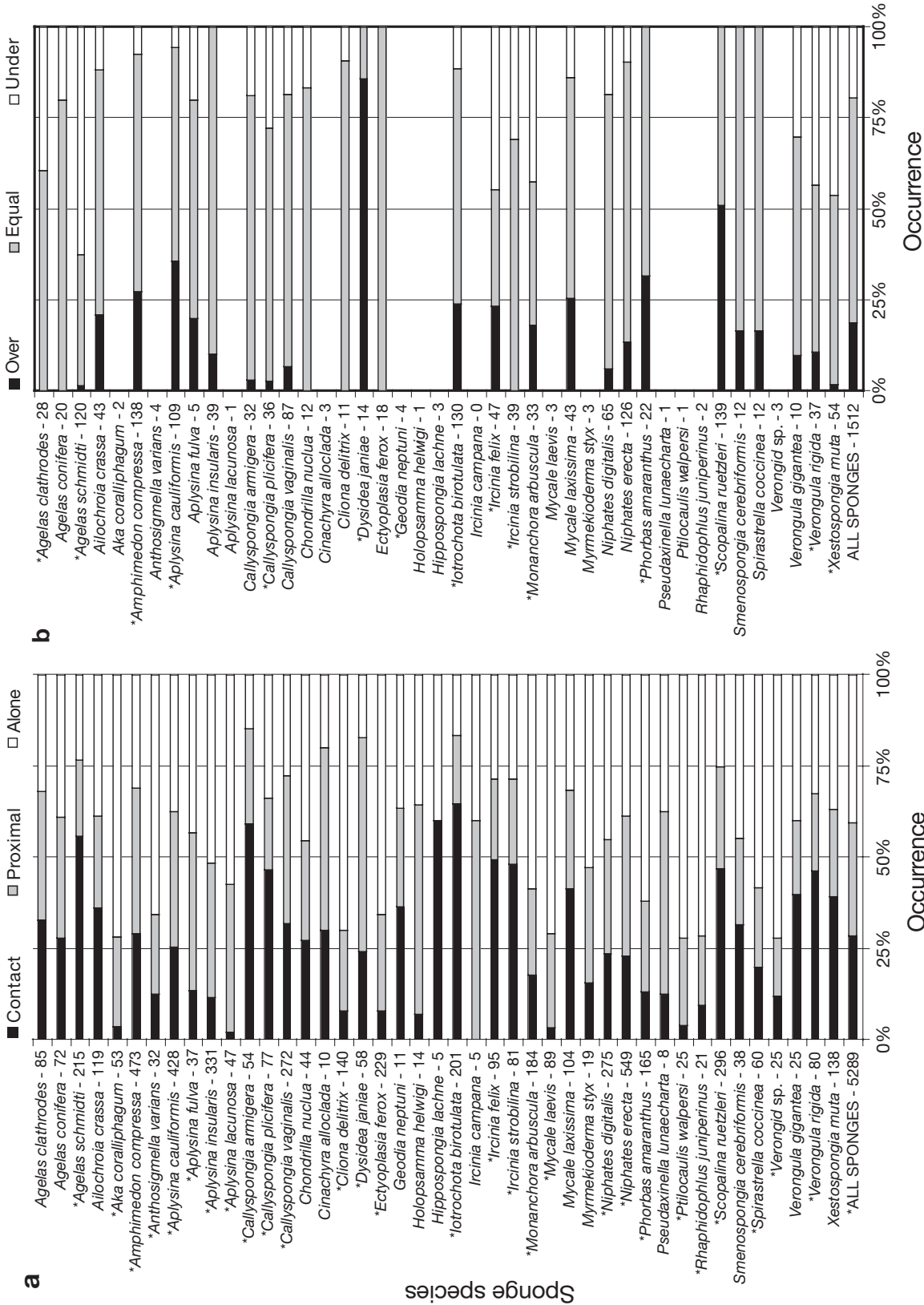


Fig. 4. Percentage occurrence of (a) contact, proximal, and no interactions (Alone) and (b) each contact category (Over, Equal, Under) for all sponges and individual species. Total number of individuals is given next to the species name. *: significant results from the chi-square goodness of fit test (a) with H_0 of equal frequency and (b) conducted on assigned points with H_0 of no difference in overgrowth ability

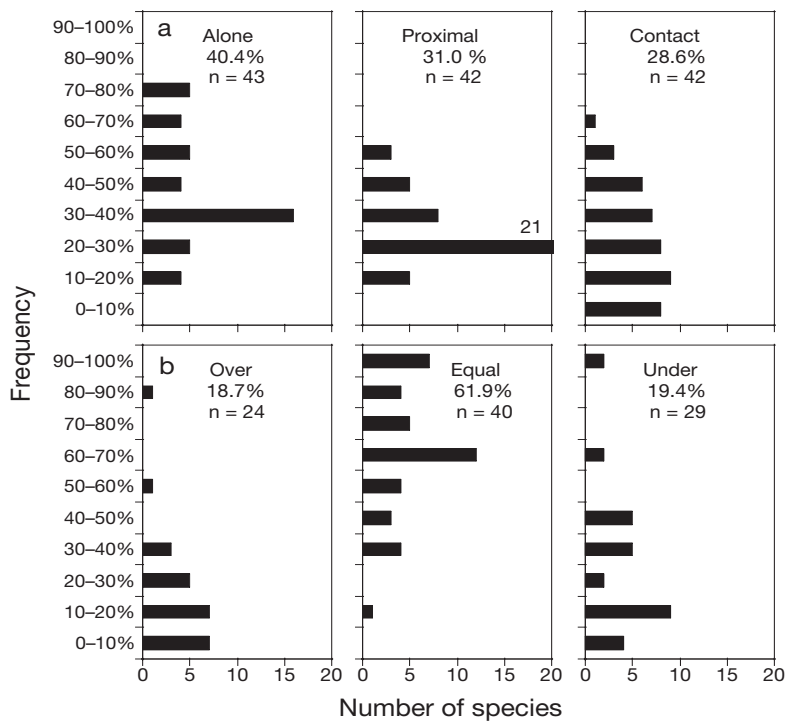


Fig. 5. (a) Frequencies of each interaction category and (b) each contact category displayed by the number of reef species encountered in each category. Frequency data were pooled in increments of 10%. Overall percentage occurrence and total number of species (n) for each category is given

Dysidea janiae overgrew other species in >85%, while *Agelas schmidti* was overgrown by other species in >50% of all contact interactions (Figs. 4b & 5b).

The overgrowth ability for the 21 most abundant species occurring in contact interactions was further examined by statistically analyzing the frequencies of contact categories between each species pair. The chi-square test results for each interacting sponge pair are presented in a matrix of interspecific contact interactions along with the calculated overgrowth index for each species (Fig. 6). *Dysidea janiae*, *Phorbos amaranthus*, and *Scopalina ruetzleri* were the only species with an overgrowth index of 0.5 or greater because they were rarely overgrown and frequently overgrew species with which they came into contact (Fig. 6). *Ailochroia crassa* was also rarely overgrown; however, its overgrowth index of 0.4 reflects a relative increase in 'equal' interactions (Fig. 6). Positive overgrowth indices were also observed for *Amphimedon compressa*, *Aplysina cauliformis*, *Iotrochota birotulata*, and *Niphates erecta* (Fig. 6). *Mycale laxissima* was the only species with an overgrowth index of 0 because it was equally likely to overgrow and be overgrown by other sponge species (Fig. 6). The remaining sponge species surveyed in this study had negative overgrowth indices because they were most frequently overgrown

by sponges with which they came into contact (Fig. 6).

All sponge species were grouped into 7 categories defined by distinct morphological growth characteristics (Jackson 1979, Boury-Esnault & Rützler 1997) (Table 3). Overall, 39.5% of all species were lobate, 20.9% were branching, 11.6% were encrusting, 9.3% were globular, 7% were tubular, 7% were barrel shaped, and 4.7% were turbinata (Table 3). The average overgrowth index of each species in each category was used to assess the overgrowth ability of each morphological growth form (Fig. 7). The only encrusting sponge observed in contact interactions was *Scopalina ruetzleri*, which was epibiotic on 9 of the 13 species with which it interacted (Fig. 6), and ranked at the top of the overgrowth hierarchy with and overgrowth index of 0.69 (Fig. 7). The branching sponges observed in contact interactions included *Amphimedon compressa*, *Aplysina cauliformis*, *Iotrochota birotulata*, and *Niphates erecta* (Table 3); these sponges had an average overgrowth index of 0.25, overgrowing most sponges in the other categories except for the encrusting sponge *S. ruetzleri*, and the lobate sponges *Dysidea janiae* and *Phorbos amaranthus* (Figs. 6 & 7).

Lobate sponges comprised the largest group of morphologically similar species occurring in contact interactions (Table 3). The average overgrowth index of all lobate species was 0.07, reflecting clear differences in the overgrowth ability of lobate species over branching or globular sponge species (Fig. 7). All tubular and turbinata sponges averaged a combined overgrowth index of -0.25 because they were frequently overgrown by encrusting and branching sponges and only in some cases were found growing on globular and barrel sponges (Figs. 6 & 7). No significant overgrowth ability was observed between lobate, tubular, or turbinata sponges. Globular and barrel sponges ranked lowest in the overgrowth hierarchy, with average overgrowth indices of -0.5 and -0.54, respectively (Figs. 6 & 7). The globular sponges *Ircinia felix* and *Ircinia strobilina* and the barrel sponges *Verongula gigantea* and *Xestospongia muta* were frequently overgrown by encrusting, branching, tubular, and turbinata sponges (Fig. 7).

DISCUSSION

The competitive dominance of sponges over other sessile marine invertebrates is well documented (e.g. Jackson & Buss 1975, Jackson 1977, Russ 1982,

	XMUT	VRIG	VGIG	SRUE	PAMA	NERE	NDIG	MLAX	MARB	ISTR	IFEL	IBIR	DJAN	CVAG	CPLI	ACAU	ACOM	ACRA	ASCH	ACON
ACLA				NS 2 3		2	2 1		1		← 1 5			1 1		1	NS 4 2	← 6 5	NS 1 2	
ACON			2			1				NS 6		← 3 4				1	1	NS 5 2		
ASCH	1			← 25 92		NS 7	2 1		← 3 7	2		NS 5		2	NS 7	NS 1 3	← 1 7 9		1	
ACRA	2	1		1 2	2	← 5 7	2		1 1		NS 5	2 1	2					NS 3 1		
ACOM	1 1	NS 5 1		← 10 7	1	↑ 12 20 3	NS 10	NS 1 5 2	← 6 6	↑ 5 2	NS 1 7 2	NS 4 18 11	← 2 5	NS 3 12 1	↑ 4 2	NS 12 47 20				
ACAU	↑ 7 3	1		← 5 8	← 2 4	NS 19	NS 7 1	↑ 5 4	NS 3	NS 2 5	↑ 1 2	↑ 7 16		↑ 16	NS 5					
CPLI	NS 3 4			1				NS 7 4			1				← 3 5					
CVAG	↑ 6 3	NS 6		← 4 4		NS 8 1	NS 7		1		NS 1 3 2	← 26 11								
DJAN	1	↑ 6				1		1					1							
IBIR	1 1			← 5 12	1	NS 5 12 2	↑ 5 3	2	↑ 5 2	NS 6	↑ 7 4 1									
IFEL	1	1		← 2 5	1	← 4 5	1			1										
ISTR		1		← 4 5	2	← 3 5	← 4 4	← 2 6	1											
MARB				NS 8 2	NS 6 2	NS 4	1													
MLAX	2	1		1 2		NS 2 6	NS 5 1													
NDIG	NS 5	NS 3 2		← 4 7		1	3													
NERE	↑ 9 11 1	↑ 13 5	↑ 4 1	NS 26 3	← 4 5															
PAMA				NS 6 1																
SRUE	↑ 6 3	1																		
VGIG	NS 1 4																			
VRIG	2																			

ACLA – *Agelas clathrodes* (–0.4; LO)
 ACON – *Agelas conifera* (–0.33; TU)
 ASCH – *Agelas schmidti* (–0.38; LO/TU)
 ACRA – *Ailochroia crassa* (0.4; LO)
 ACOM – *Amphimedon compressa* (0.19; BR)
 ACAU – *Aplysina cauliformis* (0.21; BR)
 CPLI – *Callyspongia plicifera* (–0.33; TR)
 CVAG – *Callyspongia vaginalis* (–0.22; TU)
 DJAN – *Dysidea janiae* (1; LO)
 IBIR – *Ictochota birotulata* (0.33; BR)
 IFEL – *Ircinia felix* (–0.38; GL)
 ISTR – *Ircinia strobilina* (–0.63; GL)
 MARB – *Monanchora arbuscula* (–0.14; LO)
 MLAX – *Mycale laxissima* (0; LO)
 NDIG – *Niphates digitalis* (–0.11; TR)
 NERE – *Niphates erecta* (0.27; BR)
 PAMA – *Phorbis amaranthus* (0.5; LO)
 SRUE – *Scopalina ruetzleri* (0.69; EN)
 VGIG – *Verongula gigantea* (–0.5; BA)
 VRIG – *Verongula rigida* (–0.4; LO)
 XMUT – *Xestospongia muta* (–0.57; BA)

Fig. 6. Matrix of interspecific contact interactions for 21 sponge species occurring in overgrowth interactions 5 or more times. Each cell in the matrix represents the interactions between a pair of sponge species. The top number in each cell represents the total number of occurrences in which the species in the vertical column is observed overgrowing the species in the horizontal column. Middle numbers represent the number of equal occurrences. Bottom numbers represent the total number of occurrences in which the species in the vertical column is observed to be overgrown by the species in the horizontal column. Arrows represent results from the chi-square goodness of fit test, and point to the species that is more likely to be overgrown by the other. Blank cells did not have enough interactions to be considered for statistical analysis. Overgrowth index and morphology of each sponge species are given in parentheses next to the species name. NS = no significant overgrowth ability, EN = encrusting, LO = lobate, GL = globular, TU = tubular, TR = turbinate, BR = branching, BA = barrel (see Table 3)

Suchanek et al. 1983, Aerts 1998, Hill 1998); however, not much is known about interference interactions among sponge species. To date, most studies investigating interspecific interactions among sponges have only focused on mutualistic associations (Rützler 1970, Sará 1970, Pansini & Pronzato 1990, Wulff 1997). The relatively stable and non-transitive nature of most sponge interactions often makes it difficult to identify epi- from basibiotic species (Rützler 1970, Sará 1970, Pansini & Pronzato 1990). This difficulty was mirrored in our study, where over 86 % of all sponge species in

contact interactions occurred in 'equal' rather than clear overgrowth interactions (Figs. 4b & 5b). However, our large sample size among diverse sponge populations (Tables 1 & 2) allowed us to examine the remaining contact interactions that resulted in the overgrowth of one species by another.

The majority of sponge species were encountered alone or in close proximity to one another (Fig. 4a). Only 28.6 % of all sponge individuals were observed in direct contact with other species (Fig. 4a), limiting our analysis of interspecific contact interactions to

Table 3. Percentage occurrence of the 7 basic sponge morphologies in Key Largo, Florida. Morphological growth characteristics and descriptions modified from Jackson (1979)

Growth form	Description	Examples
Encrusting (EN) (11.6%)	Flat, 2-dimensional encrustations Lateral growth only Completely attached to substratum	<i>Aka coralliphagum</i> <i>Cliona deletrix</i> <i>Scopalina ruetzleri</i>
Lobate (LO) (39.5%)	Irregular encrustations Lateral and vertical growth Most basal area is attached	<i>Ailochroia crassa</i> <i>Dysidea janiae</i> <i>Mycale laxissima</i> <i>Verongula rigida</i>
Globular (GL) (9.3%)	Regular encrustations Lateral and vertical growth Most basal area is attached	<i>Geodia neptuni</i> <i>Ircinia felix</i> <i>Ircinia strobilina</i>
Tubular (TU) (7.0%)	Regular or irregular branching tubes Vertical and minimal lateral growth One restricted zone of basal attachment	<i>Agelas conifera</i> <i>Aplysina lacunosa</i> <i>Callyspongia vaginalis</i>
Turbinate (TR) (4.7%)	Erect vase forms Vertical and minimal lateral growth One restricted zone of basal attachment	<i>Callyspongia plicifera</i> <i>Cribrorchalina vasculum</i> <i>Niphates digitalis</i>
Branching (BR) (20.9%)	Linear or branching forms Vertical and lateral growth One or multiple restricted zones of basal attachment	<i>Amphimedon compressa</i> <i>Aplysina cauliformis</i> <i>Iotrochota birotulata</i> <i>Niphates erecta</i>
Barrel (BA) (7.0%)	Erect barrels Vertical and lateral growth Most basal area attached to substratum	<i>Ircinia campana</i> <i>Verongula gigantea</i> <i>Xestospongia muta</i>

21 of the 43 species surveyed in this study. Of 210 possible interaction pairs among 21 species, only 81 species pairs interacted frequently enough to be considered for statistical analysis (Fig. 6). Of all statisti-

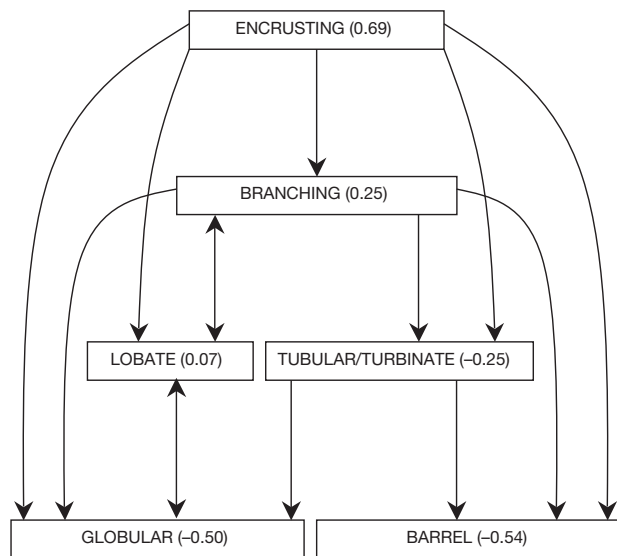


Fig. 7. Overgrowth ability for each morphological growth category defined in Table 3. Average overgrowth indices of all species in each category are given in parentheses. Arrows point from categories that are likely to overgrow to categories that are likely to be overgrown

cally tested interaction pairs, 41 resulted in overgrowth by 1 of the interacting species (Fig. 6). While sponge morphology was a good indicator of the overgrowth ability of some species (Fig. 7), several interactions could not be explained by morphological differences alone. In these cases, sponges in contact interactions appeared to resist overgrowth by other species through the production of allelochemicals (Engel & Pawlik 2000).

The top of the overgrowth hierarchy was occupied by *Dysidea janiae*, *Phorbas amaranthus*, and *Scopalina ruetzleri*, which were never observed to be overgrown by other species. Among these 3 species, *S. ruetzleri* was the most abundant (Fig. 3) and interacted with more species than either *D. janiae* or *P. amaranthus* (Fig. 6). The tissue of *S. ruetzleri* is delicate and thinly encrusts the substratum, including many other sponge species. The overgrowth ability of *S. ruetzleri* is likely a result of its ability to laterally overgrow available substrata, and the apparent inability of other sponges to overgrow such delicate tissue. In contrast, *D. janiae* and *P. amaranthus* have a lobate growth form, which does not lend itself to lateral overgrowth as readily as an encrusting growth form. Instead, the overgrowth ability of *D. janiae* and *P. amaranthus* appears to be mediated by allelochemicals that prevent overgrowth by other sponges. In a previous study investigating allelopathic interactions

among sponges, extracts from *P. amaranthus* inhibited the lateral overgrowth of 3 other species (Engel & Pawlik 2000). While extracts of *D. janiae* were not tested in this study, extracts of the related sponge *Dysidea etheria* also inhibited the overgrowth of the same 3 sponge species (Engel & Pawlik 2000). In addition, a study conducted by Thacker et al. (1998) demonstrated that a sponge of the genus *Dysidea* produces a secondary metabolite that causes tissue necrosis in field assays which therefore facilitates its ability to overgrow other species.

The sponges *Niphates erecta*, *Amphimedon compressa*, *Iotrochota birotulata*, and *Aplysina cauliformis* all have a branching growth form that provides a good mechanism for escaping overgrowth by others 'in height' (Meesters et al. 1996). These species were among the most abundant (Fig. 3) and occurred in more contact interactions than any other sponge species (Fig. 6). Overgrowth by these sponges was usually the result of branches attaching to the side of other species and subsequently 'wrapping' around or 'creeping' up and over them (Wulff 1979, 1997). Both *A. cauliformis* and *I. birotulata* were often observed wrapping around the tubular sponge *Callyspongia vaginalis*, and the turbinate sponges *Callyspongia plicifera* and *Niphates digitalis* (Fig. 6). In contrast, *N. erecta* is usually found 'creeping' over lobate sponges such as *Ailochroia crassa* and *Verongula rigida* as well as both globular sponges *Ircinia felix* and *I. strobilina* (Fig. 6). *Niphates erecta* was also observed 'creeping' up larger sponges such as the barrel sponges *Verongula gigantea* and *Xestospongia muta* (Fig. 6). Interestingly, both *N. erecta* and *I. birotulata* were frequently overgrown by *A. compressa* and *A. cauliformis*, respectively (Fig. 6). Further, the extracts from *A. compressa* and *A. cauliformis* inhibited overgrowth by other sponge species; however, extracts from *N. erecta* and *I. birotulata* did not have allelopathic effects on sponge growth (Engel & Pawlik 2000). While morphology enhanced the overgrowth ability of some branching sponges, the production of allelopathic metabolites appears to play an important role in preventing overgrowth by other, morphologically similar, species.

Lobate, tubular, and turbinate sponges did not rank high in their ability to overgrow other species (Fig. 7). In only 2 cases were tubular or turbinate sponges observed to overgrow other sponges: tubular *Callyspongia vaginalis* was observed growing on the giant barrel sponge *Xestospongia muta*, and turbinate *Niphates digitalis* was observed growing on the globular sponge *Ircinia strobilina* (Fig. 6). In both cases it is clear that overgrowth did not occur via the lateral growth of sponge tissue; rather, the sponges were observed growing on top of the other species. Similar

cases were observed with the sponge *Ircinia felix* growing on the surface of *Agelas clathrodes* (Fig. 6). These overgrowth interactions are most likely a result of larval settlement or the secondary attachment of the epibiont sponge on the basibiont. In all cases, globular and barrel sponges were likely to be overgrown by all other species with which they came into contact (Figs. 6 & 7).

The sponges *Aka coralliphagum*, *Cliona delitrix*, *Mycale laevis*, and *Ectyoplasia ferox* were observed to occur alone more frequently than in proximity to or in direct contact with other sponge species (Fig. 4a). *C. delitrix* and *A. coralliphagum* are boring and burrowing sponges, respectively, and are usually found growing in coral mounds and ledges. While the sponge *M. laevis* is not classified as a boring sponge, it has strong similarities to both *C. delitrix* and *A. coralliphagum* in that it is usually found growing among the branches of many different coral species. All 3 species are often described as occurring in contact with different coral species (Aerts 1998). The sponge *E. ferox* is a low-growing and lobate species known to produce triterpene glycosides that prevent overgrowth by other species (Engel & Pawlik 2000, Kubanek et al. 2002). Because of the low frequency of contact interactions, it is hard to assess the overgrowth ability of *E. ferox* with other sponges. However, given the abundance of *E. ferox* (Fig. 3), the probability of interspecific interactions is high. Therefore, the ability of *E. ferox* to prevent overgrowth appears to be mediated by the production of allelochemicals.

In conclusion, interference interactions among reef sponges frequently resulted in encounters in which it was not possible to distinguish the epi- from the basibiotic species. However, interspecific overgrowth interactions revealed 2 trends in the overgrowth ability of a species: (1) sponge morphology provided a good indicator of the overgrowth ability of some species, and (2) the production of allelochemicals appears to play an important role in preventing overgrowth by others.

Acknowledgements. This study was funded by grants from the NOAA/National Undersea Research Program (UNCW9523, 9812) and from the Biological Oceanography Program of the National Science Foundation (OCE-9711255, 0095724). Permits to perform this research were provided by the NOAA/Florida Keys National Marine Sanctuary and the State of Florida. We thank Greg McFall and the staff of NOAA/NURC in Key Largo, Florida, for logistical support. Special thanks to Robyn M. Palmer for her daily assistance with the collection of transect data. This research benefited from the advice of Timothy P. Henkel regarding data interpretation and presentation. We also thank William G. O'Neal for his assistance in the field. Dedicated to the memory of Sophie.

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Editorial responsibility: Otto Kinne (Editor-in-Chief), Oldendorf/Luhe, Germany

*Submitted: February 14, 2005; Accepted: July 28, 2005
Proofs received from author(s): October 15, 2005*