



Friend or foe? No evidence that association with the sponge *Mycale laevis* provides a benefit to corals of the genus *Montastraea*

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ABSTRACT: Competition for space is intense among sessile benthic organisms on coral reefs. Despite this, the commonly observed interaction between the sponge *Mycale laevis* and scleractinian corals has been considered a mutualism in which the sponge gains substratum for growth on the undersides of coral colonies, and corals receive protection from boring sponges as well as increased food supply from the exhalant water of surrounding sponge oscules. In previous studies, we demonstrated that *M. laevis* is chemically undefended from predators and gains a refuge from sponge-eating fishes by growing among the branches and plates of hard corals. In this study, we investigated the putative benefits of the sponge to the coral host in the presence and absence of spongivores. Specifically, we examined whether the sponge reduced infestation of the coral skeleton by boring sponges, whether corals associated with sponges had higher reproductive output reflecting enhanced food availability and whether the boundary between the 2 species was stable over time. Regardless of the presence of spongivores, association with *M. laevis* neither affected the frequency of colonization of *Montastraea annularis* by boring sponges, nor increased reproductive output of *Montastraea franksi*. On overfished reefs off Panama, *M. laevis* overgrew its coral hosts, while off the Florida coast, where sponge-eating fishes are abundant, the sponge had a semi-cryptic growth form and little impact on associated corals. Corals do not gain any benefit from *M. laevis* on reefs protected from overfishing, but suffer negative effects when sponge predators are removed.

KEY WORDS: Mutualism · Symbiosis · Context dependence · Conditional · Caribbean · Overgrowth · *Montastraea*

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INTRODUCTION

The complexity of marine ecosystems has been partially attributed to facilitation among interacting species (Stachowicz 2001, Bruno et al. 2003). Facilitation is defined as a relationship in which at least one species benefits, with no negative impacts on either (Stachowicz 2001). Mutualism is defined as a subset of facilitation in which the 2 species are in close proximity, and both benefit from the interaction. Although competition and predation are traditionally regarded as the primary biotic structuring forces in

biological communities (Estes & Palmisano 1974, Paine 1974, Estes et al. 2011, Kotler & Holt 2012), mutualisms also structure ecosystems through the establishment of cooperative networks that minimize competition (Bastolla et al. 2009), and facilitation ameliorates the stresses of living in non-optimal environments, increasing biodiversity and stabilizing communities (Bertness 1997, Bruno et al. 2003).

Despite the foregoing, facilitative interactions are not always easy to define. It has become increasingly apparent that most interactions between species are not static but vary as other components of the ecosys-

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tem are altered. These context-dependent interactions may change the costs and benefits to associates as the ecosystem changes. Non-obligate mutualisms are more likely to display conditional outcomes, as well as interactions subject to third-party influences such as predation; therefore, net benefits or costs should be aggregated over the total temporal and spatial range of any interaction (Bronstein 1994, Leung & Poulin 2008).

Even some well-known mutualisms are now considered conditional. For example, ants become antagonistic towards their host acacia trees when predators are removed, and the association between cleaner gobies and their much larger host fishes may devolve to parasitism when resources are limited (Cheney & Côté 2005, Palmer et al. 2008). In this study, we turn our attention to the conditional outcomes of a putative sponge–coral mutualism on Caribbean coral reefs.

In highly diverse coral reef ecosystems, sessile organisms have to compete for limited space. Sponges currently dominate Caribbean reefs in terms of abundance, biodiversity and biomass, concurrent with the decline in cover of scleractinian corals over the past few decades (Diaz & Rützler 2001, Gardner et al. 2003, Maliao et al. 2008, Pawlik 2011). Faster-growing sponges frequently outcompete reef-building corals for space by overgrowing live coral polyps or by producing allelopathic secondary metabolites (Rützler & Muzik 1993, Aronson et al. 2002, Pawlik et al. 2007, Fujii et al. 2011). Despite the competitive nature of most sponge–coral interactions, the orange icing sponge *Mycale laevis*, which ranks among the 10 most common sponges on Caribbean reefs (Pawlik et al. 1995), is frequently observed to grow on the undersides or among branches of scleractinian coral colonies (Goreau & Hartman 1966, Hill 1998). This sponge–coral association has been characterized as a mutualism in which the sponge gains space for growth on the undersides of coral colonies, while the coral colony is protected from colonization by bioeroders, notably clionaid boring sponges, an assertion based on observations that sponge-associated coral colonies in Jamaica did not have clionaid infestations (Goreau & Hartman 1966). As an added benefit, exhalant water from sponge oscules surrounding the coral colony were purported to enhance the food supply for the coral and increase coral growth, especially for coral polyps at the colony edge next to the sponge (Goreau & Hartman 1966). Although the mutualism hypothesis was based solely on non-experimental observations, recent studies have described the association

between *M. laevis* and scleractinian corals as an example of a sponge–coral mutualism (Wulff 2006a, 2012).

From previous field observations and settlement assays with larvae of *Mycale laevis*, we know that the sponge is not an obligate associate of corals. *M. laevis* is not selectively distributed on coral colonies on the reef and bears no specific settlement response to the presence of live coral (Loh & Pawlik in press). In its associations with scleractinian coral, *M. laevis* is typically described as semi-cryptic and encrusting (Wulff 1997). Elsewhere, *M. laevis* also has a fleshy, non-cryptic growth form described as massive (Goreau & Hartman 1966, Randall & Hartman 1968, Wulff 2006b, Loh & Pawlik 2009), and molecular analyses has demonstrated no genetic differences between the 2 growth forms at the species level (Loh et al. 2012). Laboratory and field assays have established that *M. laevis* is chemically undefended and is a preferred food item for spongivorous predators (Pawlik et al. 1995, Loh & Pawlik 2009). The massive form of *M. laevis* is only found in severely overfished areas that lack spongivorous fish, usually growing on top of coral colonies instead of being restricted to the undersides of colonies (Fig. 1; Loh & Pawlik 2009). As coral skeletons provide an effective physical refuge from predation, *M. laevis* benefits from associating with reef-building corals in areas of high spongivore density. When sponge predators are rare or absent, the association with scleractinian corals becomes less important for the sponge. In either case, the potential positive benefits of the sponge to the coral host have not been empirically tested since they were proposed by Goreau & Hartman (1966).

To investigate the putative benefits to sponge-associated corals across a spatial scale that varied in

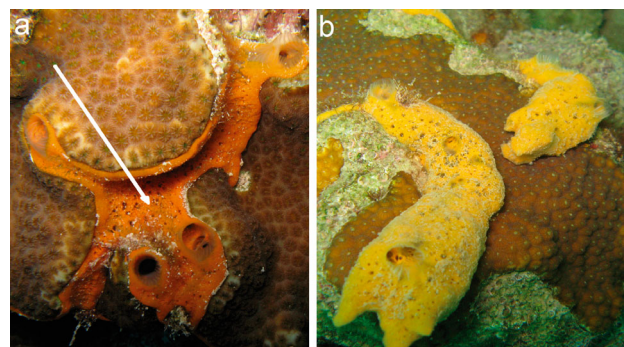


Fig. 1. *Mycale laevis*. The (a) semi-cryptic and (b) fleshy growth forms of the sponge. Photographs were taken at Key Largo, Florida (less fished), and Bocas del Toro, Panama (overfished), respectively. Arrow: the position of *M. laevis* under a colony of *Montastraea franksi*

spongivore densities, interactions between *Mycale laevis* and *Montastraea* spp. were assessed on reefs off Key Largo, Florida, Little San Salvador Island, Bahamas, and Bocas del Toro, Panama. Reefs off Key Largo and the Bahamas are protected from excessive fishing pressure, while reefs off Bocas del Toro are severely overfished and lack important spongivores such as angelfishes or parrotfishes (Burke & Maidens 2004, Loh & Pawlik 2009). We conducted surveys to determine whether colonies of *Montastraea annularis* associated with *M. laevis* are less infested by boring sponges, and we monitored the stability of species boundaries between corals and *M. laevis* under varying densities of sponge-eating fishes. As the undersides of coral colonies provide a competitor-free space for *M. laevis*, we expected that *M. laevis* would grow in tandem with the expansion of its coral host to maintain the mutualistic association. Coral colonies associated with *M. laevis* may receive additional food from the exhalant water of the sponge (Goreau & Hartman 1966), which may include elevated levels of dissolved nitrogen (Southwell et al. 2008); thus, relative coral fitness was examined by measuring the reproductive output of *Montastraea franksi* with and without an associated sponge, on both overfished and less-fished reefs.

METHODS

Are sponge-associated coral colonies less infested by boring sponges?

Colonies of the *Montastraea annularis* species complex (hereafter *Montastraea annularis* s.l.) were surveyed at Conch Reef, Key Largo, Florida (24° 56.996' N, 80° 27.223' W), in November 2006 at depths of 12 to 23 m and at Punta Caracol, Bocas del Toro, Panama (9° 22.638' N, 82° 18.152' W) in September 2007 at depths of 5 to 8 m. On each reef, coral colonies that were either associated or not associated with *Mycale laevis* (n = 50) were haphazardly selected, and the entire colony was monitored for infestation by *Cliona* spp. Colonies that were monitored were spaced at least 3 m apart on the reef, and the survey swim continued until 50 colonies were encountered. For each site, the frequency of infestation by *Cliona* spp. was compared between colonies of *M. annularis* s.l. with and without a sponge associate using the Fisher's exact test. Any overgrowth of the coral colonies by *M. laevis*, defined as sponge tissue covering coral polyps on the upper surface of the colony, was also noted at both sites.

Does *Mycale laevis* increase coral reproductive output?

To assess coral reproductive output, samples of *Montastraea franksi* were collected using an underwater pneumatic holesaw drill or a hammer and chisel from colonies at Little San Salvador, the Bahamas (24° 34.848' N, 75° 57.622' W), and Casa Blanca, Bocas del Toro, Panama (9° 21.461' N, 82° 16.273' W), in July 2010 at depths of 7 to 9.5 m. Coral pieces were sampled from colonies that were either associated with *Mycale laevis* or had no sponge association (n = 18 to 20). Pieces were collected 2.5 to 3.0 cm from the colony edge, as coral polyps close to the colony edge are presumably most affected by the sponge association. Edges of coral colonies associated with *M. laevis* were located closest to sponge oscules and assume a folded shape around each oscule of the sponge (Goreau & Hartman 1966).

Immediately after collection, coral samples were relaxed in 50% MgCl₂ for 30 min and then fixed in 20% Z-fix solution. Samples were refrigerated overnight at 4°C, the Z-fix solution was replaced and samples were stored at 4°C until they were processed for histology. Before decalcification, remnants of *Mycale laevis* were removed from sponge-associated corals by vigorous scrubbing and rinsing in tap water. Corals were decalcified in a 10% (v/v) HCl solution buffered with 0.1% (w/v) EDTA. The decalcifying solution was replaced every 24 h until the entire coral skeleton was dissolved for each sample. The coral tissues were rinsed twice in tap water and stored in 70% ethanol at room temperature. Four adjacent polyps were excised from each sample with a scalpel, and coral tissues were dehydrated in an ethanol series, cleared in toluene and embedded in paraffin. Starting from the oral surfaces of the coral polyps, the paraffin blocks were sectioned with a microtome until the coenosarcs were removed. Eight to 10 sections, each 10 µm thick, were taken from 3 layers from each block of 4 polyps: the top layer, immediately under the coenosarcs; the middle layer, 160 µm under the top layer; and the bottom layer, 160 µm under the middle layer. Sections were stained in hematoxylin, eosin Y and orange G, and cover slips were attached using Permount.

Coral sections were scanned under a compound light microscope for the presence of oocytes, which were identified as in Szmant-Froelich et al. (1985). If oocytes were present for a coral sample, the section with the highest surface area of oocytes was selected and each polyp photographed under 40× magnification. Photographs were stamped with a scale to allow

for calibration in image analysis. Oocytes were outlined using the program Adobe Photoshop, and oocyte area and total polyp area were measured using the 'Analyze Particles' command in the software program ImageJ. Mean proportional oocyte area (oocyte area / total polyp area) over 4 polyps was calculated for each gravid sample and compared between gravid coral colonies associated with *Mycale laevis* and those without the association for each study site. Proportions were used instead of absolute oocyte area to standardize reproductive output among colonies as coral polyp sizes varied among colonies. Similar methods have been used to compare reproductive output in sponges (Whalan et al. 2007, Leong & Pawlik 2011). Comparisons were carried out with arcsine-transformed data using the Student's *t*-test. The numbers of gravid versus non-gravid samples were also compared between associated and non-associated coral colonies for each site using the Fisher's exact test.

Assessing the species boundary between *Mycale laevis* and associated corals

Ten colonies of *Montastraea franksi* were tagged and their upper surfaces photographed with a linear scale on each reef at North Dry Rocks, Key Largo (25° 07.850' N, 80° 17.521' W), and Punta Caracol, Bocas del Toro, in May and August 2008, respectively. All the selected coral colonies were associated with *Mycale laevis*, which surrounded at least 50% of the colony circumference, and all colonies were at least 20 cm in diameter. Coral colonies were photographed again 1 yr later, and the surface areas of both sponge and coral were measured using image analysis in ImageJ. To track sponge coverage of their coral hosts, differences in proportional sponge surface area (sponge area / total sponge and coral area) over 1 yr on each reef were compared with arcsine-transformed data using a paired *t*-test. The number of coral colonies with increased sponge cover after 1 yr was compared between sites using the Fisher's exact test.

RESULTS

Are sponge-associated coral colonies less infested by boring sponges?

Levels of infestation by clionaid sponges were similar whether colonies of *Montastraea annularis* s.l. surveyed at Conch Reef, Florida, were associated with *Mycale laevis* or not associated with the sponge ($p =$

1.000, Fisher's exact test). Ten of 50 coral colonies associated with *M. laevis* and 11 of 50 non-associated colonies had clionaid infestations. Nineteen infestations were by the boring sponge *Cliona delitrix*, and the other 2 coral colonies were infested by *C. varians*.

At Punta Caracol, Panama, the levels of clionaid infestation between associated and non-associated corals were also not significantly different ($p = 0.611$), and 8 of 50 associated corals and 11 of 50 non-associated corals were infested with clionaid sponges. Most of the boring sponges that were infesting *Montastraea annularis* s.l. at Punta Caracol were *Cliona aprica* (16 of 19 coral colonies), and 3 additional coral colonies were infested by *C. delitrix*. Because *Mycale laevis* has a fleshy, non-cryptic growth form at Punta Caracol, overgrowth of *M. annularis* by associated *M. laevis* was also observed here (8 of 50 coral colonies), but not at Conch Reef.

Does the sponge–coral association boost coral reproductive output?

At Little San Salvador, Bahamas, oocytes were present in 10 of 19 and 10 of 20 colonies of *Montastraea franksi* that were associated and not associated with *Mycale laevis*, respectively. Non-associated corals had approximately twice the mean proportional oocyte surface area relative to associated corals, and oocytes comprised $1.33 \pm 0.35\%$ (mean \pm SE) of total polyp area compared with $0.74 \pm 0.35\%$ in colonies associated with *M. laevis* (Fig. 2). However, because

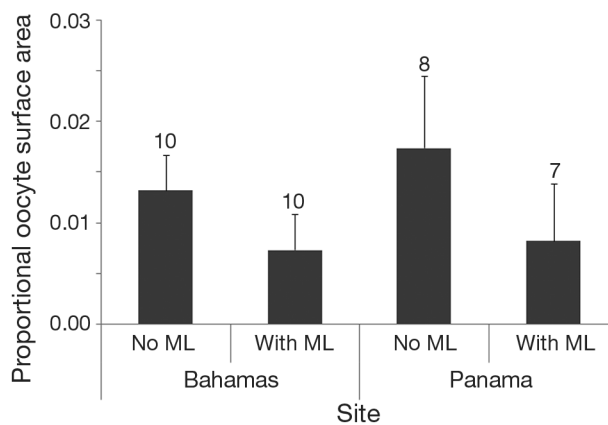


Fig. 2. *Montastraea franksi* and *Mycale laevis*. Proportional oocyte surface area from histological sections of coral colonies either associated ('With ML') or not associated ('No ML') with the sponge. The proportional surface area of oocytes relative to total tissue was determined for each microscopic frame, with a mean of 4 frames (1 for each of 4 polyps) per sample. Means \pm SE. Numbers above columns: number of samples of gravid coral colonies. Colonies were sampled from Little San Salvador, Bahamas, and CasaBlanca, Panama

of high variance, this difference was not statistically significant ($p = 0.248$, 2-tailed t -test). Eighteen associated coral colonies and 19 non-associated colonies of *M. franksi* were sampled at Casa Blanca, Panama. Of these, 7 associated colonies and 8 non-associated colonies were found to be gravid. Mean percent oocyte area in non-associated colonies was, again, approximately double that in associated colonies, at $1.74 \pm 0.71\%$ versus $0.83 \pm 0.56\%$, but this difference was also not significant ($p = 0.328$, 2-tailed t -test). At both Little San Salvador and Casa Blanca, the proportion of gravid colonies was not significantly different between associated and non-associated coral colonies ($p = 1.000$ for both sites, Fisher's exact test).

Assessing the sponge-coral species boundary

At North Dry Rocks, Florida, only 8 colonies of *Montastraea franksi* were recovered after 1 yr, and the mean proportional surface area of *Mycale laevis* declined significantly from 0.112 ± 0.036 (mean \pm SE) to 0.076 ± 0.027 ($p = 0.0289$, 2-tailed paired t -test; Fig. 3).

The colonies of *Montastraea franksi* monitored at Punta Caracol, Panama, had more than twice the mean initial and final proportional sponge cover than those at North Dry Rocks. Proportional sponge cover (mean \pm SE; $n = 10$) increased from 0.259 ± 0.050 to 0.390 ± 0.098 after 1 yr (Fig. 3), and 1 coral colony was completely overgrown by *Mycale laevis* (Fig. 4). However, this increase was not statistically significant ($p = 0.146$, 2-tailed paired t -test).

When individual coral colonies were scored for proportional sponge cover over 1 yr, significantly

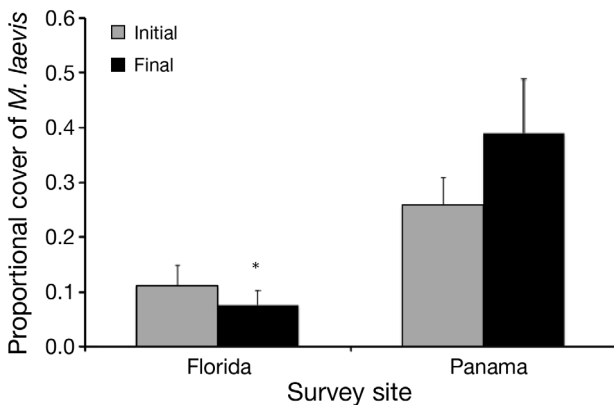


Fig. 3. *Mycale laevis* and *Montastraea franksi*. Differences in proportional surface area of *M. laevis* growing over the upper surfaces of associated colonies of *M. franksi* after 1 yr of monitoring at North Dry Rocks, Florida ($n = 8$), and Punta Caracol, Panama ($n = 10$). *: significant difference in proportional cover of *M. laevis* after 1 yr (paired t -test); mean \pm SE

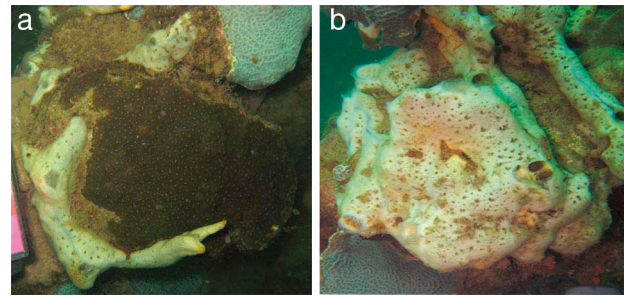


Fig. 4. *Montastraea franksi* and *Mycale laevis*. (a) Coral colony of sponge-associated *M. franksi* at start of monitoring, and (b) completely overgrown by *M. laevis* within 1 yr at Punta Caracol, Panama. The white morph of *M. laevis* is genetically identical to the orange morph shown in Fig. 1 and co-occurs with it, along with intermediate color morphs

more colonies of *Montastraea franksi* had increased proportional sponge cover at Punta Caracol compared with colonies at North Dry Rocks ($p = 0.0248$, Fisher's exact test). Proportional surface area of *Mycale laevis* increased for 7 coral colonies out of 10 at Punta Caracol, while proportional sponge cover increased for only 1 of 8 colonies at North Dry Rocks.

DISCUSSION

Contrary to the hypothesis of Goreau & Hartman (1966) that the association between *Mycale laevis* and scleractinian corals is mutualistic, the actual relationship between sponge and coral is more complicated when investigated across a spatial range, and is a good example of context-dependence of a symbiotic relationship. It is certainly advantageous for *M. laevis* to grow in close proximity to reef-building corals, especially in areas where spongivorous fish are abundant (Loh & Pawlik 2009), but benefits appear to strongly favor the sponge.

Regarding the putative benefit of protection of the coral host from boring sponges, we found no differences in the frequency of clonoid infestations whether or not coral colonies were associated with *Mycale laevis*. While it is likely that *M. laevis* acts as a physical barrier to invasion of the undersides of coral skeletons by boring sponges, this feature is not unique to *M. laevis* and may be accomplished by a variety of other encrusting organisms (MacGeachy 1977, López-Victoria & Zea 2005). This type of protection would also not be effective if boring sponge larvae colonize patches of dead skeleton on top of coral colonies. For example, the common Caribbean boring sponge *Cliona delitrix* propagates mainly by sexual

reproduction (Zilberberg et al. 2006), and new recruits are commonly found growing on dead skeleton patches on top of colonies (Chaves-Fonnegra & Zea 2011). Most of the coral colonies we surveyed (~80%) were free of infestation by clionaid sponges regardless of whether colonies were associated with *M. laevis*, indicating that other protective mechanisms are probably more effective. For example, *Montastraea cavernosa* can extend mesenterial filaments to digest tissues of encroaching boring sponges (McKenna 1997). Although *M. laevis* may establish a physical barrier that deters colonization of the cryptic underside of coral skeletons by boring sponges, this level of protection is probably not different from that offered by other cryptic fouling organisms.

Another putative advantage to coral from associating with *Mycale laevis* is enhanced feeding owing to exhalant currents issuing from sponge oscules surrounding the coral colony (Goreau & Hartman 1966). Sponges are very efficient at removing particulate organic matter from the water (Reiswig 1971, Pile et al. 1996), but can release dissolved inorganic nitrogen (Southwell et al. 2008), which may increase the productivity of coral zooxanthellae and thus coral fitness. Despite that, our results did not indicate a clear pattern of higher reproductive output in sponge-associated corals. Rather, there was a trend towards lower proportional surface areas of oocytes in corals associated with *M. laevis*, regardless of sponge growth form and spongivore density. This may be further examined through sampling additional coral colonies and polyps per colony. Where the sponge and coral interact, *M. laevis* tends to overgrow coral polyps on the edge of the colony, even when growing on the underside of the coral colony in a semi-cryptic form (T. Loh pers. obs.), possibly causing reproductive stress to the coral. During our study period, food resources may be diverted to coral growth instead of reproduction, but oocytes are nutritionally dense and probably resource limiting for corals. Moreover, we have observed sponge-eating fishes biting at the oscules and edges of *M. laevis* that protrude from coral colonies, resulting in the incidental removal of coral tissue and thin skeletal fragments, both of which are likely to have negative consequences for coral fitness.

While *Mycale laevis* grows in a semi-cryptic form on reefs where sponge predators are numerous, the situation changes dramatically in overfished areas where sponges are released from predation pressure. The proportional cover of coral by sponges was more than double in Panama relative to Florida (Fig. 3). We reported that *M. laevis* has a fleshy growth form, and

spongivore density is very low in Panama (Loh & Pawlik 2009), but the extent to which the sponge overgrows its coral host was not previously quantified (Figs. 3 & 4). Not all coral colonies monitored had substantial overgrowth when sponge predators were absent, but there were more colonies with increased sponge cover in Panama compared with Florida. The greater occurrence of overgrowth by *M. laevis* on its host corals in Panama happens because sponge growth is not restricted to cryptic refugia in the absence of predation. On reefs protected from fishing (Florida and Bahamas), predation restricts the growth of *M. laevis* such that associated corals are able to increase in area relative to the sponge. As *M. laevis* did not appear to have died back over the year when sponge–coral interaction boundaries were monitored in Florida, the decrease in proportional sponge cover implies an increase in skeletal linear extensions of the coral colonies.

Results of previous larval settlement assays and field observations of adult *Mycale laevis* indicate that larvae of the sponge do not settle specifically in response to the presence of live scleractinian corals, nor is the adult distribution skewed toward proximity to corals (Loh & Pawlik in press). It seems clear, then, that instead of a mutualism, the interaction between *M. laevis* and scleractinian corals is a conditional association driven by predation pressure on the palatable sponge. Where spongivorous fishes are abundant, the association tends toward commensalism, in that there is less harm to corals associated with the sponge because fish predators graze the sponge down and prevent it from overgrowing coral, while the sponge gains a predator refuge. In overfished areas where spongivore density is very low, the sponge–coral association is negative for the coral, and *M. laevis* competes with corals for space. The sponge is not restricted by predators to a semi-cryptic growth form and has a higher frequency of coral overgrowth, which may further stress corals by suppressing coral reproductive output.

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