Journal of Experimental Marine Biology and Ecology 374 (2009) 45–50

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Bitten down to size: Fish predation determines growth form of the Caribbean coral reef sponge *Mycale laevis*

Tse-Lynn Loh, Joseph R. Pawlik *

Center for Marine Science, University of North Carolina Wilmington, 5600 Marvin K Moss Lane, Wilmington, NC 28409, USA

ARTICLE INFO

Article history:
Received 8 August 2008
Received in revised form 6 April 2009
Accepted 7 April 2009

Keywords:
Chemical defense
Growth form
Predation
Refugia
Trophic cascade

ABSTRACT

Interactions between organisms add complexity to ecosystem function, particularly on coral reefs. The Caribbean orange icing sponge *Mycale laevis* is semi-cryptic, often growing under coral colonies or between coral branches. This association is reportedly a mutualism, with the sponge deterring boring sponges from invading the coral skeleton and the coral providing an expanding surface for sponge growth. But is there an alternative explanation for the proximity of sponge and coral? We examined the importance of fish predation on the growth of the sponge. While the semi-cryptic growth form of *M. laevis* predominates on reefs off the Florida Keys and the Bahamas Islands, *M. laevis* grows with a non-cryptic, erect morphology off Bocas del Toro, Panama. Surveys revealed that sponge-eating fishes were rare or absent at Bocas del Toro compared to sites in the Florida Keys. Because past studies were inconsistent about the palatability of *M. laevis* to fish predators, we conducted feeding experiments with sponges from all three sites. Crude organic extracts of *M. laevis* from all three sites were palatable to generalist fish predators in aquarium assays, and field feeding assays and caging experiments conducted in the Florida Keys confirmed that spongivorous fishes readily ate exposed fragments of *M. laevis*. Our results suggest that *M. laevis* is restricted to its semi-cryptic growth form by spongivorous predators, with corals providing a physical refuge from predation. This alternative explanation supports the broader hypothesis that Caribbean reef sponges can be categorized on the basis of chemical defense into defended, palatable, and preferred species, the last of which are restricted to refugia.

1. Introduction

Ecological interactions contribute to the resilience and biodiversity of ecosystems, as evidenced by trophic cascades when one component of the system is perturbed (Dulvy et al., 2004; Burkepile and Hay, 2007). More than the sum of individual species, ecosystems are complicated by interspecific and interconnecting interactions, such as competition, predation, and facilitation (Stachowicz, 2001; Bruno et al., 2003). The nature of the interaction between two species can vary over time and space in response to prevailing physical and biotic conditions. One example is the conditional mutualism reported between insect-tending ants and their aphid charges, in which aphids only benefit when their predators are present in large numbers (Cushman and Whitham, 1989).

Mycale laevis, one of the 10 most common Caribbean reef sponge species (Pawlik et al., 1995), is described as having a semi-cryptic growth form (Wulff, 1995) and is commonly found growing on the underside of scleractinian corals or in-between coral branches (Goreau and Hartman, 1966; Hill, 1998). It was hypothesized that *M. laevis* has a mutualistic relationship with corals, in which *M. laevis* protects the coral skeleton from invasion by bioeroding sponges while obtaining space on the underside of coral colonies for growth (Goreau and Hartman, 1966). However, *M. laevis* is not restricted to a semi-cryptic habit, and fleshy, erect forms growing on top of substrata have been observed on reefs off Bocas del Toro, Panama (Loh, pers. obs). Growth forms of *M. laevis* in Panama and Jamaica were also described as “massive” in previous studies (Randall and Hartman, 1968; Wulff, 2001).

Why do these different growth forms of *M. laevis* exist? Sponges display great variability in color and morphology, even within the same species, influenced by both physical and biological factors. Sponges inhabiting high-energy environments modify their morphology to increase strength and stiffness (Palumbi, 1986), and individuals of *Haliclona caerulea* that were protected from predation had more branches compared to exposed individuals (Carballo et al., 2006). The coral reefs of Panama and Jamaica, where *M. laevis* has been described as “massive,” are characterized as having depauperate reef fish populations because of over-fishing (Burke et al., 2004). If *M. laevis* is palatable to spongivorous fishes, the low fish density may explain the difference in the growth form of *M. laevis* in these areas.

There is some evidence that *M. laevis* is palatable to fish predators, but the data have been equivocal. Whole sponge organic solvent extracts of *M. laevis* were palatable to the generalist reef predatory fish *Thalassoma bifasciatum* in laboratory feeding assays (Pawlik et al., 1995), but pieces of *M. laevis* were ignored by spongivorous fish when

---

* Corresponding author. Tel.: +1 910 9622377; fax: +1 910 9622410.
E-mail address: pawlikj@uncw.edu (J.R. Pawlik).

0022-0981/$ – see front matter © 2009 Elsevier B.V. All rights reserved.
doi:10.1016/j.jembe.2009.04.007

Table 1
List of fish species previously cited as spongivorous and counted in surveys performed on coral reefs off the Florida Keys and Bocas del Toro, Panama.

Fish species	Common name	Source
Chaetodipterus faber	Atlantic spadefish	Randall and Hartman (1968)
Holacanthus ciliaris	Queen angelfish	Randall and Hartman (1968)
Holacanthus tricolor	Rock beauty	Randall and Hartman (1968)
Holacanthus bermudensis	Blue angelfish	Dunlap and Pawlik (1996)
Pomacanthus arcuatus	Gray angelfish	Randall and Hartman (1968)
Pomacanthus paru	French angelfish	Randall and Hartman (1968)
Cantherhines macrocerus	Whitespotted filefish	Randall and Hartman (1968)
Cantherhines pullus	Orangespotted filefish	Randall and Hartman (1968)
Acanthostracion polygonius	Honeycomb cowfish	Randall and Hartman (1968)
Acanthostracion quadricornis	Scrawled cowfish	Randall and Hartman (1968)
Lactophrys triqueter	Smooth trunkfish	Randall and Hartman (1968)
Lactophrys bicaudalis	Spotted trunkfish	Dunlap and Pawlik (1996)
Canthigaster rostrata	Sharpnose puffer	Randall and Hartman (1968)
Sparisoma aurofrenatum	Redband parrotfish	(Dunlap and Pawlik, 1996, Wulff, 1997a)
Sparisoma viride	Stoplight parrotfish	(Dunlap and Pawlik, 1996, Wulff, 1997a)
Sparisoma chrysopterum	Redtail parrotfish	(Dunlap and Pawlik, 1996, Wulff, 1997a)

the outer surface of the sponge was intact, yet consumed when the outer surface was removed (Wulff, 1997a), indicating a possible defense mechanism in the outer tissues of the sponge. Contrarily, whole pieces of sponge tissue from *M. laevis* did not deter feeding by other predators such as the hermit crab *Paguristes punticeps* (Waddell and Pawlik, 2000), the reticulated sea star *Oreaster reticulatus* (Wulff, 1995, 2000), or the pufferfish *Arothron hispidus* (Wulff, 1997b).

The objective of this study was to investigate the relationship between growth form, tissue palatability and predation pressure for *M. laevis* from Key Largo, Florida, the Bahamas, and Bocas del Toro, Panama. We quantified the abundance of potential predators at the Key Largo and Bocas del Toro study sites using surveys of spongivorous fish, with corresponding surveys of differences in the morphology of *M. laevis* at the same sites. While aquarium assays have previously been conducted using organic extracts of *M. laevis* from other locations, we tested samples of *M. laevis* from our study sites to investigate whether chemical defenses of *M. laevis* varied as a function of growth form and predator abundance. We investigated differences in the palatability of extracts of external and internal tissues of *M. laevis* to assay fish, to clarify whether the ectoderm of *M. laevis* is defended against predation. Finally, field assays of fish feeding were carried out within the Florida Keys National Marine Sanctuary to determine whether *in situ* feeding by fishes on tissue of *M. laevis* corroborated the results of aquarium assays.

2. Materials and methods

2.1. Fish and sponge surveys

Fish abundance was recorded following the Reef Check Fish Survey Methodology (http://www.reefcheck.org). Four 20 m line transects were laid along two reef sites at each location, Punta Caracol (9°22.638′N 82°18.152′W) and Adriana's Reef (9°14.8′N 82°10.7′W) at Bocas del Toro, Panama, and Conch Reef (24°56.996′N, 80°27.223′W) and North Dry Rocks (25° 07.850′N 80°17.521′W) at Key Largo, Florida. Transects were laid at depths of 6, 5, 13, and 8 m at each site, respectively. Surveys were conducted 10–15 min after each transect was laid. Target fish in a volume subtended by 2.5 m on either side of the transect line and 5 m above were counted as the surveyor swam along the transect. Every 5 m, a 3 min waiting period was observed during which time no fish were counted. The total volume surveyed per transect was 2000 m^3. The list of 16 target spongivorous fish species were obtained from Randall and Hartman (1968), Dunlap and Pawlik (1996), and Wulff (1997a) (Table 1).

For the surveys of *M. laevis*, the growth forms of 50–78 haphazardly encountered individuals were recorded at the 2 sites in each location. Individuals of *M. laevis* were identified as one of 3 forms: semi-cryptic, when more than half of the sponge was hidden or difficult to access; exposed, when the sponge was mostly exposed but thinly encrusting; and erect, when the sponge exhibited an exposed upright or branching form (Fig. 1).

2.2. Feeding assays

Samples of *M. laevis* were collected from Sweetings Cay (26°33.664′N 77°52.538′W) and Little San Salvador (24°34.848′N 75°57.622′W) in the Bahamas in June 2007, Punta Caracol, Adriana's Reef and STRI Point (9°21.113′N 82°15.543′W) at Bocas del Toro in September 2007, and Dixie Shoals (25°4.28′N 80°19.05′W), North Dry Rocks (25°07.850′N 80°17.521′W) and Conch Wall (24°57.01′N 80°27.25′W) off Key Largo, Florida from November to December 2007, at depths of 5–17 m. Only tissue from the non-cryptic, erect forms of *M. laevis* was collected at Bocas del Toro. Sponge samples were stored at −20 °C before extraction. The ectoderm of the *M. laevis*, which was approximately 3 mm thick in all samples, was separated from the endoderm using a scalpel. The volumes of both

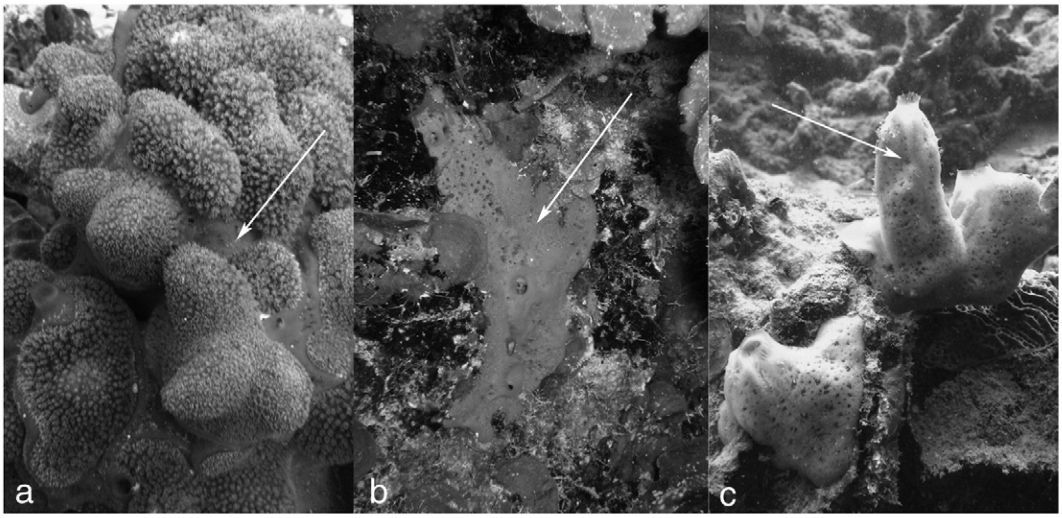

Fig. 1. The (a) semi-cryptic, (b) exposed and (c) erect forms of *M. laevis*. Arrows mark the location of the sponge. Photographs were taken at Key Largo, Florida (a), the Bahamas (b), and Bocas del Toro, Panama (c) respectively.

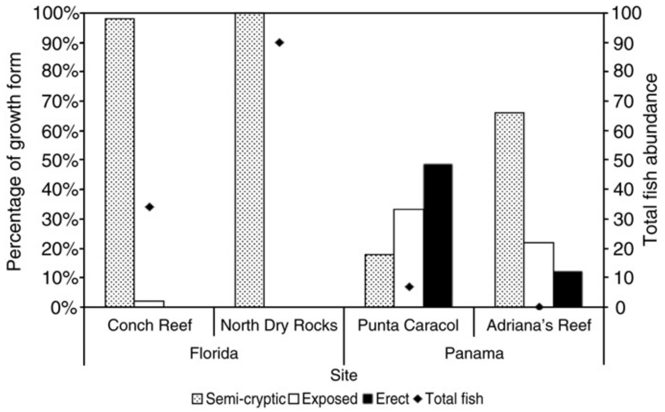

Fig. 2. The total abundance of spongivorous fish (◆) recorded over four 20 m line transects and proportions of the different growth forms of *M. laevis* (bars) present at each survey location.

tissue types were then measured by volumetric displacement. Two to ten milliliters of each tissue type was processed from each site.

For the aquarium assay, extracts were prepared using tissue from several individuals from each site, yielding an average representation for each site. Sponge tissue from the Bahamas and Florida was processed according to the methods described in Pawlik et al. (1995), with sponge tissue extracted in three successive solvent mixtures of 1:1 dichloromethane and methanol, methanol only, and methanol and 5% v/v deionized water. The extracts were decanted and filtered at each step before rotary evaporation at low heat (<40 °C). The extracts from each step combined into a 20 ml vial and any remaining solvent was removed using a vacuum evaporator. As a minor modification of this protocol, samples of *M. laevis* collected at Bocas del Toro were first extracted with diethyl ether, which was rapidly evaporated by bubbling air through the extract.

Laboratory feeding assays were carried out as described in Pawlik et al. (1995) on board the 'R/V Seward Johnson' and at the Center for Marine Science at the University of North Carolina Wilmington. Organic solvent extracts of the outer and inner tissues of *M. laevis* were mixed at twice the natural volumetric concentration found in the sponge tissue into a food matrix of alginic acid, powdered squid mantle and deionized water. Food pellets ~4 mm in length were cut from strands formed when the mixture was extruded into a 0.25 M calcium chloride solution through a syringe. Control pellets were made the same way but without the addition of sponge extract. Orange food coloring was added to the control mixture to match the color of the sponge extract. Control and treated pellets were offered to groups of 3–4 bluehead wrasses, *Thalassoma bifasciatum*, in 10 separate aquarium compartments. Control pellets were offered first to determine if the fish were feeding. If consumed, a treated pellet was offered. A rejection was scored if the one or more fish attempted three times to take the pellet into their mouth cavity but spat it out each time, or if a fish attempted to eat the pellet, spat it out, and subsequently ignored the pellet. A control pellet was offered after each rejection to determine if the fish had ceased feeding. Ten control and 20 treated pellets (10 for each treatment of inner and outer tissue extracts) were offered in each assay for each reef site, and the treated pellets were considered significantly deterrent if 4 or more pellets were rejected in the assay (Fisher exact test, $p \leq 0.043$, 1-tailed test).

Observations of fish feeding on *M. laevis* were carried out at North Dry Rocks, Key Largo in November 2007. Twenty-five pieces of *M. laevis* were collected, with each piece at least 5.0×2.5 cm^2 in surface area. Pieces were either folded in half or rolled up, carefully making certain that only outer tissue was exposed, and a plastic cable tie was fastened around each piece. The ends of each cable tie were then inserted into a length of polypropylene rope (~20 m in length) suspended on the reef flat. Three divers stationed at least 15 m from the rope observed the sponge pieces for 1 h, recording both the fish species biting the pieces and the number of bites.

2.3. Predator exclusion experiments

Twenty pieces of coral rubble encrusted with *M. laevis* were collected at North Dry Rocks, Key Largo in November 2007, taking care to ensure minimal damage to the outer tissue of *M. laevis*. Ten pieces were exposed to predators, and an additional 10 were similarly exposed but secured in cages made from 1.89 l plastic food containers with holes to allow water flow. Rubble pieces with and without cages were attached to bricks using plastic cable ties. A digital photograph of the surface area of each sponge was taken, together with a scale bar, at the initiation of the experiment and again after 24 h.

The initial and final surface areas of the intact outer tissue of *M. laevis* on each rubble piece were measured using ImageJ 1.38× for Macintosh OSX, and the proportional loss of surface area was calculated for each sponge. Mean proportional loss in surface area

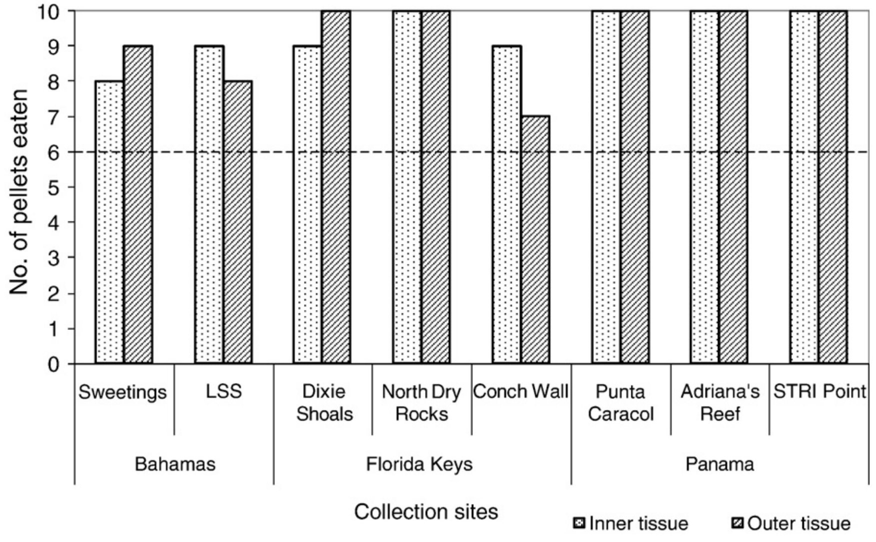

Fig. 3. Number of pellets (out of 10) treated with extracts of the inner and outer tissue of *M. laevis* eaten by *Thalassoma bifasciatum* in aquarium assays. The dashed line indicates the number of treated pellets eaten below which extracts are considered significantly deterrent, compared to 10 control pellets (Fisher exact test, $p \leq 0.043$, 1-tailed test) (LSS = Little San Salvador).

Table 2
Number of fish bites on 25 pieces of *M. laevis* in 1 h.

Fish type	Number of bites
Parrotfish (*Sparisoma* spp.)	405
Damselfish (*Stegastes* sp.)	8
Thalassoma bifasciatum	1
Total number of bites	414

Pieces of *M. laevis* were cut from substrata and suspended from a rope on the reef while observers counted fish bites. Observations were carried out at North Dry Rocks, Florida.

was compared between caged and uncaged sponges using 1-way ANOVA (JMP 6.0.2) with arc-sine transformed data to reduce heterogeneity in residual variances, which was then checked in a residual plot.

3. Results

3.1. Fish and sponge surveys

A higher proportion of the non-cryptic, erect growth form of *M. laevis* occurred where there were fewer spongivorous fishes (Fig. 2). In total, 34 and 90 spongivorous fishes were recorded in the Florida Keys at Conch Reef and North Dry Rocks, respectively, the majority of which were the parrotfish *Sparisoma aurofrenatum*. Nine angelfishes of the species *Holocanthus tricolor*, *H. ciliaris*, *Pomacanthus arcuatus* and *P. paru* were also recorded between the two sites. Correspondingly, 98% and 100% of individual *M. laevis* encountered were of the semi-cryptic growth form at the two sites.

On Panamanian reefs, only 7 spongivorous fish (*Sparisoma* spp. and *Canthigaster rostrata*) were recorded at Punta Caracol, none were recorded at Adriana's Reef, and no angelfishes were encountered at either site. The percentages of the erect growth form encountered were 48.7% and 12% respectively. There was a high proportion of the semi-cryptic form at Adriana's Reef (66%) compared to Punta Caracol even though no spongivorous fishes were recorded there. However, the sponge-eating sea star *O. reticulatus* was present in large numbers (50 individuals in 400 m^2) at Adriana's Reef, and some individuals were observed to be feeding on *M. laevis* (Loh, pers. obs).

3.2. Feeding assays

When incorporated into artificial food, organic extracts of *M. laevis* from both inner and outer tissue were found to be palatable for all sites, with no significant deterrence of feeding by *Thalassoma bifasciatum* in laboratory assays, even when assays were performed using twice the natural volumetric concentration (Fig. 3). Extracts from the erect form of *M. laevis* collected at Bocas del Toro were also palatable, with 10 out of 10 treatment pellets offered consumed in all cases.

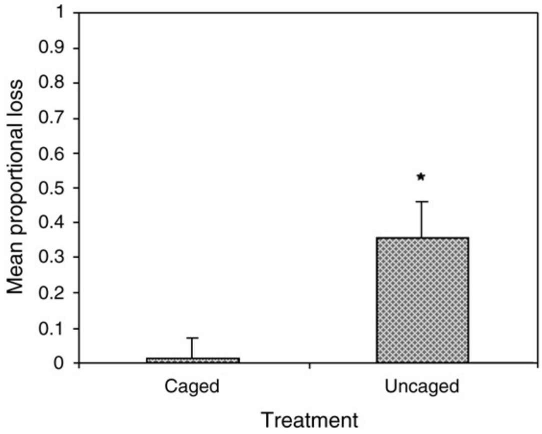

Fig. 4. Proportional loss of surface area of outer tissue of *M. laevis* for caged and uncaged sponges ($N = 10$), North Dry Rocks, Florida. Error bars represent standard errors (* = significant difference between treatments using 1-way ANOVA for arc-sine transformed data, $p = 0.0083$).

Fig. 5. Uncaged individual of *M. laevis* (a) before and (b) after exposure to predators for 24 h, North Dry Rocks, Florida.

In field feeding experiments, 7 of 25 pieces of *M. laevis* were completely consumed within 1 h of being exposed to spongivorous fishes at North Dry Rocks. A total of 414 fish bites were tallied, with most bites coming from the parrotfish *Sparisoma aurofrenatum* and *S. viride* (Table 2).

In field enclosure experiments, caged *M. laevis* had a mean percentage loss of outer tissue surface area of 1.2% after 24 h, and 35.9% by uncaged sponges (Fig. 4). The proportional loss was significantly higher for uncaged sponges (1-way ANOVA, $N = 10$, $^{**}p < 0.01$). Contrary to the results reported in Wulff (1997a), exposed individuals of *M. laevis* that were collected on rubble and had completely intact ectoderms after the collection process were also eaten over the duration of the experiment (Fig. 5).

4. Discussion

Predation is the predominant factor structuring the community of sponges on Caribbean coral reefs (Pawlik, 1997; 1998; Pawlik et al., 2008). As sessile animals, sponges have evolved a number of mechanisms in response to predation. Some sponges produce distasteful secondary metabolites to deter predators (Pawlik et al., 1995; Becerro et al., 2003; Sokolover and Ilan, 2007). Others are able to tolerate some level of predation, and have higher rates of reproduction, growth, or wound healing (Walters and Pawlik, 2005; Pawlik et al., 2008). Based on these strategies, three categories of sponges have been identified (Pawlik, 1997; Pawlik et al., 2008): (1) chemically defended sponges, which are avoided by generalist predators, (2) palatable sponges, which are undefended but grow fast enough to overcome tissue loss due to predation, and (3) preferred sponges, which are rapidly consumed by predators when exposed and consequently inhabit cryptic refugia. Accordingly, several field studies have demonstrated that undefended Caribbean sponges are restricted to refuge habitats by fish predation (Dunlap and Pawlik, 1996; Wulff, 1997a; Pawlik, 1998).

The combination of its semi-cryptic growth form and palatability to sponge-eating fishes indicates that *M. laevis* should be categorized as a preferred sponge using the criteria defined above (Pawlik et al., 2008). No evidence of a chemical defense was detected in the aquarium feeding assays for sponges sampled from all three collection sites. Samples of *M. laevis* similarly yielded palatable extracts in Pawlik et al. (1995), and these were collected from Belize and the Bahamas (J. Pawlik pers. comm.). However, assays of organic extracts do not account for other defenses, such as spicules or lack of nutritional quality (Burns and Ilan, 2003). These alternative strategies were accounted for using the field feeding experiments, simulating a scenario in which rubble pieces would be overturned during storm events, and sponges exposed. Contrary to Wulff (1997a), there was no evidence that the outer tissue of *M. laevis* offered a defense against fish predators. On reefs where they are present, sponge predators target exposed *M. laevis*, causing substantial tissue loss in a very short time.

Our surveys of Panamanian reefs revealed that a higher proportion of the erect growth form of *M. laevis* was found where sponge predators were rare or absent, indicating that predation alters sponge growth form. Therefore, *M. laevis* is not limited to a semi-cryptic growth form, and is not restricted to growing in tandem with the underside and interstitial surfaces of corals, as proposed by the mutualism hypothesis (Goreau and Hartman, 1966). Moreover, aquarium feeding assays demonstrate that the apparent growth form of *M. laevis* does not comprise a chemically deterrent population from a different geographic locality, because they are just as palatable to sponge-eating fishes as the semi-cryptic form.

Despite the absence of sponge-eating fishes along transects at Adriana's Reef in Panama, 66% of *M. laevis* observed there were semi-cryptic, likely because of the presence of another sponge predator, the sea star *O. reticulatus*. Sea stars were never found on sponges growing on more topographically complex or raised substrata (Loh, pers. obs.), which may explain the limited predatory effect of seastars on *M. laevis* in Panama compared to the more complete predatory effect of fishes in Florida. It is interesting that in the absence of spongivorous fishes, *O. reticulatus* has become the dominant sponge predator on Panamanian reefs, because in other parts of the Caribbean, these sea stars are usually found in rubble or sand flats and seagrass beds, and not on the reef (Wulff, 1995). While *O. reticulatus* is abundant in the seagrass beds of the Bahamas, it has not been seen in similar habitats off the Florida Keys in more than 20 years, probably because of over-collecting (Pawlik, pers. obs.).

Predation is responsible for the semi-cryptic growth form of *M. laevis* among scleractinian corals, and this association is commonly observed in the field (e.g. Hill, 1998). Nevertheless, *M. laevis* has also been observed to grow on other hard substrata such as dead coral, on other species of sponges, and on gorgonian bases (Loh, pers. obs.). The specificity of the association and the actual costs or benefits to the coral host are under investigation in order to further test the mutualism hypothesis. Nevertheless, while *M. laevis* benefits from growing in a semi-cryptic state among corals under high predation pressure, this association appears to lose its advantage for the sponge in the absence of predators.

Sponges now dominate contemporary Caribbean reefs in terms of diversity and abundance (Reiswig, 1973; Diaz and Rützler, 2001), yet little is known of their ecology and interactions with other reef organisms. Interspecific interactions greatly impact ecosystem function (Baskett et al., 2007), and need to be better understood, especially in the face of global coral reef decline (Hughes et al., 2003). Our study highlights a complex interaction among a Caribbean sponge, spongivores, and scleractinian corals. With over-fishing a widespread problem on coral reefs (Burke et al., 1998, Pauly et al., 2002), understanding the responses of populations of *M. laevis* and other sponge species to changes in predation pressure may provide a useful index for the level of ecological function of spongivores on coral reefs.

Acknowledgments

This research was funded by the National Science Foundation (OCE-0550468) and NOAA/NURC (NA96RU-0260), with additional support from the UNCW-GSA travel award.

We thank T. Henkel, S. McMurray, W. Leong, D. Hines, and S. Lopez-Legentil for assistance in the field and the laboratory. Thanks also go out to R. Thacker, C. Diaz and staff members at the Smithsonian Tropical Research Institute, Bocas del Toro, staff members of NOAA/NURC at Key Largo, and the crew of the R/V Seward Johnson II. Comments from two anonymous reviewers helped to improve the manuscript. **[SS]**

References

Baskett, M.L., Micheli, F., Levin, S.A., 2007. Designing marine reserves for interacting species: insights from theory. Biol. Conserv. 137, 163–179.

Becerro, M.A., Thacker, R.W., Turon, X., Uriz, M.J., Paul, V.J., 2003. Biogeography of sponge chemical ecology: comparisons of tropical and temperate defenses. Oecologia 135, 91–101.

Bruno, J.F., Stachowicz, J.J., Bertness, M.D., 2003. Inclusion of facilitation into ecological theory. Trends Ecol. Evol. 18 (3), 119–125.

Burke, L., Bryant, D., McManus, J., Spalding, M., 1998. Reefs at Risk: A Map-Based Indicator of Potential Threats to the World's Coral Reefs. World Resources Institute, Washington D.C.

Burke, L., Maidens, J., Spalding, M., Kramer, P., Green, E., Greenhalgh, S., Nobles, H., Kool, J., 2004. Reefs at Risk in the Caribbean. World Resources Institute, Washington D.C.

Burkepile, D.E., Hay, M.E., 2007. Predator release of the gastropod *Cyphoma gibbosum* increases predation on gorgonian corals. Oecologia 154, 167–173.

Burns, E., Ilan, M., 2003. Comparison of anti-predatory defenses of Red Sea and Caribbean sponges. II. Physical defense. Mar. Ecol. Prog. Ser. 252, 115–123.

Carballo, J.L., Avila, E., Enriquez, S., Camacho, L., 2006. Phenotypic plasticity in a mutualistic association between the sponge *Haliclona caerulea* and the calcareous macroalga *Jania adherens* induced by transplanting experiments. I: morphological responses of the sponge. Mar. Biol. 148, 467–478.

Cushman, J.H., Whitham, T.G., 1989. Conditional mutualisms in a membracid–ant association: temporal, age-specific, and density-dependent effects. Ecology 70, 1040–1047.

Diaz, M.C., Rützler, K., 2001. Sponges: an essential component of Caribbean coral reefs. Bull. Mar. Sci. 69, 535–546.

Dulvy, N.K., Freckleton, R.P., Polunin, N.V.C., 2004. Coral reef cascades and the indirect effects of predator removal by exploitation. Ecol. Lett. 7, 410–416.

Dunlap, M., Pawlik, J.R., 1996. Video-monitored predation by Caribbean reef fish on an array of reef and mangrove sponges. Mar. Biol. 126, 117–123.

Goreau, T.F., Hartman, W.D., 1966. Sponge: effect on the form of reef corals. Science 151, 343–344.

Hill, M.S., 1998. Spongivory on Caribbean reefs releases corals from competition with sponges. Oecologia 117, 143–150.

Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J.B.C., Kleypas, J., Lough, J.M., Marshall, P., Nytröm, M., Palumbi, S.R., Pandolfi, J.M., Rosen, B., Roughgarden, J., 2003. Climate change, human impacts, and the resilience of coral reefs. Science 301, 929–933.

Palumbi, S., 1986. How body plans limit acclimation: responses of a demosponge to wave force. Ecology 67, 208–214.

Pauly, D., Christensen, V., Guénette, S., Pitcher, T.J., Sumaila, R.U., Walters, C.J., Watson, R., Zeller, D., 2002. Towards sustainability in world fisheries. Nature 418 (8), 689–695.

Pawlik, J.R., 1997. Fish predation on Caribbean reef sponges: an emerging perspective of chemical defenses. Proc. 8th Int. Coral Reef Sym. Panama 2, 1255–1258.

Pawlik, J.R., 1998. Coral reef sponges: do predatory fishes affect their distribution? Limnol. Oceanogr. 43, 1396–1399.

Pawlik, J.R., Chanas, B., Toonen, R.J., Fenical, W., 1995. Defenses of Caribbean sponges against predatory reef fish. I. Chemical deterrency. Mar. Ecol. Prog. Ser. 127, 183–194.

Pawlik, J.R., Henkel, T.P., McMurray, S.E., López-Legentil, S., Loh, T., Rohde, S., 2008. Patterns of sponge recruitment and growth on a shipwreck corroborate chemical defense resource trade-off. Mar. Ecol. Prog. Ser. 368, 137–143.

Randall, J.E., Hartman, W.D., 1968. Sponge feeding fishes of the West-Indies. Mar. Biol. 1, 216–225.

Reiswig, H.M., 1973. Population dynamics of three Jamaican Demospongiae. Bull. Mar. Sci. 23, 191–226.

Sokolover, N., Ilan, M., 2007. Assessing anti-predatory chemical defences among ten East Mediterranean sponges. J. Mar. Biol. Assoc. U.K. 87, 1785–1790.

Stachowicz, J.J., 2001. Mutualism, facilitation, and the structure of ecological communities. Bioscience 51, 235–246.

Waddell, B., Pawlik, J.R., 2000. Defenses of Caribbean sponges against invertebrate predators: I. Assays with hermit crabs. Mar. Ecol. Prog. Ser. 195, 125–132.

Walters, K.D., Pawlik, J.R., 2005. Is there a trade-off between wound-healing and chemical defenses among Caribbean reef sponges? Integr. Comp. Biol. 45, 352–358.

Wulff, J.L., 1995. Sponge-feeding by the Caribbean starfish *Oreaster reticulatus*. Mar. Biol. 123, 313–325.

Wulff, J.L., 1997a. Parrotfish predation on cryptic sponges of Caribbean coral reefs. Mar. Biol. 129, 41–52.

Wulff, J.L., 1997b. Causes and consequences of differences in sponge diversity and abundance between the Caribbean and Eastern Pacific of Panama. Proc. 8th Int. Coral Reef Sym. Panama 2, 1377–1382.

Wulff, J.L., 2000. Sponge predators may determine differences in sponge fauna between two sets of mangrove cays, Belize Barrier Reef. Atoll Res. Bull. 477, 250–263.

Wulff, J.L., 2001. Rapid diversity and abundance decline in a Caribbean coral reef sponge community. Biol. Conserv. 127, 167–176.