Accepted: 17 September 2016

DOI: 10.1111/maec.12410

SHORT COMMUNICATION

WILEY marine ecology

Defense by association: Sponge-eating fishes alter the small-scale distribution of Caribbean reef sponges

Michael K. Wooster | **Micah J. Marty** | **Joseph R. Pawlik**

Department of Biology and
Marine Biology, Center for Marine
Science, University of North Carolina
Wilmington, Wilmington, NC, USA

Correspondence
Joseph R. Pawlik, Department of Biology
and Marine Biology, Center for Marine
Science, University of North Carolina
Wilmington, Wilmington, NC, USA.
Email: pawlikj@uncw.edu

Funding information
NSF, Grant/Award Number: OCE-1029515

Abstract

Recent studies have demonstrated that sponge-eating fishes alter the community of sponges on coral reefs across the Caribbean. Sponge species that lack chemical defenses but grow or reproduce faster than defended species are more abundant on reefs where sponge-eating fishes have been removed by overfishing. Does predator-removal have an effect on the distribution of sponges at smaller spatial scales? We conducted transect surveys of sponge species that are palatable to sponge predators in proximity to refuge organisms that are chemically or physically defended (fire coral, gorgonians, hard corals) on the heavily overfished reefs of Bocas del Toro, Panama, and a reef in the Florida Keys where sponge-eating fishes are abundant. In Panama, palatable sponge species were not distributed in close association with refuge organisms, while in the Florida Keys, palatable sponge species were strongly associated with refuge organisms. The presence of fish predators alters the meter-scale pattern of sponge distribution, and defense by association enhances biodiversity by allowing palatable sponges to persist on reefs where sponge-eating fishes are abundant.

KEYWORDS

associational defense, coral reefs, indirect effects, overfishing, predation, sponges

1 | INTRODUCTION

The factors that alter biodiversity in ecosystems have long been of interest to ecologists (Stachowicz, Bruno, & Duffy, 2007). Among the mechanisms that enhance biodiversity is indirect facilitation, which occurs when the survival or fitness of one organism is enhanced indirectly through the presence or behavior of another (Wootton, 2002). One example of indirect facilitation is predator-avoidance by prey species that grow in or among other species that have anti-predatory defenses. This defense by association, or use of associational defenses, is well described in terrestrial ecosystems. For example, removal of chemically defended herbaceous plants from a mixed-species community resulted in the loss of undefended species through herbivory, thereby reducing overall plant biodiversity (Callaway, Kikodze, Chiboshvili, & Khetsuriani, 2005).

For marine ecosystems, among the best examples of associational defenses are described for marine algae. For example, seaweeds growing on a rocky jetty off North Carolina exhibited seasonal changes that reflected herbivory by fishes, with several palatable species persisting only in association with two seaweed species that are chemically defended from herbivorous fishes (Hay, 1986; Pfister & Hay, 1988). In another study conducted on the Mesoamerican barrier reef off Belize, 11 species of seaweeds had greater survivorship when in proximity to sea fans or fire coral than when these seaweed species were more distant from defended cnidarians, with twice the species diversity of algae in association with defended cnidarians than away from them (Littler, Littler, & Taylor, 1987).

Associational defense has also been described in marine invertebrates. In the rocky subtidal of the San Juan Islands in Washington State, solitary ascidians with morphological defenses provide refuge habitat for the undefended ascidians *Boltenia villosa* and *Styela gibbsii*, whose distribution is otherwise restricted to habitats that lack the predatory snail *Fusitriton oregonensis* (Young, 1986). Another example of associational defense in invertebrates is the Caribbean orange icing sponge, *Mycale laevis*, which lacks chemical defenses. This species is found growing under coral colonies or between coral branches on Caribbean reefs where sponge-eating fishes are abundant, but on the reefs off of Bocas del Toro, Panama, where spongivores are absent, *M. laevis* grows in a non-cryptic, erect form (Loh & Pawlik, 2009). Field feeding experiments confirmed that spongivorous fishes readily ate *M. laevis*, and caging experiments demonstrated that this sponge would grow out of its refuge if protected from predators.

Predation has recently been shown to structure the community of sponges on Caribbean reefs, with sponge-eating fishes removing sponge species that lack chemical defenses (Loh & Pawlik, 2014). On reefs where sponge-eating parrotfishes and angelfishes were removed by intensive fish-trapping, fast-growing sponge species that lacked chemical defenses dominated the sponge community, and these sponge species were more likely to contact or overgrow reef-building corals than at sites where sponge predators were more abundant (Loh, McMurray, Henkel, Vicente, & Pawlik, 2015). While these studies demonstrated differences in sponge community composition across large spatial scales, they did not address changes that might occur at smaller scales, on the order of meters and on individual reefs. Associational defenses have been described for one sponge species (*M. laevis*, above), but how do the grazing activities of sponge predators alter the distributions of other sponge species at small spatial scales? To answer this question, we conducted transect surveys of sponge species palatable to sponge-eating fishes in relation to potential refuge organisms at two locations having markedly different abundances of sponge-eating fishes. We predicted that palatable sponge species would be clumped near refuge organisms on reefs with a high abundance of sponge-eating fishes, but that this would not occur on reefs without sponge predators.

2 | MATERIAL AND METHODS

Transect surveys were conducted on reefs adjacent to two locations in the Caribbean: Bocas del Toro, Panama, and Key Largo, Florida. These locations were chosen because a recent study had established the relative abundances of sponge-eating fishes (primarily angelfishes and parrotfishes of the genus *Sparisoma*) at each location, with the heavily overfished Panama reefs having the mean lowest abundance of 69 sites across the Caribbean, and the Key Largo sites having the mean highest abundance (spongivore index in dataset S3 of Loh & Pawlik, 2014).

Belt transects, 30 m in length, were run parallel to the shore and each other, ~10 m apart (English, Wilkinson, & Baker, 1997). In December 2013, 20 surveys in total were conducted on two reefs off Bocas del Toro, Panama: 12 surveys at Punta Caracol (09°22.690′ N, 82°18.230′ W; eight at depths ranging from 5–10 m and four in shallow water <3 m) and eight surveys at Airport Reef (09°20.242′ N, 82°15.555′ W; four at 5–10 m and four at ~2 m depth). In June 2014, 15 transects were conducted on Conch Reef (24°56.996′ N, 80°27.223′ W) off Key Largo, Florida, where sponge-eating fishes are abundant. Beyond the differences in abundance of sponge-eating fishes, the survey depth was different for each location (Panama: 2–10 m; Florida Keys: 15–20 m), but the benthic fauna at both sites was remarkably similar, as previously documented (Loh & Pawlik, 2014; Loh et al., 2015; Pawlik & Loh, 2016).

Palatable sponge species were identified at both locations using a photographic taxonomic key (Zea, Henkel, & Pawlik, 2014) in combination with data on chemical defenses for 106 Caribbean sponge species presented in Loh and Pawlik (2014). For each transect survey, all palatable sponges (undefended and variably defended species, see Loh & Pawlik, 2014) within a meter on both sides of the transect line were located and identified, it was noted whether they were associated with a refuge organism, and the identity of the refuge organism was recorded. Refuge organisms were chosen based on previous studies (Littler et al., 1987; Loh & Pawlik, 2014; O'Neal & Pawlik, 2002). Four different categories of refuge organisms were recorded: octocorals, hard corals, fire corals and chemically defended sponges; of these, Caribbean octocorals are all known to be chemically defended (O'Neal & Pawlik, 2002), while the chemically defended sponge species were identified using Loh and Pawlik (2014). A palatable sponge was considered associated with a refuge organism if >50% of its volume was in direct proximity (<2 cm distance) to a refuge organism; this included sponges growing within the branches of, or under, or intertwined within the refuge organism. To analyse the survey data for significant differences between the number of palatable sponges found associated and not associated with refuge organisms, a *t* test was conducted on the abundance data for each sponge species at each location. A *G* test of independence with William's correction was applied to values in a contingency table of sponge abundances to determine if the presence of sponge-eating fishes and association were correlated or independent of each other.

3 | RESULTS AND DISCUSSION

The number of palatable sponge species observed in transects at each location was eight for sites at Bocas Del Toro, Panama, and 11 for sites at Key Largo, Florida, with four sponge species being found at both locations (species listed in the legends for Figures 1 and 2). On reefs in Panama, where sponge-eating fishes were absent, six of the eight sponge species were more frequently not associated with refuge organisms (t test, $p < .05$), while there was no difference in distribution for the other two species (Figure 1). Palatable sponges on Panama reefs appeared to be distributed randomly, although the survey technique did not permit testing of the spatial distribution of palatable sponge species relative to a random distribution, as that would have required mapping the sponges, which was beyond the specific goal of the present study. Considering that space in proximity to a refuge organism represented a smaller fraction of the total space available to benthic organisms on the reef, palatable sponges distributed in a randomized manner would be expected to occur more frequently away from refuge organisms. Nevertheless, this was not true for two palatable sponge species, *Haliclona vansoesti* and *M. laevis*, for which there was no significant difference in distribution

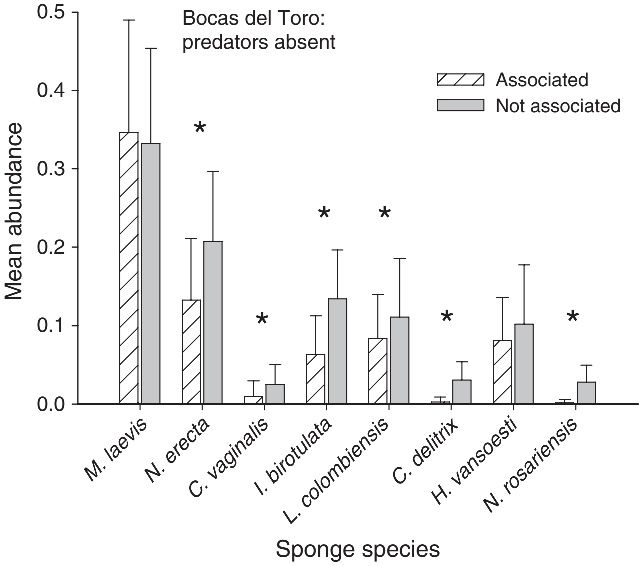

FIGURE 1 Abundance of palatable sponge species per m^2 for reef sites off Bocas del Toro, Panama. Error bars are *SD*. Striped bars indicate sponges counted that were associated with refuge organisms, and gray bars indicate sponges not associated with refuge organisms. An asterisk indicates species that were significantly more likely not to be associated with refuge organisms ($p < .05$). Palatable sponge species recorded were: *Mycale laevis*, *Niphates erecta*, *Callyspongia vaginalis*, *Iotrochota birotulata*, *Lissodendoryx colombiensis*, *Cliona delitrix*, *Haliclona vansoesti*, *Neopetrosia rosariensis*

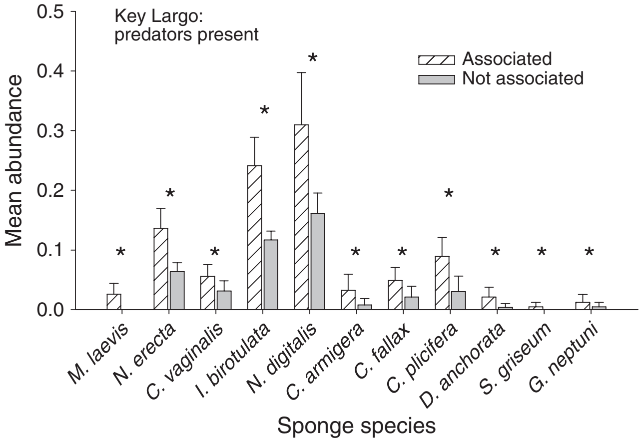

FIGURE 2 Abundance of palatable sponge species per m^2 for reef sites on Conch Reef, off Key Largo, Florida Keys. Error bars are *SD*. Striped bars indicate sponges counted that were associated with refuge organisms, and gray bars indicate sponges not associated with refuge organisms. An asterisk indicates species that were significantly more likely to be associated with refuge organisms ($p < .05$). Palatable sponge species recorded were: *Mycale laevis*, *Niphates erecta*, *Callyspongia vaginalis*, *Iotrochota birotulata*, *Niphates digitalis*, *Callyspongia armigera*, *Callyspongia fallax*, *Callyspongia plicifera*, *Desmapsamma anchorata*, *Strongylacidon griseum*, *Geodia neptuni*

in association or not associated with refuge organisms. Both of these species are soft, fragile and grow close to hard substrata; hence, their tendency to grow on or among coral skeletons likely enhanced their distribution in association with living, as well as dead, reef-building corals.

On Florida reefs, where sponge-eating fishes were abundant, all 11 palatable sponge species that were counted inside transects were significantly more often associated with refuge organisms (Figure 2). Palatable sponges at these sites often exhibited bite marks on their surfaces, particularly those that were not associated with refuge organisms. Lobate or encrusting palatable sponge species such as *M. laevis* were more commonly found associated with coral, while branching and tube sponges like *Iotrochota birotulata* and *Callyspongia vaginialis* were more commonly associated with erect or branching defended sponges (often *Amphimedon compressa* and *Aplysina cauliformis*) and upright octocorals (such as *Iciligorgia schrammi*, *Plexaura* spp. and *Gorgonia ventalina*).

A conceptual model of the ecology of sponges on Caribbean reefs (Pawlik, 2011) successfully predicted that sponge communities are controlled by sponge-eating fishes, resulting in indirect effects on reef-building corals (Loh & Pawlik, 2014; Loh et al., 2015). These studies demonstrated that predation alters sponge community structure among reef locations across the Caribbean. The goal of the present study was to examine the effect of predation at much smaller spatial scales. We predicted a skewed distribution of palatable sponges near refuge organisms at the Florida location where sponge-eating fishes are abundant and consume palatable sponge species that are easily accessible, leaving only those that are protected by refuge organisms that are chemically (sponges, gorgonians) or physically (fire coral, hard coral) defended. Across all species, 69% of the palatable sponges recorded in Florida were scored as being in association with refuge organisms, while in Panama, where sponge-eating fishes are nearly absent, only 43% of palatable sponges were in association with refuge organisms. Spongivore abundance and palatable sponge association with refugia were highly correlated with each other (*G* test of independence, $G = 206.81$, $df = 1$, $p < .0001$).

The orange icing sponge, *M. laevis*, was the most abundant palatable sponge species in surveys of Panama sites, and occurred almost equally in association and not associated with refuge organisms, but was one of the least abundant palatable sponges in the Florida Keys, where it was only found in associational refugia. These results corroborate those of previous studies on this sponge species, which was once thought to be in a mutualistic symbiotic relationship with the reef-building corals on which it is often found growing (Loh & Pawlik, 2009). Not only is the cryptic growth form of this sponge species a direct consequence of grazing by sponge-eating fishes on reefs where these predators are abundant, no particular advantage could be demonstrated for the coral in locations where the sponge is cryptic, and this sponge species rapidly grows outward and smothers corals when predators are absent or removed in manipulative experiments (Loh & Pawlik, 2009, 2012).

This study is further demonstration that indirect facilitation is an important mechanism for enhancing biodiversity. When sponge-eating fishes are abundant, associational refuges enhance species richness by permitting the survival of sponge species that would otherwise be removed by predation. Overfishing, however, removes top-down control by sponge-eating fishes and allows palatable sponge species to grow on any acceptable substratum. Sponges are aggressive competitors for space on reefs (Aerts, 1998). Space is one of the prime limiting resources for sessile organisms, so those that can out-compete or grow faster will tend to dominate. Without predators to control the abundance of palatable sponges, they begin to overgrow reef-building corals; surveys of reefs across the Caribbean demonstrate a three-fold increase in overgrowth of corals by sponges on overfished reefs (Loh et al., 2015).

In summary, this study found support for the hypothesis that predation forces palatable sponge species into associational refuges, thereby altering small-scale distributions of these species in sites where predators are abundant. Without predation palatable sponges are relieved of their top-down control and can persist wherever they recruit. While the removal of predators may diminish biodiversity on Caribbean reefs as fast-growing palatable sponges smother other benthic organisms, defense by association enhances biodiversity by allowing palatable sponges to persist in association with refuge organisms on healthy reefs with abundant sponge-eating fishes.

ACKNOWLEDGEMENTS

This project was completed by M.K.W. as part of an undergraduate degree at the University of North Carolina Wilmington for graduation with Honors. Funding was provided by the National Science Foundation (OCE-1029515 to J.R.P.) and field work in Panama was supported as part of a field course at the Tropical Conservation Consortium.

REFERENCES

Aerts, L. A. M. (1998). Sponge/coral interactions in Caribbean reefs: Analysis of overgrowth patterns in relation to species identity and cover. *Marine Ecology-Progress Series*, *175*, 241–249.

Callaway, R. M., Kikodze, D., Chiboshvili, M., & Khetsuriani, L. (2005). Unpalatable plants protect neighbors from grazing and increase plant community diversity. *Ecology*, *86*, 1856–1862.

English, S., Wilkinson, C., & Baker, V. (1997). *Survey manual for tropical marine resources*. Townsville, Australia: Australian Institute of Marine Sciences.

Hay, M. E. (1986). Associational plant defenses and the maintenance of species diversity: Turning competitors into accomplices. *American Naturalist*, *128*, 617–641.

Littler, M. M., Littler, D. S., & Taylor, P. R. (1987). Animal-plant defense associations: Effects on the distribution and abundance of tropical reef macrophytes. *Journal of Experimental Marine Biology and Ecology*, *105*, 107–121.

Loh, T.-L., McMurray, S. E., Henkel, T. P., Vicente, J., & Pawlik, J. R. (2015). Indirect effects of overfishing on Caribbean reefs: Sponges overgrow reef-building corals. *PeerJ*, *3*.

Loh, T.-L., & Pawlik, J. R. (2009). Bitten down to size: Fish predation determines growth form of the Caribbean coral reef sponge *Mycale laevis*. *Journal of Experimental Marine Biology and Ecology*, *374*, 45–50.

Loh, T.-L., & Pawlik, J. R. (2012). Friend or foe? No evidence that association with the sponge *Mycale laevis* provides a benefit to corals of the genus *Montastraea*. *Marine Ecology Progress Series*, *465*, 111–117.

Loh, T.-L., & Pawlik, J. R. (2014). Chemical defenses and resource trade-offs structure sponge communities on Caribbean coral reefs. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, 4151–4156.

O'Neal, W., & Pawlik, J. R. (2002). A reappraisal of the chemical and physical defenses of Caribbean gorgonian corals against predatory fishes. *Marine Ecology-Progress Series*, *240*, 117–126.

Pawlik, J. R. (2011). The chemical ecology of sponges on Caribbean reefs: Natural products shape natural systems. *BioScience*, *61*, 888–898.

Pawlik, J. R., & Loh, T.-L. (2016). Biogeographical homogeneity of Caribbean coral reef benthos. *Journal of Biogeography*. doi:10.111/jbi.12858

Pfister, C. A., & Hay, M. E. (1988). Associational plant refuges: Convergent patterns in marine and terrestrial communities result from differing mechanisms. *Oecologia*, *77*, 118–129.

Stachowicz, J. J., Bruno, J. F., & Duffy, J. E. (2007). Understanding the effects of marine biodiversity on communities and ecosystems. *In Annual Review of Ecology Evolution and Systematics*, *38*, 739–766.

Wootton, J. T. (2002). Indirect effects in complex ecosystems: Recent progress and future challenges. *Journal of Sea Research*, *48*, 157–172.

Young, C. M. (1986). Defenses and refuges: Alternative mechanisms of coexistence between a predatory gastropod and its ascidian prey. *Marine Biology*, *91*, 513–522.

Zea, S., Henkel, T. P., & Pawlik, J. R. (2014). *The Sponge Guide: a picture guide to Caribbean sponges*.