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## Coral reef sponges: Do predatory fishes affect their distribution?

**Abstract**—The predatory activities of fishes are thought to have little impact on the distribution and abundance of sponges on Caribbean coral reefs. To test this premise, 15 species of sponges were transplanted from mangrove and grassbed habitats, where spongivorous fishes are rare, to shallow patch reefs, where spongivorous fishes are common. Twelve of these 15 sponge species could also be found in cryptic locations, but not in conspicuous locations, on nearby reefs. After 3 d, there was significant loss of wet mass of uncaged sponges versus caged sponges for nine sponge species because of consumption by spongivores, primarily angelfishes. A mean of >50% of the sponge tissue was consumed for seven species: *Chondrilla nucula*, *Chondrosia collectrix*, *Geodia gibberosa*, *Halichondria* sp., *Halichondria melanodocia*, *Myriastra kalititilla*, and *Tedania ignis*. These results, in addition to other recent data on the chemical defenses of Caribbean reef sponges against generalist predatory fishes, suggest that predation plays an important role in structuring the reef sponge community and that predation limits the distribution of some Caribbean sponges.

Sponges are important components of benthic communities ranging from polar seas (Dayton et al. 1974; McClintock 1987) to temperate and tropical waters (Reiswig 1973; Wenner et al. 1983) but are particularly prominent on coral reefs, where they often rival both hard and soft corals in diversity and abundance. For example, Schmahl (1991) reported transect means of 10.5 species and 17.5 individual sponges m<sup>-2</sup> on a 20-m-deep reef off the Florida Keys. In addition to

being diverse and abundant, sponges are important to the ecology of coral reefs because they are significant filter feeders, competitors, agents of bioerosion, and sources of nutrients derived from cyanobacterial symbionts (Bergquist 1978; Rützler 1990).

Our conventional understanding of fish predation on Caribbean reef sponges comes from an exhaustive study of fish gut contents conducted by Randall and Hartman (1968). Of 212 species of Caribbean fishes, only 11 contained sponge remains that comprised 6% or more of the gut volume. The paucity of spongivorous species prompted the authors to comment that “the Porifera of the West Indies appear to enjoy relative freedom from predation by fishes” (Randall and Hartman 1968). The lack of predation on sponges by generalist predators was ascribed to the defensive properties of sponges, most notably “mineralized sclerites, noxious chemical substances, and tough fibrous components,” with the few spongivorous fish species belonging to highly specialized teleost families (e.g., angelfishes, boxfishes, and filefishes). These spongivores frequently had several different species of sponges represented in their gut contents, prompting Randall and Hartman (1968) to propose that spongivores used a “smorgasbord” feeding strategy of eating small amounts of many sponges so that they “never run the risk of eating large quantities of a sponge species that is toxic or relatively low in nutritive value.” The same conclusion was reached by Wulff (1994) after recording each bite that

fishes took of sponges on a Panamanian reef. With the feeding activities of the few spongivorous fishes spread out over a large number of sponge species, the impact of spongivory on any one species was believed to be negligible.

We recently performed a survey of the chemical defenses of 73 species of Caribbean sponges against a generalist predatory reef fish (Pawlik et al. 1995) and discovered that reef sponge species yielded crude organic extracts that were more effective at deterring fish predation than extracts from mangrove or grassbed sponge species. After further investigation, we discovered that many of the sponge species that occurred as large, conspicuous specimens in mangrove or grassbed habitats, where spongivorous fishes are rare or absent, could also be found growing as small or encrusting specimens in cryptic reef habitats (e.g., under coral rubble). To test whether the foregoing differences are due to spongivory, we conducted the following experiments.

Transplantation experiments were conducted periodically from May to September 1993–1997 on 7- to 12-m-deep patch reefs off Sweetings Cay, Grand Bahama Island; off Acklins Island, Bahamas; or off Key Largo, Florida. Sponges were collected from mangrove habitats (*Aaptos aaptos*, *Chondrilla nucula*, *Chondrosia collectrix*, *Dysidea etheria*, *Geodia gibberosa*, *Halichondria* sp., *Halichondria melanodocia*, *Lissodendoryx sigmata*, *Myriastrra kalitetilla*, *Tedania ignis*, and *Tethya actinia*) or from seagrass beds (*Anthosigmella varians*, *Cinachyra alloclada*, *Haliclona hogarthi*, and *Spongia obscura*) within 4 km of the patch reefs where the experiments were conducted. Sponges were carefully collected to minimize tissue damage. Fist-sized portions were gently removed from the substratum or cut from larger sponges with a razor blade so that the cut surface was only a small part of the overall surface area. Detached sponges were placed in plastic bags underwater, then transferred underwater into large containers of flowing, aerated seawater for transport to the laboratory.

For each species, 30 sponge portions were tagged and weighed in the laboratory. Each portion was skewered underwater with a numbered, 30-cm cable tie, removed from seawater for 3 s, placed in a pretared container of seawater, and weighed on an electronic balance. Sponges were then returned to large containers for transport to the patch reef site. Sponges were returned to the field as quickly as possible, usually 3–4 h after initial collection. At the patch reef sites, each sponge portion was attached by its cable tie to a 20- × 10- × 6-cm brick, and 15 of these were placed inside 40-cm<sup>3</sup> cages made of Vexar mesh with 2-cm<sup>2</sup> openings. Sponge portions were attached to bricks so that the cut surface of the sponge was against the brick surface (i.e., the cut surface was not exposed to predators). Fifteen pairs of caged and uncaged sponges were haphazardly deployed on the patch reef, with the uncaged sponges within 1 m of the caged sponges. Feeding activity was periodically monitored at the site during each experiment. After 72 h, the sponges were collected with their cable ties intact, bagged, transported, and weighed as before. These experiments did not require partial cages or other controls for separating cage artifacts from the effects of predation (e.g., Steele 1996) because the experi-

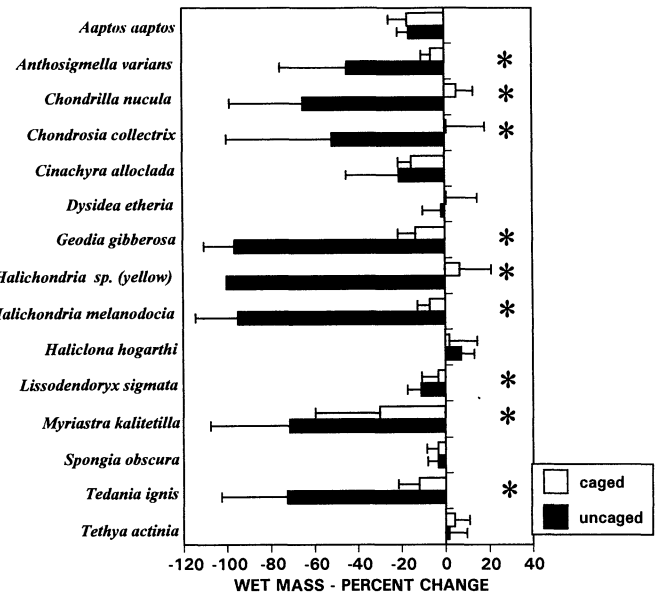


Fig. 1. Mean percentage change ( $\pm$ SD;  $N = 15$ ) in wet mass after 72 h of Caribbean grassbed and mangrove sponges transplanted to patch reefs. \* Significant difference in mass between paired caged and uncaged sponges ( $P < 0.05$ , Wilcoxon paired-sample test).

mental time period was too short for factors other than predation to produce spurious results (such as growth differences between the caged and uncaged sponges) and because spongivory could be readily observed and its effects were obvious. The significance of differences in the percentage change of the wet mass of caged versus uncaged sponges was determined using the Wilcoxon paired-sample test (Zar 1984).

Of 15 sponge species transplanted from mangrove or grassbed environments to patch reefs, 9 lost a significant amount of mass during the 72 h (Fig. 1). For all but one of these species, tissue loss was clearly the result of spongivory by fishes; angelfishes, primarily *Pomacanthus paru* and *Pomacanthus arcuatus*, were observed feeding on these species as soon as they were deployed on the reef. Others, including parrotfishes (*Sparisoma* spp.), filefishes (*Catherhines* spp.), and trunk- and cowfishes (*Lactophrys* and *Acanthostracion* spp.), were also observed feeding on these species. Spongivory was also evident by bite marks left in remaining uncaged sponge portions. Only uncaged portions of *L. sigmata* lost a significant percentage of mass relative to caged portions without obvious evidence of spongivory; fishes were not observed consuming this species, and bite marks were not evident on uncaged sponge portions. It is possible that predation by smaller fishes or invertebrates was responsible for the small but significant loss of mass observed for uncaged *L. sigmata*. At the same time that a majority of the uncaged sponges used in these transplant experiments lost weight because of predation, specimens of 6 of 15 species grew (gained mass) in only 72 h when protected by cages from spongivorous fishes. Because not all sponge species responded as well to transplantation, some lost mass in cages over the course of the 3-d experiment, but the loss was minor

compared to the loss experienced because of predation on uncaged sponge pieces.

Predation by spongivorous fishes clearly limits the distribution and abundance of some sponge species. Of the nine species that were consumed in this study, six can be found in cryptic habitats on the reef but not in exposed locations (Meesters et al. 1991; Dunlap and Pawlik 1996; Wulff 1997). *A. varians* is found in grassbed environments as an upright, amorphous sponge with portions extending below the sediment, but on the reef it is only found boring into coral rock, with little or no soft tissue exposed. Similarly, *C. nucula* is found as large, fleshy lobes covering mangrove roots but as thinly encrusting patches in reef environments. Species such as *C. collectrix*, *G. gibberosa*, and *T. ignis* can be found only in small patches under coral rubble (Meesters et al. 1991; Dunlap and Pawlik 1996; Wulff 1997). When coral rubble was overturned to expose cryptic specimens of *Chondrosia collectrix* and *Tedania ignis* on reefs in the Florida Keys, 63 of 67 sponges were completely consumed within 24 h (Dunlap and Pawlik 1996). Predation can account for the absence of these species from exposed locations on Caribbean reefs; in the absence of spongivorous fishes, these species would likely grow out of cryptic locations. The fact that 8–14% of the sponge contents in the stomachs of four of the six most common spongivorous fishes on Caribbean reefs was made up of sponges restricted to cryptic locations (*C. collectrix*, *G. gibberosa*, and *T. ignis*) (Randall and Hartman 1968) suggests that these fish continuously remove preferred sponge species as rubble is overturned or as sponges grow out of concealed locations.

Predation may not be the only factor restricting the distribution of some sponges to cryptic or nonreef sites. Some species are probably too delicate to withstand the hydrodynamic conditions of the exposed reef. Two easily damaged sponges, *D. etheria* and *H. hogarhi*, are found in cryptic locations on the reef yet were not consumed in our experiments, suggesting that other factors restrict their distributions. *T. actinia*, also not consumed in this study, has the capacity to move slowly over the substratum and has a marked preference for shaded locations. Besides physical limitations, other biological factors may restrict the distribution of some sponges, including predation by invertebrates (Wulff 1995). The short-term experiments described in this study would have likely missed the effects of low-level, persistent spongivory.

The results of this and other recent investigations of spongivory and sponge chemical defenses suggest that the conventional view of the ecology of sponges on Caribbean coral reefs needs to be reexamined (Randall and Hartman 1968; Wulff 1994). Surveys of the defensive roles of chemistry, spicules, tissue toughness, and nutritional quality (Chanas and Pawlik 1995; Pawlik et al. 1995) suggest that generalist fish predators are deterred by sponge chemistry but not by structural or nutritional defenses. Spongivorous fishes, such as angelfishes and filefishes, do not generally circumvent sponge chemistry by smorgasbord feeding (Randall and Hartman 1968; Wulff 1994) but instead choose to feed predominantly on chemically undefended sponge species (Pawlik et al. 1995; Pawlik and Dunlap 1996). Most importantly, fish predators have a ma-

JOR IMPACT ON THE DISTRIBUTION AND ABUNDANCE OF SPONGES ON CARIBBEAN REEFS BECAUSE FISH PREDATORY ACTIVITIES RESTRICT SOME SPONGE SPECIES TO REFUGIA.

Joseph R. Pawlik

Department of Biological Sciences  
Center for Marine Science Research  
University of North Carolina  
Wilmington, North Carolina 28403-3297

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