

**FISH PREDATION ON CARIBBEAN REEF SPONGES:  
AN EMERGING PERSPECTIVE OF CHEMICAL DEFENSES**

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**ABSTRACT**

New data on the chemical defenses of Caribbean sponges against fish predators, and on fish predation on sponges transplanted to reefs, suggest that the traditional view of reef fish predation on sponges needs to be re-examined. Generalist predatory reef fishes are deterred by sponge chemistry, but not by structural elements, toughness, or the nutritional quality of sponge tissue. Spongivorous fishes are not "smorgasbord" feeders (circumventing sponge chemistry by eating small amounts of many different species), but instead choose to eat chemically undefended apparent and cryptic sponge species. Most importantly, the traditional view that fish predators have little impact on the distributions and abundances of sponges on Caribbean reefs is incorrect, because it can be demonstrated that the activities of spongivores restrict some sponge species to refugia. The elaboration of chemical defenses plays an important role in the ecology of sponges on Caribbean reefs.

**INTRODUCTION**

Sponges constitute a diverse and abundant component of tropical reef ecosystems, where they are important filter feeders, competitors, agents of bioerosion, and sources of nutrients (reviewed in Pawlik et al. 1995). In terms of percentage cover, they often rival scleractinian and gorgonian corals (Targett and Schmahl 1984), but unlike these taxa, the often soft and fleshy tissue of reef sponges seems defenseless in an environment noted for intense levels of predation (Huston 1985).

Sponge tissues have yielded more novel and unusual organic compounds (natural products, secondary metabolites) than those of any other group of marine organisms (Faulkner 1995 and preceding reviews). Chemical defense has long been suggested as an important mechanism protecting sponges (Pawlik 1993), but other defensive strategies have also been proposed (Randall and Hartman 1968). I wish to take the opportunity afforded by this Symposium on the Chemical Ecology of Reef Invertebrates to broadly review the "conventional wisdom" regarding predation by fishes on Caribbean reef sponges, and propose some new perspectives based on recent research on sponge chemical defenses against fish predators. To accomplish this overview, I take the liberty of comparing data sets from research conducted through the years on reefs from many sites in the Caribbean, taking advantage of the general uniformity of species of fishes and sponges represented on these reefs.

**THE ORGANISMS**

In order to facilitate a discussion of predation on Caribbean sponges, it is useful to define a set of terms that generally describe the organisms referred to in this overview.

**THE PREY.** *Reef sponges* are species that grow in apparent (non-cryptic) locations on the reef. Reef sponges are generally not found growing in mangrove habitats, probably because of physical factors (variable salinity and temperatures, high turbidity, etc.), but some species are found in grassbed habitats, which are more physically stable. *Cryptic sponges* are species of sponges that grow in cryptic locations on the reef, generally under coral or rock rubble adjacent to the reef crest. Some cryptic sponge species are only found in cryptic locations on the reef, but several species (e.g., *Chondrosia collectrix*,

*Dysidea etheria*, *Geodia gibberosa*, *Tedania ignis*) are also found in mangrove habitats (Meesters et al. 1991). *Mangrove sponges* are species of sponges that grow in apparent locations in mangrove habitats, usually attached to mangrove prop roots. Although some mangrove sponges are only found in mangrove and grassbed habitats, many species are also cryptic sponges.

**THE PREDATORS.** Fishes appear to be the most important consumers in tropical benthic reef communities (Hixon 1983, Hay 1991). Little is known about the importance of invertebrate predation on sponges. Although dorid nudibranchs may be important sponge predators on Pacific reefs (Thompson, 1976), they are rarely encountered in the Caribbean. The Caribbean seastar *Oreaster reticulatus* is known to eat sponges, but is restricted to grassbed habitats (Wulff 1995). Turtles, particularly the hawksbill (*Eretmochelys imbricata*), consume sponges (Meylan 1988), but these predators are very rare, and their effects appear to be broadly spread out over the reef habitat. For the purposes of this overview of Caribbean reef sponge predation, only fish predators will be considered. *Generalist predators* include a wide array of predatory fishes that feed opportunistically on reefs, including wrasses, snappers, grunts, damselfishes, and basses. Generalist predators are also found in non-reef habitats, such as mangroves, but the species represented are often different. *Spongivores* make up 10-15 species of fishes that feed predominantly or opportunistically on sponges. These primarily include members of the genera *Holacanthus* and *Pomacanthus* (angelfishes), *Catherhines* (filefishes), and *Lactophrys* (=Acanthostracion; trunkfishes) (Randall and Hartman 1968; Wulff 1994; Dunlap and Pawlik 1996). In addition, it has recently been discovered that some parrotfishes are important sponge predators, particularly *Sparisoma aurofrenatum* and *S. chrysopteron* (Dunlap and Pawlik 1996). Among the spongivorous fishes, there do not appear to be any "specialists", in the sense that some insects feed on one species of plant, or some opisthobranch molluscs feed exclusively on one species of sponge (cf. Wulff 1994). Although some fish species clearly prefer certain sponges over others (Wulff 1994), the guts of these species generally contain many other types of organisms (Randall and Hartman 1968). Spongivores are common in reef habitats, but are rarely seen away from the reef in grassbed or mangrove habitats.

**TRADITIONAL CONCEPTS OF PREDATION ON REEF SPONGES**

Our conventional understanding of predation on sponges primarily comes from a herculean study of reef fish gut contents conducted by Randall and Hartman (1968). A similar pairing of such accomplished taxonomists of fishes and sponges is not likely to be repeated. Randall and Hartman (1968) analyzed the stomach contents of 212 species of Caribbean fishes and found sponge remains that comprised over 6% of the contents in only 11 fish species, prompting them to comment that "...the Porifera of the West Indies appear to enjoy relative freedom from predation by fishes". Randall and Hartman (1968) ascribed the lack of predation on sponges by generalist predators to the defensive properties of sponges, most notably "...mineralized sclerites, noxious chemical substances, and tough fibrous components...". They reported no obvious correlation between the color or shape of sponges and their tendency to be eaten by fishes.

Among the few species that Randall and Hartman (1968) found were spongivorous, sponges comprised over 95% of the diet of angelfishes of the genus *Holacanthus*, over 70% of angelfishes of the genus *Pomacanthus*, and more than 85% of

the filefish *Cantherhines macrocerus*. These spongivores belong to highly specialized teleost families, suggesting to Randall and Hartman (1968) that spongivory had evolved geologically recently. Spongivores frequently had several different species of sponges represented in their gut contents, with up to 9 species identified from the stomach of one specimen of *Holacanthus ciliaris*. In order to circumvent sponge defensive characteristics, Randall and Hartman (1968) believed 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."

Wulff (1994) investigated predation in the field, and recorded each bite that fishes took of sponges in a 16 m<sup>2</sup> observation area on a Panamanian reef. Although this study did not document what fish actually consumed (fishes often bite at objects without eating them), the results matched those of Randall and Hartman (1968) for the major spongivores, and Wulff (1994) also concluded that spongivores are smorgasbord feeders. Wulff (1994) dismissed the importance of sponge secondary chemistry in deterring spongivores, suggesting that "[T]hese fish clearly choose what to eat with care; but their goal is not to avoid particular species, but to eat a variety of species." She further hypothesized that spongivores use sponge color to actively alternate feeding on various sponge species (i.e., they only take a few bites of a sponge of one color before switching to a sponge of another color), thereby avoiding a toxic dose of metabolites from any one species.

In general, conventional ideas on reef fish predation on sponges could be summarized as follows: (1) Generalist predators are deterred from eating sponges because sponge tissue contains spicules, defensive metabolites, tough fibers, or poor nutritional quality. (2) Spongivores are smorgasbord feeders, eating small amounts of many differently colored species. (3) Sponge chemistry has little impact on spongivores because of smorgasbord feeding. (4) Fish predators (generalists and spongivores) have little impact on the distribution and abundances of sponges on Caribbean reefs.

#### AN EMERGING PERSPECTIVE OF CHEMICAL DEFENSES

We have recently completed a survey of the chemical antipredatory defenses of 73 species of Caribbean sponges using a common generalist predatory fish, the bluehead wrasse *Thalassoma bifasciatum*, as an assay organism (Pawlik et al. 1995). In parallel studies of subsets of this same group of sponges, we assessed the defensive properties of spicules and determined the tensile strength, the protein, lipid, and carbohydrate content, and the total caloric value of sponge tissues (Chanas and Pawlik 1995). To date, these surveys represent the most complete study of chemical and structural defenses for a group of organisms common to one biogeographic region, and provide an important set of data for comparisons with earlier work on Caribbean sponge predation.

Surprisingly, there was no evidence that generalist predators are deterred by the glass spicules found in many Caribbean demosponges (Chanas and Pawlik 1995). This was true whether or not the spicules were assayed in their natural conformations in combination with the proteinaceous skeleton of the sponge; in fact, the presence of spongin actually enhanced the palatability of nutritionally poor foods (Chanas and Pawlik 1996). Organic solvent extracts of a majority of sponge species deterred feeding, however, and the number of deterrent species was greater in reef habitats than in mangrove or grassbed habitats (Pawlik et al. 1995). There was no relationship between sponge color and detergency, suggesting that sponges are not aposematic and that color variation is the result of other factors. But more surprising, there was no evidence that sponge species lacking in chemical defenses were more likely to have tougher tissues or tissues with lower nutritional quality than chemically deterrent species. In fact, sponge tissues proved to have a high concentration of soluble protein (mean of 20.7 mg protein/ml tissue, N=71; Chanas and Pawlik 1995).

The results of the foregoing studies are perhaps more interesting in light of what they tell us about the feeding preferences of the spongivores, not just the generalist predators. It is safe to assume that sponge extracts that are palatable to generalists would also be palatable to spongivorous species. And indeed, spongivores appear to prefer species that yielded palatable extracts in assays with generalist predators (Pawlik et al. 1995). Combining the data from Randall and Hartman (1968) with those of Pawlik et al. (1995), the majority of the sponges found in the stomachs of the most common spongivores are those that lack chemical defenses (Fig. 1). This suggests that, rather than circumventing or tolerating toxic sponge chemistry, spongivores preferentially select sponge species that lack deterrent chemistry. Rather than spreading their predatory activity out over a large number of species, only one or two sponge species make up 25-56% of the sponge tissue in the stomachs of four of the six major spongivores (Table 1), and these sponge species are notable because (1) they have palatable crude extracts and (2) they are among the ten most common sponge species on Caribbean reefs (Pawlik et al. 1995). If spongivorous fishes were truly smorgasbord feeders, one would expect a long list of sponge species in their diet, each comprising a low percentage of the total gut contents, but this is not the case (Randall and Hartman 1968, Table 1). Estimates of feeding based on the number of fish bites have also been used to support the smorgasbord feeding hypothesis (Wulff 1994), but the act of biting a sponge does necessarily result in the consumption of tissue. When we video-recorded fish feeding on an array of mangrove and reef sponges (Dunlap and Pawlik 1996), we found that fishes took large bites of soft mangrove species (*Tedania ignis* and *Halichondria* sp.), small bites of tough mangrove species (*Chondrosia collectrix* and *Geodia gibberosa*) and apparently removed no tissue when they bit at reef species (reef species were

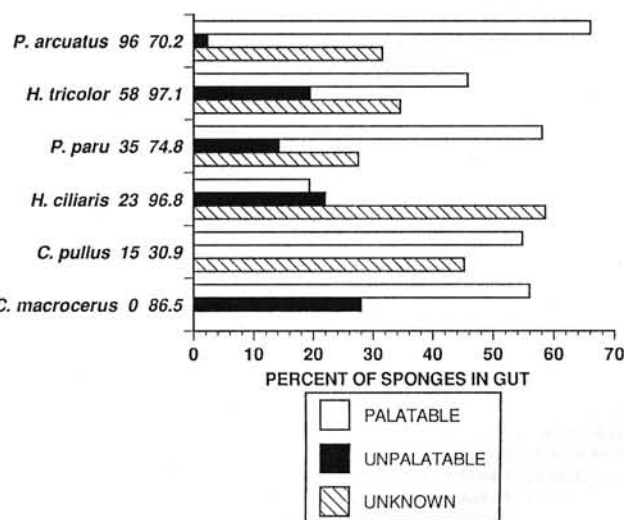


Fig. 1. Chemical detergency of sponge tissue in the stomachs of the six most common spongivorous Caribbean reef fishes: anglefishes: *Pomacanthus arcuatus*, *Holacanthus tricolor*, *P. paru*, *H. ciliaris*; filefishes: *Catherhines pullus*, *C. macrocerus*. The first number after the fish species name is the random point sample frequency of the species at Looe Key, Florida (Bohnsack et al. 1987). The second number is the percentage of gut contents made up of sponge tissue (Randall and Hartman 1968). The sponge species identified from the guts (Randall and Hartman 1968) are divided into chemically palatable, unpalatable, or unknown based on assays with generalist predators (Pawlik et al. 1995). Unknown samples were either not fully identified by Randall and Hartman (1968) or not assayed by Pawlik et al. (1995). Trunkfishes not included in this analysis because they are less common and feed so as to avoid ingesting tissue (Wulff 1994). Parrotfishes were not included in Randall and Hartman (1968), but do eat sponges (Dunlap and Pawlik 1996) and are very abundant on reefs: frequencies of *Sparisoma aurofrenatum* = 180, *S. chrysopteron* = 84 (Bohnsack et al. 1987).

**Table 1:** Percentage of sponge tissue made up of chemically undefended species in the stomachs of the six most common spongivorous reef fishes: angelfish: *Pomacanthus arcuatus*, *Holacanthus tricolor*, *P. paru*, *H. ciliaris*; filefish: *Catherhines pullus*, *C. macrocerus*. Data from Randall and Hartman (1968) and Pawlik et al. (1995). <sup>1</sup>Most abundant species in gut. <sup>2</sup>Second most abundant in gut.

PERCENTAGE OF GUT CONTAINING PALATABLE SPONGES	SPONGIVORE					
	<i>P. arc</i>	<i>H. tri</i>	<i>P. par</i>	<i>H. cil</i>	<i>C. pul</i>	<i>C. mac</i>
<b>Reef species</b>						
<i>Callyspongia vaginalis</i>	21.9 <sup>1</sup>	10.0 <sup>2</sup>	27.0 <sup>1</sup>	1.6	15.0	54.0 <sup>1</sup>
<i>Mycale laevis</i>				1.1		
<i>Niphates erecta</i>	12.1		8.0	0.6		2.0
<i>Iotrochota birotulata</i>	1.8	15.6 <sup>1</sup>		0.5		
TOTAL	35.8	25.6	35.0	3.8	15.0	56.0
<b>Cryptic/mangrove species</b>						
<i>Tedania ignis</i>	8.3	9.7	2.3	0.7		
<i>Geodia gibberosa</i>				0.2	2.8	
<i>Chondrosia collectrix</i>			11.5		6.0	
TOTAL	8.3	9.7	13.8	0.9	8.8	0.0

never replaced on the array over 4 days, mangrove species were replaced 3-4 times per day). Therefore, it took many more bites for fishes to remove tough mangrove sponges from the array than soft mangrove sponges. Fishes may bite some sponges in order to feed on epibionts or detritus, rather than sponge tissue. Studies that document feeding using fish bites also need to monitor tissue loss, as in Dunlap and Pawlik (1996).

It is also clear that spongivores have a dramatic effect on sponge distributions and abundances. When mangrove sponges were transplanted to the reef alongside similarly transplanted reef sponges, spongivores quickly located mangrove species and consumed them (Dunlap and Pawlik 1996; Pawlik, in prep). There was no evidence that spongivores used color to maintain diversity in their diets, because although transplant experiments were conducted with color-matched pairs of mangrove and reef sponges that were black, brown, yellow and red, spongivores very specifically attacked one or two mangrove species, biting them repetitively until completely consumed (Dunlap and Pawlik 1996). We subsequently discovered that two of these preferred mangrove species (*Chondrosia collectrix* and *Tedania ignis*) could also be found under coral rubble. When the rubble was overturned, colonies of these species were quickly eaten, as they had been in the transplant experiments (Dunlap and Pawlik 1996). *Tedania ignis*, *Chondrosia collectrix* and another species we have commonly found under reef rubble, *Geodia gibberosa*, all yielded palatable crude extracts (Pawlik et al. 1995) and have never been encountered by us in apparent locations on reefs in the Bahamas, Belize, or in the Florida Keys (although they are commonly found in mangrove habitats), yet tissue from these species made up 8-14% of the sponge contents in the stomachs of 4 of the 6 most common spongivores surveyed by Randall and Hartman (1968) (Table 1). The most likely explanation is that the predatory activities of spongivores restrict the distribution of these otherwise "mangrove sponge" species to cryptic refugia on reefs. It seems unlikely that spongivores make forays into mangrove habitats to feed on sponges, because (1) spongivores are seldom seen in mangrove habitats, (2) mangrove sponges show no evidence of grazing, and (3) spongivore reef habitats are frequently several km away from mangrove habitats. Despite our inability to find these cryptic sponges growing in apparent locations on the reef, spongivores are locating enough of these species, as the sponges grow out of refugia or as rubble is overturned, that these sponges constitute ~10% of spongivore diets.

We hypothesize that spongivores prefer to feed on palatable cryptic species, but that their predatory activity limits the amounts of these species that they can find. In lieu of these preferred species, spongivores turn their attention to the common, chemically undefended reef species, such as *Callyspongia vaginalis* and *Niphates erecta* (or, in the case of the parrotfishes *Sparisoma aurofrenatum* and *S. chrysopterus*, they turn to algae; Dunlap and Pawlik 1996). Because these undefended reef sponges are readily

available, they make up the largest component of spongivore diets. The presence of small amounts of chemically deterrent species in the diets of spongivores may reflect some immunity to deterrent sponge metabolites, or it may simply represent incidental grazing of these species when they are found in association with palatable species. Therefore, spongivores clearly affect the distribution of some sponge species, and the diversity of spongivore diets is more an indication of the limited availability of preferred sponge species.

Predation by spongivores, and the effect of predation on reef sponge communities, may best be likened to the effect of sheep grazing on the plants of an enclosed pasture. Sheep preferentially graze the most palatable plants, and these quickly become absent or rare in the enclosure, but may be abundant outside the enclosure (analogous to fish feeding on scarce, palatable cryptic sponges). Next, sheep graze on fast-growing grasses, which remain abundant in the enclosure despite grazing (analogous to fish feeding on palatable reef species, such as *Callyspongia vaginalis*). Finally, sheep avoid eating noxious plants, which become more abundant and apparent in enclosures as sheep graze down the grasses (analogous to the abundance and apparency of chemically defended sponges on reefs).

In summary, the emerging view of sponge predation on Caribbean reefs can be summarized as follows: (1) Generalist predators are generally deterred by sponge chemistry, but not by structural elements, toughness, or the nutritional quality of sponge tissue. (2) Spongivores are not smorgasbord feeders, but focus their predatory activities on preferred cryptic sponge species and palatable reef species. (3) Spongivores do not generally circumvent sponge chemistry, but choose chemically undefended sponge species. (4) Fish predators have a major impact on the distributions and abundances of sponges on Caribbean reefs because fish predatory activities restrict some sponge species to refugia.

#### AREAS FOR FURTHER RESEARCH

The foregoing is a rapidly developing, generalized perspective on sponge predation that is likely to undergo revision as further study is undertaken. Many questions remain to be resolved, and some of these are more open to experimentation than others. Some of these questions, along with some possible answers, are as follows: Why don't generalist predators eat chemically undefended sponges, particularly the common species on reefs? Similarly, given that spongivores eat these undefended reef species, why do these sponges persist at such high abundances on reefs when other palatable species are relegated to refugia? It is possible that undefended reef sponges grow and reproduce faster than their chemically defended neighbors, using energy otherwise spent on the synthesis of complex metabolites for growth and reproduction? Bite marks on species like *Callyspongia*



*vaginalis* appear to heal quickly; these species may simply endure a modest level of grazing. We have observed that pieces of sponge are completely digested as they are tracked through the lengthy, dissected guts of angelfishes. Generalists may not eat species like *C. vaginalis* because their guts have a fairly rapid through-put, and highly condensed proteinaceous fibers cannot be digested in such a short time.

Although most spongivores feed primarily on chemically undefended sponges, there appear to be some species that feed to a considerable extent on chemically rich sponges. For example, Wulff (1994) reported that trunkfishes preferred *Aplysina fistularis*, a chemically defended species, although, in another study, trunkfishes readily devoured palatable mangrove sponges (Dunlap and Pawlik 1995). Randall and Hartman (1968) found that over 20% of the stomach contents of the queen angelfish, *Holacanthus ciliaris*, were sponges of the genus *Agelas*, a group that contains deterrent brominated pyrrol compounds (Pawlik et al. 1995; Chanas et al. 1996). Whether these less common spongivores actively detoxify sponge metabolites, or simply tolerate low-level toxic effects, remains to be determined.

The foregoing may generally apply to predation on Caribbean reef sponges, but how different is sponge predation on tropical reefs in the Indo-Pacific? Differences have been observed in the chemical defenses of seaweed communities on Caribbean vs. Pacific reefs, perhaps because of the greater diversity of herbivorous fishes in the Pacific (Paul 1992). Spongivore diversity may be similarly greater in the Pacific. In addition to fishes, invertebrate spongivores, particularly nudibranch molluscs and seastars, likely have a greater effect on the sponge community of Pacific reefs. In addition, predation is certainly not the only factor that influences the distributions and abundances of sponges in tropical ecosystems. Many reef species cannot survive the physical extremes of inshore environments, and some mangrove and cryptic species cannot endure the surge and currents of reefs. It remains to be seen whether the generalities concerning predation on sponges put forward in this overview withstand further investigations, or whether they are applicable to tropical reefs worldwide.

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