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Video-monitored predation by Caribbean reef fishes on an array of mangrove and reef sponges

Abstract Although predation by fishes is thought to structure benthic invertebrate communities on coral reefs, evidence to support this claim has been difficult to obtain. We deployed an array of eight sponge species on Conch Reef (16 m depth) off Key Largo, Florida, USA, and used a remote video-camera to record fish activity near the array continuously during five daylight periods (6 h for 1 d, at least 11.5 h for 4 d) and one night period (11 h). Of the eight sponge species, four were from adjacent reefs (*Agelas wiedenmayeri*, *Geodia neptuni*, *Aplysina fistularis*, and *Pseudaxinella lunaecharta*), and four were from a nearby mangrove habitat (*Chondrosia collectrix*, *Geodia gibberosa*, *Halichondria* sp., and *Tedania ignis*). Each species of reef sponge was chosen to match the corresponding mangrove species in form and color (black, brown, yellow, and red, respectively). Predation events only occurred during daylight hours. Tallies of the number of times fishes bit sponges revealed intense feeding by the expected species of sponge-eating fishes, such as the angelfish *Holacanthus bermudensis*, *H. tricolor*, and *Pomacanthus arcuatus*, the cowfish *Lactophrys quadricornis*, and the filefish *Cantherhines pullus*, but surprisingly also by the parrotfish *Sparisoma aurofrenatum* and *S. chrysopterum*. Of 35 301 bites recorded, 50.8% were taken by angelfish, 34.8% by parrotfish, and 13.7% by trunkfish and filefish. Mangrove sponges were preferred by all reef fishes; 96% of bites were taken from mangrove species, with angelfish preferring *Chondrosia collectrix* and parrotfish preferring *Geodia gibberosa*. Fishes often bit the same sponge repetitively, and frequently consumed entire samples within 30 min of their deployment. Sponge color did not influence fish feeding. Two of the four mangrove sponge-species deployed on the array were also found living in cryptic habitats on adjacent reefs and were rapidly consumed by fishes when exposed. Our results demonstrate the importance of fish predation in controlling the distribution of sponges on Caribbean reefs.

Introduction

The community structure of coral-reef ecosystems is strongly influenced by the feeding activity of fishes (Hay 1983, 1991; Hixon 1983). While the importance of herbivory on the distribution of algae on coral reefs has been experimentally investigated for over a decade (Hay 1991; Hay and Steinberg 1992), the same scope and rigor has not been applied to studies of predation by fishes on coral-reef benthic invertebrates (Jones et al. 1991). Nevertheless, for seven studies of reef fish diets, 27 to 56% of all fish species were benthic invertebrate feeders, while 7 to 26% were herbivores (reviewed in Jones et al. 1991). Moreover, the wide variety of morphological, physiological, and behavioral defensive characteristics displayed by reef invertebrates testify to the selective impact of fish predation (Vermeij 1978; Bakus 1981).

Sponges are abundant and conspicuous members of Caribbean coral-reef communities, where their biomass, diversity and abundance often exceeds that of scleractinian and alcyonarian corals (Goreau and Hartman 1963; Rützler 1978; Suchanek et al. 1983; Targett and Schmahl 1984). On an 18 m-deep reef off the Florida Keys, Schmahl (1991) recorded transect means of 10.40 sponge species m^{-2} and 17.45 sponges m^{-2}. In a photographic survey of the benthos of Salt River Canyon, Virgin Islands, nearly half of all taxa recorded were sponges (Suchanek et al. 1983).

Despite being sessile, fleshy, and nutritious organisms (Bergquist 1978; Chanas and Pawlik 1995), and despite growing in the presence of large numbers of

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predatory reef fishes (Hixon 1983), sponges on coral reefs appear to suffer very little predation. In the tropics, the only major sponge predators are opistho-branch mollusks (Pawlik et al. 1988; Paul 1992), hawksbill turtles (Meylan 1988), and a few fish species (Randall and Hartman 1968). In an extensive survey of the gut contents of 212 species of Caribbean fishes, Randall and Hartman found that only 21 species had sponge remains in their guts, and in only 11 species did sponge remains comprise > 6% of the gut contents. These sponge-eating fishes belong to a few, highly specialized teleost families, including angelfish (*Holacanthus* and *Pomacanthus* spp.), trunkfish (*Lactophrys* spp.), and filefish (*Cantherhines* spp.) (Randall 1967).

Marine sponges have been a major source of unusual secondary metabolites (Faulkner 1994, and previous reviews cited therein), and it has been assumed that these compounds play an important role in protecting sponges from predation (Pawlik 1993). Among the con-clusions of Randall and Hartman (1968) was that spongivorous fishes tend to sample a wide variety of sponge species in order to lower the risk of eating large quantities of one or a few chemically-defended species; as a result, sponge-eating fishes do not significantly influence sponge distributions. Angelfish guts in par-ticular indicated this "smorgasbord" type of feeding, with > 20 species of sponges represented in gut con-tents (Randall and Hartman 1968). More recently, Wulff (1994) observed fish spongivores on a Panamanian coral reef, and found that angelfish tended to bite a sponge only a few times before moving to another sponge, usually of a different color. She com-pared her results of spongivory on the reef to the activity of herbivorous primates that diversify their diet of chemically-defended plants. Wulff reasoned that spe-cifics of sponge chemistry may be unimportant if smor-gasbord predators eat only a small amount of many differently colored sponges.

In a recent survey of the chemical antipredatory defenses of 73 species of Caribbean sponges, Pawlik et al. (1995) discovered that crude organic extracts from most reef sponge-species strongly deterred feeding by predatory reef fish in aquarium assays. Surprisingly, several common reef sponges yielded palatable extracts, and these species were the same ones that Randall and Hartman (1968) listed as the major com-ponents of the diet of sponge-eating fishes (Pawlik et al. 1995). These results suggest, therefore, that spongivor-ous fishes target chemically-undefended sponge species rather than tolerating small quantities of many chemic-ally-defended species. Another outcome of the survey of the chemical defenses of Caribbean sponges (Pawlik et al. 1995) was that the majority of sponges from mangrove habitats (where predatory reef fishes are ab-sent) yielded palatable extracts. Are mangrove habitats a refuge from fish predation for chemically undefended sponge species, or are other factors (light, temperature,

sedimentation, etc.) more important in controlling sponge distributions?

To examine the importance of fish predation on sponge distributions on coral reefs, we placed an array of four replicate pieces of each of four mangrove and four reef sponge species on a reef (16 m depth) and recorded predation on them. Remote video equipment was used to make continuous observations of feeding on the array by a natural reef-fish assemblage. Pairs of mangrove and reef sponge-species were matched by color to assess the propensity for smorgasbord feeding. In addition, we searched for mangrove sponge-species on the undersides of coral rubble on adjacent reefs, and when sponges were found, we overturned the rubble and monitored the fate of the sponges. Our goals were to identify sponge predators on the reef, examine the preferences of predators for reef or mangrove sponge-species and determine the importance of sponge color in prey selection.

Materials and methods

Study sites

All field work was carried out in the vicinity of the National Undersea Research Center in Key Largo, Florida, USA (25° 10'N; 80° 20'W). Sponge collection sites included Adam's Cut and Jewfish Creek for mangrove species, and Molasses Reef for reef species. Video-taping of the sponge array was undertaken on Conch Reef, ≃60 m distant from the Aquarius Undersea Habitat (hereafter "habitat") in a sand plain between two coral rock outcrops at 16 m depth. Video-taping occurred from 26 through 30 July 1994. Over-turning of coral rubble to expose sponges was carried out at Pickles, White Banks, and Grecian Rocks reefs.

Collection and deployment of sponge samples

Fist-sized portions of eight sponge species (~ 400 ml volume each) were collected from mangrove and reef habitats throughout the experiment. Four replicate samples of each of the eight sponge species were deployed on the array. Four colors of sponges were represented, a mangrove and a reef species for each color (Table 1). During collection, sponge portions were sliced from colonies so that little or no interior tissue was exposed when sponges were attached to the array. If present, epibionts were removed from the surfaces of mangrove sponges. Samples were placed in plastic bags during collection dives, but were stored in plastic tote-boxes with seawater during transport to the habitat.

Table 1 Eight sponge species in array at Conch Reef from 26 to 30 July 1994. Two similarly colored sponge species from different habitats were collected for four colors. The unidentified *Halichondria* species is a yellow, beehive-shaped sponge that grows on man-grove prop-roots

Color	Mangrove species	Reef species
Black	*Chondrosia collectrix*	*Agelas wiedenmayeri*
Brown	*Geodia gibberosa*	*Geodia neptuni*
Yellow	*Halichondria* sp.	*Aplysina fistularis*
Red	*Tedania ignis*	*Pseudaxinella lunaecharta*

At Conch Reef, surface divers carried sponges to the habitat for deployment on the array. Samples not used immediately were stored at 16 m depth on the "porch" of the habitat in plastic garbage cans with holes punched in them to provide flow. The containers were weighted and a lid was placed on each to exclude fish. Divers carried sponges to the experimental site in the sand plain.

At the experimental site, divers attached sponges to four 0.5 × 0.5 m plastic plates by inserting cable ties through the tissue and through holes drilled in the plates. The cut edge of sponge samples was placed against the plates so as to expose as little of the interior tissue as possible. Each plate had one replicate of each of the eight sponge species arranged in the same manner. The four plates were placed together to form a single array of 32 sponges, and the position of each replicate was mapped for use while viewing the video. The array was positioned horizontally, ~5 cm from the sand bottom, with its bottom surface attached to lead weights. A silicon-intensified target (SIT) video camera was positioned 2 m away and 1 m off the bottom, with its lens focused to include the array and ~0.5 m on each side. The camera was tethered to the mobile support barge (MSB) directly above the habitat. To examine nocturnal feeding behavior, two red-filtered lights were positioned on cinder blocks on either side of the array, equidistant from the array and camera.

Sponges removed from the array by feeding fishes were replenished three times a day: in the morning, midday, and evening, except on 27 and 29 July 1994, when sponges were replenished four times, twice in the morning. Video output was continually monitored by a technician in the MSB. Night-time taping and use of the red-filtered lights were discontinued after the first night of taping revealed no feeding on the sponges.

Video analysis

Tape was analyzed at the video facilities of the National Undersea Research Center, University of North Carolina, Wilmington, North Carolina, USA. For every 10 min period, the total number of times each species of fish bit each species of sponge on the array was tallied. Bites were counted only when it was obvious the fish was removing tissue from the sample. The time at which any species of sponge was depleted from the array was recorded, as was the time that divers arrived to replenish sponges.

Rubble-overturning experiment

Some sponge species that form large, exposed colonies in mangrove habitats were also located on the undersides of pieces of dead coral rubble on shallow reefs (< 8 m depth), where these same species form small or encrusting colonies. Sponges were identified as in Pawlik et al. (1995). Rubble pieces were overturned to expose their undersides to predation, and sponge positions were recorded. After 1 h exposure to the natural reef fish-assemblage, the fate of each sponge was recorded. If any sponges remained after 1 h, they were left exposed for a total of 24 h and then checked again.

Results

Reef fishes fed almost exclusively on sponges collected from mangrove habitats. Of the 35 301 fish bites recorded on video tape during the experiment, 96% were taken from mangrove sponges (Fig. 1). Fishes fed on two species in particular, *Chondrosia collectrix* and *Geodia gibberosa*, often removing all samples of these

species from the plates within 30 min of their deployment. Mangrove sponges were replenished on the array 3 to 4 times during each daylight period.

Parrotfish of the genus *Sparisoma* took 34.6% of the bites (Table 2, Fig. 2). Redband parrotfish, *S. aurofrenatum*, took 24.9% of all bites recorded, second only to the 26.6% taken by the blue angelfish *Holacanthus bermudensis*. Redband parrotfish made frequent attacks on the mangrove sponge *Geodia gibberosa*, from which they took five to ten consecutive bites before leaving. Redtail parrotfish, *S. chrysopterum*, made similar visits to the array, although their visits were much shorter and consisted of only 2 or 3 bites. Parrotfish of the genus *Scarus* took < 1% of all bites on the sponge array (Table 2). Overall, parrotfish preferred *G. gibberosa* over the other species of mangrove sponges (Fig. 3).

Nineteen species of fishes fed on the array (Table 2), but the angelfish *Holacanthus bermudensis*, *H. tricolor*, *H. ciliaris*, *Pomacanthus arcuatus*, and *P. paru* took > 50% of the bites (Fig. 2). Angelfish preferred the mangrove sponge *Chondrosia collectrix* (Fig. 3), and were the most obvious predators during the experiment. Unlike the parrotfish, angelfish positioned
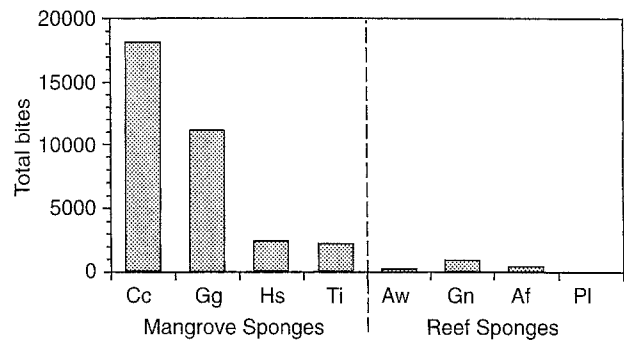

Fig. 1 Total number of reef-fish bites on each of eight species of sponges attached to an array on Conch Reef, 26 to 30 July 1994. Fish bites were tallied from a continuous video recording (*Cc Chondrosia collectrix*, *Gg Geodia gibberosa*; *Hs Halichondria* sp.; *Ti Tedania ignis*; *Aw Agelas wiedenmayeri*; *Gn Geodia neptuni*; *Af Aplysina fistularis*; *Pl Pseudaxinella lunaecharta*)
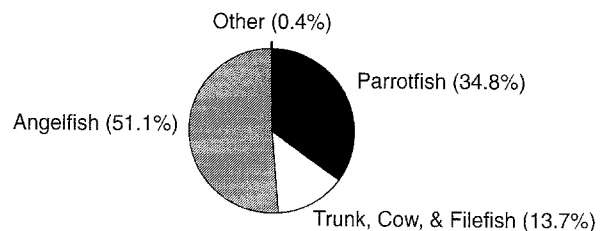

Fig. 2 Percentage of total bites by reef fishes on all sponges attached to an array on Conch Reef, 26 to 30 July 1994. Fish bites were tallied from a continuous video recording. Reef fishes grouped as in Table 2, which gives specific names

Table 2 Predators observed feeding on sponges attached to array on Conch Reef from 26 to 29 July 1994

| Scientific name	Common name	% of bites
Angelfish		
Holacanthus bermudensis	Blue angelfish	26.6
Holacanthus tricolor	Rock beauty	7.4
Holacanthus ciliaris	Queen angelfish	6.9
Pomacanthus arcuatus	Grey angelfish	6.7
Pomacanthus paru	French angelfish	3.5
Parrotfish		
Sparisoma aurofrenatum	Redband parrotfish	24.9
Sparisoma chrysopterum	Redtail parrotfish	7.2
Sparisoma viride	Stoplight parrotfish	2.5
Scarus vetula	Queen parrotfish	0.1
Scarus taeniopterus	Princess parrotfish	0.1
Trunkfish		
Lactophrys quadricornis	Scrawled cowfish	5.1
Lactophrys bicaudalis	Spotted trunkfish	2.2
Lactophrys trigonus	Trunkfish	0.2
Lactophrys polygonia	Honeycomb cowfish	0.2
Lactophrys triqueter	Smooth trunkfish	< 0.1
Filefish		
Cantherhines pullus	Orangespotted filefish	5.6
Cantherhines macrocerus	Whitespotted filefish	0.4
Puffer		
Canthigaster rostrata	Sharpnose puffer	_[a]
Sea turtle		
Eretmochelys imbricata	Hawksbill turtle	_[a]

[a] Bites not counted
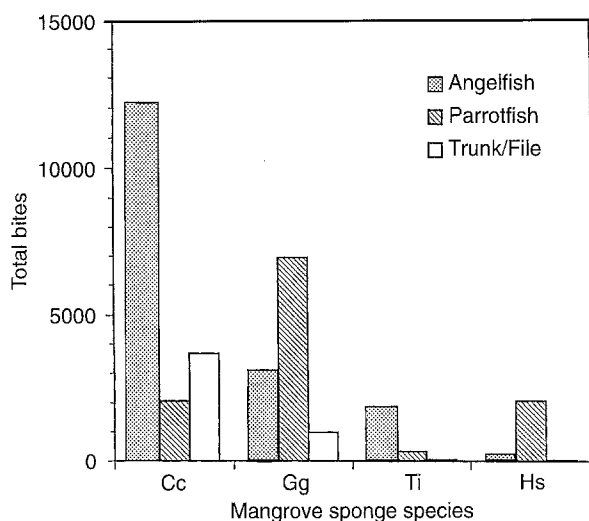
Fig. 3 Total number of reef-fish bites on each of four mangrove sponge species. Reef fishes grouped as in Table 2, which gives specific names (*sponge abbreviations* as in Fig. 1)

themselves above the plates and fed almost continuously. Angelfish were usually the first species to arrive after fresh sponges were deployed, but were not as plentiful once *C. collectrix* had been completely consumed.

Several species of trunk-, cow-, and filefish took 13.7% of the bites. Sharpnose puffers, *Canthigaster rostrata*, and a hawksbill turtle, *Eretmochelys imbricata*, fed intermittently, but were not counted because their bites could not be distinguished on the videotape.

Feeding was intense, up to 420 bites per 10 min period, at all times of the day whenever the sponge array was replenished (Fig. 4). Fish feeding began within 10 min of sunrise, and continued until sunset whenever palatable sponges were on the array. No feeding on sponges was observed at night. The fishes fed by biting directly into the exterior surface of sponges. Frequently, *Chondrosia collectrix* and *Geodia gibberosa* were missing from the array because each of the four replicates had been eaten (Fig. 4). At these times, feeding continued on other sponge species, but at a much slower rate.

In the rubble-overturning experiments, which were conducted on reefs > 3 km distance from the habitat site at Conch reef, 89% of colonies of *Tedania ignis* and 100% of colonies of *Chondrosia collectrix* were completely eaten within 24 h. Angelfish, parrotfish, and trunkfish investigated rubble shortly after it was flipped over and often began feeding immediately. Of 29 colonies of *C. collectrix* exposed, 14% were completely eaten within 1 h and 100% were eaten within 24 h. Of 38 colonies of *T. ignis*, 21% were completely eaten within 1 h and 68% were eaten within 24 h, while four were not completely eaten.

Discussion and conclusions

Intense feeding by coral-reef fishes on sponges transplanted from mangrove habitats suggests that fish predation may be eliminating some sponges from reef habitats. Feeding was always higher on the mangrove species of color-matched, mangrove-reef pairs, even when the reef species (*Geodia neptuni*) was from the same genus, and had the same spicule type and growth form as the mangrove species (*G. gibberosa*). Predation, and not some other physical or biological factor, appears to be an important determinant of sponge distributions, because two sponge species used in this experiment, *Chondrosia collectrix* and *Tedania ignis*, were found living in cryptic locations on adjacent reefs and were eaten soon after being exposed. A previous study of communities inhabiting the undersides of overhanging corals and dead coral rubble on Caribbean reefs revealed 199 different sponge species, including *C. collectrix* (Meesters et al. 1991). Although other factors such as turbidity, light, and competition also probably restrict the growth of these sponges to cryptic habitats, predation by reef fishes certainly restricts the distribution of some of these sponges.

Continuous video observations permitted specific identification of the predators that fed on the sponge array. Although most of the fish recorded in this study have been previously documented as eating sponges (Randall and Hartman 1968), previous studies, including intensive studies of parrotfish foraging behavior, did not identify parrotfish as sponge-feeders (Hanley 1984; Bellwood and Choat 1990; Bruggemann et al. 1994a, b, c). Not only will parrotfish eat sponge tissue, but when given access to palatable mangrove species they will consume large amounts over short periods of time. The abundance of parrotfish and their relentless foraging on Caribbean reefs, with up to 3000 bites h^{-1} (Bruggemann et al. 1994b), would be expected to result in a significant impact on any potential food item.

The impact of predation by reef fishes on sponge populations has previously been inferred from fish gut-content analyses (Randall and Hartman 1968) and field observations of feeding (Wulff 1994). Both Randall and Hartman and Wulff concluded that specialist, sponge-eating fishes have little effect on Caribbean sponges, but neither study considered the possibility that some sponge species are absent from the reef habitat because they are quickly eaten. None of the mangrove species used in this experiment were found in exposed locations on reefs near Key Largo or in the Bahamas, yet two of the mangrove species transplanted in this experiment, *Tedania ignis* and *Chondrosia collectrix*,

Fig. 4 Time-series of fish feeding-activity on sponge array on 26,27,29 and 30 July 1994 (■ number of bites per 10 min period; ▲ period in which array was replenished with sponges; ★ time period during which *Chondrosia collectrix* or *Geodia gibberosa* had been completely consumed, and were thus absent from array)
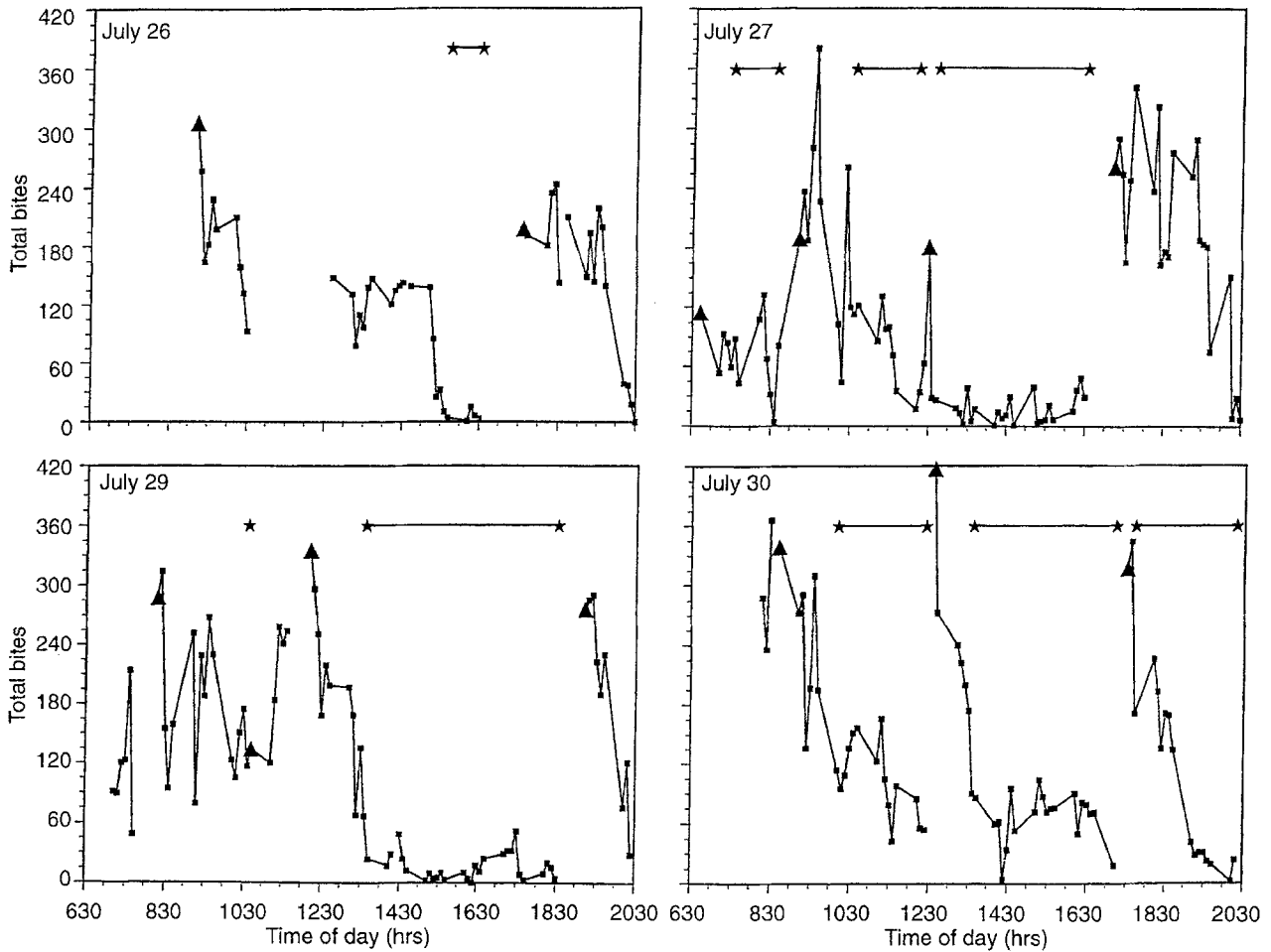

Table 3 *Chondrosia collectrix* and *Tedania ignis*. Consumption of colonies growing underneath coral rubble on Pickles, White Banks, and Grecian Rocks reefs near Key Largo, Florida, USA. Rubble was flipped over to expose sponges to predators

Sponge species	No. Completely eaten in:		Colonies with tissue remaining after 24 h
	< 1 h	< 24 h	
Chondrosia collectrix	4	25	0
Tedania ignis	8	26	4

were the seventh and thirteenth most abundant sponges, respectively, in the guts of reef fish sampled by Randall and Hartman. Moreover, *T. ignis* comprised 9.7% of all sponge material in the guts of 24 specimens of *Holocanthus tricolour*, and *C. collectrix* comprised 11.5% of all sponge material in the guts of 23 specimens of *Pomacanthus paru* (Randall and Hartman 1968). Where are reef fishes finding these sponge species? The most likely answer is that these reef fishes are adept at locating cryptic, palatable sponges on the reef or that they consume cryptic sponges as they grow around coral rubble and become exposed. A less likely possibility is that reef fishes make long-distance excursions into mangrove habitats to feed on palatable sponges, although these fishes are rarely seen in mangrove habitats and mangrove sponges show no evidence of grazing.

The behavior of predatory reef-fishes observed in the present study was not limited or specific to the Conch Reef study site. Overturning of sponge-encrusted coral rubble at several sites in the Florida Keys and the Bahamas incited the same feeding activity from the same species of reef fishes as recorded at Conch Reef. In addition, transplantation of sponges from mangrove sites to patch reefs in both Florida and the Bahamas resulted in significant predation on 7 of 13 sponge species (Pawlik in preparation).

Sponge color did not influence fish predation, nor was there any evidence that fishes actively diversified their diets. In contrast to the smorgasboard feeding strategy suggested by Randall and Hartman (1968) and Wulff (1994), fishes concentrated their predation on preferred sponge species, and bit them repetitively, until they were completely consumed. In addition, observations of video recordings of the behavior of fishes when they first encounter the array of sponges suggest that these fishes recognize palatable sponge species from several meters distance, and feed on them specifically. Two sponge species were found both in mangrove habitats, and cryptically on the reef, and were quickly consumed when made available to predatory reef-fishes. The diversity of dietary sponges recorded by Randall and Hartman is more probably the result of limited availability of preferred species, rather than active diversification of the diet of reef fishes.

This study provides further evidence that sponge-eating fishes target sponges that lack chemical defenses. Sponge species that are most common in the guts of sponge-eating fishes (Randall and Hartman 1968) are also those that yield crude tissue-extracts that are palatable to generalist predatory reef fishes (Pawlik et al. 1995). Three of the four reef species used in the present study yielded deterrent extracts (all but *Geodia neptuni*), but all the mangrove species yielded palatable extracts (Pawlik et al. 1995). Overall, sponges from reef habitats were significantly more likely to be chemically defended than those from mangrove or grassbed habitats

(Pawlik et al. 1995), perhaps as a result of the activity of sponge-eating fishes on reefs. Therefore, the production of deterrent secondary metabolites appears to play an important role in the ecology of Caribbean reef sponges.

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