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Parrotfish predation on cryptic sponges of Caribbean coral reefs

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Abstract Some sponge species that live in crevices in the reef frame appear to be restricted to their cryptic habitat by predation. When cryptic sponges were excavated, on Guigalotupo reef, San Blas, Panama, exposing them to potential predators, they were eaten by fishes that are generally considered to be herbivores, primarily parrotfishes of the genus *Sparisoma*: *S. aurofrenatum* (Cuvier & Valenciennes), *S. viride* (Bonnaterre), and *S. chrysopterum* (Bloch & Schneider). Of the 9150 bites observed to be taken by these species during paired (i.e., with sponges versus without sponges) trials conducted in defined feeding areas during 1986, 1987, and 1988, 72% (i.e. 6581 bites) were on cryptic sponges, even though these were only offered during half of the total observation time and never constituted more than 7% of the cover of the feeding observation areas. Individual parrotfish returned over and over to take bites of the exposed cryptic sponges until they were entirely consumed. They vigorously chased each other away from the sponges, but exhibited no such defense of their usual algal foods. A total of 18 sponge species were tested. Of the cryptic and semi-cryptic sponge species tested, only one of six was rejected by the parrotfish. Two of these six sponge species were consistently consumed entirely, and two were consumed entirely whenever their surfaces were sliced off with a razor blade, demonstrating that these sponges concentrate defenses against predators in their surfaces. One semi-cryptic species and one semi-exposed species were fed upon, but not entirely consumed. By contrast, 11 of 12 of the exposed and semi-exposed species were rejected. Cryptic sponges grew out of their cavities in the reef only when protected by seasonally thick mats of macroalgae or by cages that excluded fish.

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Introduction

Sponges constitute one of the most conspicuous, abundant, and diverse groups of sessile invertebrates on Caribbean coral reefs. Biomass and number of species of sponges exceed that of corals or any other group of sessile invertebrates in many reef zones (e.g., Reiswig 1973; Bonem and Stanley 1977; Hartman 1977; Rützler 1978; Wilkinson 1987; Alcolado 1990; Alvarez et al. 1990; Wulff 1991, 1994). Despite this, much remains to be learned of the ecological factors that affect the distribution and abundance of sponge species and of the selective forces shaping the evolution of sponges. Predation by fishes has been presumed to have little effect on distribution and abundance of Caribbean sponges. Even though sponges are conspicuous and relatively soft-bodied, gut content analysis of Caribbean reef fishes yielded significant (> 6% by volume) sponge remains in only 11 of the 212 species examined (Randall and Hartman 1968). These 11 species included angelfishes, trunkfishes, and filefishes, many of which specialize on sponges (Wulff 1994). Densities of these fish tend to be relatively low, and some of them feed in a "smorgasbord" fashion, taking only a small portion from each sponge individual before moving on. Their coexistence with abundant and diverse sponges further demonstrates that these fish are not controlling the distribution and abundance of conspicuous Caribbean sponges.

By contrast with this pattern on Caribbean reefs, sponges are not a conspicuous component of the sessile fauna of many tropical Pacific reefs (e.g., Bakus 1964; Glynn 1972, 1982; W.D. Hartman personal communication; author's unpublished observation). Instead the sponges are often confined to cryptic spaces within the reef frame or to undersurfaces of corals. When Bakus (1964, 1967) exposed cryptic sponges at Fanning Island

and at Eniwetok, in the central and western Pacific, by turning over corals, fishes that are not known to feed on sponges regularly devoured them rapidly. One interpretation of these data is that distribution and abundance of sponges may be controlled by fish in the tropical Pacific, but not in the Caribbean. The hypothesis that intensity of predation on sponges is greater in the tropical Pacific fits well with biogeographic patterns demonstrated in other predator–prey relationships (e.g., Glynn 1972; Vermeij 1978). However, more than one parameter varies among the previous studies of sponge-feeding or -avoidance by fishes, and so the apparent contrast between Caribbean and Pacific could be due to one or a combination of the following factors: (1) an actual biogeographic difference between the Caribbean and Pacific in the intensity of predation on sponges by fishes, (2) a difference in the effectiveness of defenses of sponges in different habitats (i.e., exposed versus cryptic), or (3) a difference in the results that can be obtained by different methods of studying predator–prey interactions (i.e., analysis of gut contents versus short-term field observations). The present study focuses on points 2 and 3 above, by examining differences between exposed and cryptic sponges in palatability to herbivorous fishes in the Caribbean, and the consequences for the distribution, abundance, and evolution of exposed and cryptic coral reef sponges.

In this study, cryptic sponges of Caribbean coral reefs were excavated to expose them to fish in the field, and feeding behavior of fish attracted to the sponges was observed. Feeding on species of normally exposed sponges was also compared to feeding on cryptic sponges. Small cages were placed over cryptic sponges to determine if they are capable of living exposed when protected from fish. The questions on which I focused are: (1) Can some Caribbean sponges serve as food for fish species that are not sponge specialists? (2) Do all generalist fishes react in the same way to sponges, in general, and to particular sponge species – i.e., are there clear distinctions (a) between sponge-feeding and sponge-avoiding fish species and (b) between protected and unprotected sponge species? (3) Do results of gut content analyses fully explain effects of fish on distribution and abundance of sponges? (4) Do cryptic sponges have less inherent protection from predators than exposed sponges, i.e., is there an inverse relationship between availability and edibility of sponges?

Methods

Study area

Shallow reefs of the ramose Caribbean coral *Porites furcata* harbor a high diversity of sponge species that are confined to crevices and within consolidated piles of rubble (e.g., Wulff 1984). All experiments in the present study were performed on one of these reefs, Guigalatupo, near the Smithsonian Tropical Research Institute's San Blas Field Station in Panama (map in Wulff 1995). The top of this reef, at its highest 0.5 m below surface at mean low water (MLW), is a mosaic of *P. furcata* rubble, in various stages of consolidation, and of widely scattered hummocks of live coral. The sides of the reef are a mixture of *Agaricia tenuifolia*, *Millepora* spp., and small thickets of almost entirely dead *Acropora cervicornis*, thickly populated with many species of exposed sponges, most commonly *Iotrochota birotulata*, *Amphimedon rubens*, *Aplysina fulva*, *Ectyoplasia ferox*, and *Xestospongia rosariensis*. During the dry season, roughly December through April, the macroalga *Dictyota divaricata* blankets parts of the top of the reef. On the leeward side, the *P. furcata* reef grades into rubble and sediment, studded with large coral heads and descending into a deep channel. On the windward side, the reef is somewhat protected by being in the lee of a small island. In the 100 m between the island and reef is a shallow (2 to 5 m below surface at MLW) seagrass meadow, of *Thalassia testudinium* mixed with *Syringodium filiforme*, and a variety of macroalgae (most in the genera *Caulerpa*, *Padina*, *Halimeda*, and *Penicillus*), exposed sponges (e.g., *Spheciospongia vesparia*, *S. cuspidifera*, *Amphimedon rubens*, and *Tectitethya crypta*), and widely spaced corals (e.g., *Montastrea annularis*, *M. cavernosa*, *Diploria strigosa*, and *Siderastrea siderea*). Experiments in which cryptic sponges were exposed to fishes were performed on this island-facing edge of the reef top during March to May 1986, November 1986 to April 1987, and July 1988.

A feeding observation area was demarcated by randomly placing a hoop of 16 gauge wire, enclosing a 0.125 m^2 circle, on a substratum of partially consolidated *Porites furcata* rubble covered with encrusting coralline algae and a variety of fleshy algae, and fish were observed feeding on these algae or on sponges that were placed within the circle. The circle was moved to a new place along the 70 m long reef edge after every trial, with the exact locations determined by reference to a list of random numbers. A wire marked boldly in centimeters was placed on the substratum within the circle to facilitate standard length measurements of visiting fish.

Feeding observations

Sponges that normally live only in cryptic spaces were excavated from crevices and within rubble piles on the top of the reef and placed in the center of the feeding circle. For each trial, a selection of sponge species was offered by laying them on the substratum within the circle. The cryptic sponges remained attached to the rubble on which they were growing and were trimmed to a common size of 2 to 3 cm^3 with a stainless steel razor blade. The actual selection of cryptic sponge species offered in a particular trial was determined by whatever species were found by making a small excavation in the top of the reef. Specific combinations of cryptic species could not be determined in advance because it is rarely possible to predict which species will be discovered in an excavation. Only one excavation was made per trial to keep numbers of excavations to a minimum, as these sponges are critical for binding together the rubble on top of the reef, preventing erosion (Wulff 1984). Thus, these experiments closely mimicked the naturally occurring situation of simultaneous exposure of a variety of cryptic sponges by localized natural disturbance to the reef surface; the only difference being that pieces of the different species of sponges were all trimmed to a standard size. Although there are many exclusively cryptic sponge species occupying *P. furcata* reefs, only three of them were sufficiently common to be used in these experiments. Feeding trials also included (1) sponges that are not entirely cryptic, but live with more than half of their tissue hidden within the reef ("semi-cryptic"); (2) sponges that live with some, but less than half of their tissue within the reef ("semi-exposed"); and (3) sponges that are entirely exposed. Sponge species were assigned to these categories on the basis of how they live in this shallow habitat, but 15 of the 18 species (listed below) remain in the same category wherever they are found. Observations of the fish, as they fed on sponges, suggested that their consumption or rejection of a sponge species was independent of the context (i.e., what other sponges were available). Therefore, offering random assortments of species at each trial does not preclude comparisons among all sponge species with respect to fish preference. As discussed in

"Results", this important assumption of independence was supported by the data.

Observers, stationed 1 to 3 m to the leeward, noted all fish that fed in the wire-demarcated circle for 20 min after sponges were added. Keeping track of individual fish was relatively easy in most cases because of the wide range of different sizes and different species represented among the fish, the small size of the circle, and the behavior of the fish, which tended to remain near the circle once they had discovered edible sponges. Standard lengths of the fish, the number of different fish of each species, the number of bites each fish took on each sponge species or on other food items, the number of times the same fish returned to feed in the circle, and chases of one fish by another that resulted in either fish leaving the circle were recorded. For the preceding 20 min, the same circle was monitored for fish-feeding in this fashion, but without adding sponges. This resulted in paired observations of the same group of fish individuals feeding at nearly the same time and in the same place, both with and without sponges available. Sponges remaining in the circle at the end of the 20-min experimental observation period were measured and left in place for 24 h to determine if they would be fed on further. The wire circle was moved to a new location for the next trial. To determine if sponges were fed on differently at different times during the day, five 40-min periods (20 min without sponges followed by 20 min with sponges) were observed during every hour between 0800 and 1700 hrs, for a total of 45 trials. An additional seven trials were run to increase sample sizes for some sponge species, for a total of 52 paired (i.e., without sponges versus with sponges) feeding trials. Specific pairwise comparisons of some sponges were made without a control circle for 22 additional trials, for a total of 49 h of quantified observations.

The cryptic sponge species used in these feeding trials were *Halichondria* cf. *lutea* Alcolado (see Wulff 1996), *Hymeniacidon caerulea* Pulitzer-Finali (capable of living as small encrustations in deeper water), and *Geodia* cf. *gibberosa* Lamarck. The semi-cryptic species were *Mycale laevis* Carter (not always a semi-cryptic species, but it is in this shallow habitat), *Adocia* sp. [black; *not Adocia carbonaria* of Hechtel (1965) or *Pellina carbonaria* of van Soest (1980), but possibly *Pellina carbonaria* of de Laubenfels (1936)], and *Pachypellina podatypa* (de Laubenfels). (Specimens, photographs, and systematic discussions of the undefined species can be obtained from the author.) Common sponges that live semi-exposed on this part of the reef [*Pellina carbonaria* (Lamarck), *Lissodendoryx colombiensis* Zea & Van Soest (lives exposed on coral heads in seagrass meadows, but semi-exposed on the shallow reef top), *Amphimedon erina* (de Laubenfels), and *Spirastrella* cf. *mollis* Verrill] were also included. The eight species of exposed sponges used were *Iotrochota birotulata* (Higgin), *Amphimedon rubens* (Pallas) [= *Amphimedon compressa* D & M, sensu Wiedenmayer (1977)], *Aplysina fulva* [= *Verongia fulva*] (Pallas), *Niphates erecta* Duchassaing & Michelotti, *Callyspongia vaginalis* (Lamarck), *Desmapsamma anchorata* (Carter), *Ectyoplasia ferox* Duchassaing & Michelotti, and *Verongula rigida* (Esper). In addition, direct comparisons were made of feeding on the semi-cryptic sponges, *Mycale laevis* and *Adocia* sp. (black), using pieces of the same individual and of similar size, with and without their outer surfaces intact, in ten trials for each species.

Caging experiments

To determine if cryptic sponges are capable of growing out of their cryptic habitat when protected from larger size classes of fish, 40 small plastic cages (10 × 10 × 6 cm, with mesh size of 1 × 2 cm) were anchored, from January to April 1987, with wire stakes over crevices in the reef, within which edges of cryptic sponges were seen. At the time of cage installation, none of the cryptic sponges protruded even 1 mm above the reef surface. Smaller meshes would have eliminated more fish, but would have reduced the vigorous water flow upon which sponge health depends. Half of these cages served as controls, with sides removed to allow fish access to the sponges.

Results

Feeding observations

Typically, the first visitors to a feeding circle with exposed cryptic sponges were the wrasses *Thalassoma bifasciatum* and *Halochoeres bivittatus*, looking for and ingesting small mobile invertebrates such as annelids, echinoderms, arthropods, and molluscs, which were exposed along with the sponges, but all wrasses combined took only 4.8 bites per trial, and only 11.1% of these were on sponges. The wrasses appeared to pick the sponges apart to further expose small invertebrates, and did not ingest the sponges. Juveniles and small adults of the damselfishes *Microspathodon chrysurus*, *Stegastes dorsopunicans*, *S. planifrons*, and *S. partitus*, which were resident in or near the circles, occasionally (an average of 5.9 bites per trial by all individuals of all four damselfish species combined) took bites on the sponges. Twice, damselfish were observed to spit out a piece of sponge they had bitten off. Butterflyfish, *Chaetodon capistratus*, took only 0.2 bites per trial within the circle, and none of these were on sponges. Surgeonfish, *Acanthurus bahianus*, took an average of 2.7 bites per trial within the circle, but 99.2% of these bites were on algae.

Parrotfishes took more than an order of magnitude more bites (an average of 263 bites per trial) in circles with cryptic sponges than any other group of fish. Most sponge-feeding (an average of 112.6 bites on sponges per trial) was done by parrotfishes, especially *Sparisoma aurofrenatum*, *S. viride*, and *S. chrysopterum* (Fig. 1). Individual *Sparisoma* spp. could be seen to roll their eyes towards the reef, and abruptly change course and increase speed to veer towards the excavated sponges. They ingested all pieces of sponges that they bit off, and showed no hesitation about which species to eat and which to avoid, even when two sponge species were on the same piece of coral rubble. The parrotfishes chased each other away from the sponges, and continued to take bites throughout the 20-min observation period or until the preferred sponges were gone. A fourth *Sparisoma* species, *S. rubripinne*, was present in the seagrass meadows, but was never observed to move onto the reef. The most common parrotfish on these reefs (K. Clifton personal communication) is the small striped parrotfish *Scarus iserti*, which frequently took bites from sponges as small schools moved across the circle (Fig. 1). Species of fish that are known to be regular sponge feeders, i.e., angelfishes, trunkfishes, and filefishes (Randall and Hartman 1968; Wulff 1994), were sometimes present in this area, but were never seen on top of the reef. They confined their feeding to the base of the reef or to patch reefs and rubble-strewn areas densely populated by exposed sponges (Wulff 1994).

By a variety of criteria, all three species of *Sparisoma* were demonstrated to feed very differently when cryptic and semi-cryptic sponges were available versus when only naturally occurring algae were available (Table 1).

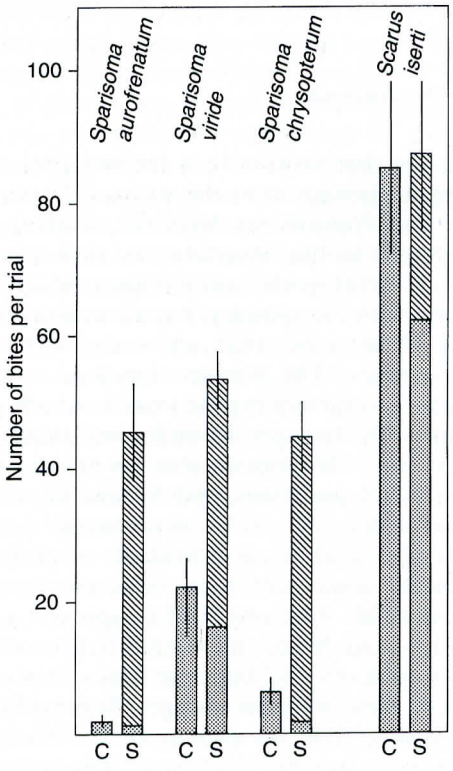

Fig. 1 *Sparisoma* spp. and *Scarus iserti*. Feeding by four species in circles with cryptic sponges versus without crytic sponges. Mean (±SE) number of bites per trial (n = 52 paired trials) taken by parrotfishes in circles with excavated cryptic sponges added (S) and in control circles without sponges (C). Bites on sponges indicated by *cross-hatching*, bites on everything else indicated by *shaded bars*. Each trial consisted of 20 min without sponges and 20 min with cryptic sponges

In circles with cryptic sponges they (1) took more bites per trial (Fig. 1), (2) took more bites per individual fish per trial (Table 1), (3) made more total visits per trial (Table 1), and (4) made more visits per fish per trial (Table 1). More individuals fed in circles with cryptic sponges (Table 1). By most of these criteria, the distinction between circles with cryptic sponges and control circles was somewhat less for *S. viride* than for the other two species (Fig. 1; Table 1). None of these distinctions between cryptic sponge and control circles were made by *Scarus iserti*. Rather than combining data from all trials to determine if fish feed differently when cryptic sponges are available, the more conservative statistical comparisons of parrotfish feeding with and without cryptic sponges were made using all paired trials (i.e., same time, site, and fish present) in which at least one individual of the fish species being analyzed fed. All three species of *Sparisoma* took significantly more bites in circles with cryptic sponges than in circles without sponges (by the t-test for paired comparisons, $p < 0.001$ for each species; Table 1). Even though cryptic sponges were only made available for half of the total observation time, 72% (6581/9150) of the total number of bites taken by *Sparisoma* species within the circles were taken on cryptic and semi-cryptic sponges (significantly different from half of the bites by the G-test, $p < 0.001$). In addition, even though sponges at most represented 7% of the surface area available for feeding within a circle, 89% of the bites taken within circles to which cryptic sponges were added were on cryptic sponges. Individuals of *Sparisoma* spp. fed in the circles throughout the day, and at all times took the majority of their bites on cryptic sponges, whenever they were available (Fig. 2).

Behavior of the parrotfishes was the same throughout the time during which experiments were made. The number of bites taken on sponges by the *Sparisoma* spp. during the very first 20-min trial on 29 March 1986 was 112, and after nearly daily trials for over a month, the number of bites taken on sponges on 6 May 1986 (both trials between 0900 and 1000 hrs, and with similar sponges offered) was 134 (not significantly different by

Table 1 *Sparisoma* spp. and *Scarus iserti*. Comparisons of parrotfish feeding in paired 20-min trials with cryptic sponges and without cryptic sponges (control). For statistical comparison of numbers of bites by the t-test for paired observations, only trials in which at least one individual of a fish species took bites within the observation circle are included, to account for the possibility that a particular fish species was not near the observation area for a particular trial. Each paired trial compares feeding at the same location, and at nearly the same time, by the same fish individuals

Trials	Paired t-test	Total bites per trial (mean ± SE)	Bites per individual per trial	Total visits per trial (mean ± SE)	Visits per individual per trial	Individuals per trial (range)
Sparisoma aurofrenatum						
With sponges		66.2 ± 8.7	21.1	14.5 ± 2.1	4.6	1–9
Control	**	10.5 ± 4.0	8.8	1.9 ± 0.3	1.6	1–2
Sparisoma viride						
With sponges		54.6 ± 4.4	19.5	10.4 ± 0.7	3.7	1–5
Control	**	28.9 ± 5.3	12.7	4.3 ± 0.7	1.9	1–5
Sparisoma chrysopterum						
With sponges		48.7 ± 5.2	20.5	10.9 ± 0.7	4.6	1–6
Control	**	17.8 ± 4.7	12.8	3.2 ± 1.1	2.3	1–2
Scarus iserti						
With sponges		93.5 ± 11.2	9.1	12.1 ± 1.2	1.2	1–33
Control	ns	106.9 ± 13.8	13.2	10.2 ± 1.1	1.2	1–24

**$p < 0.001$; *ns* not significant

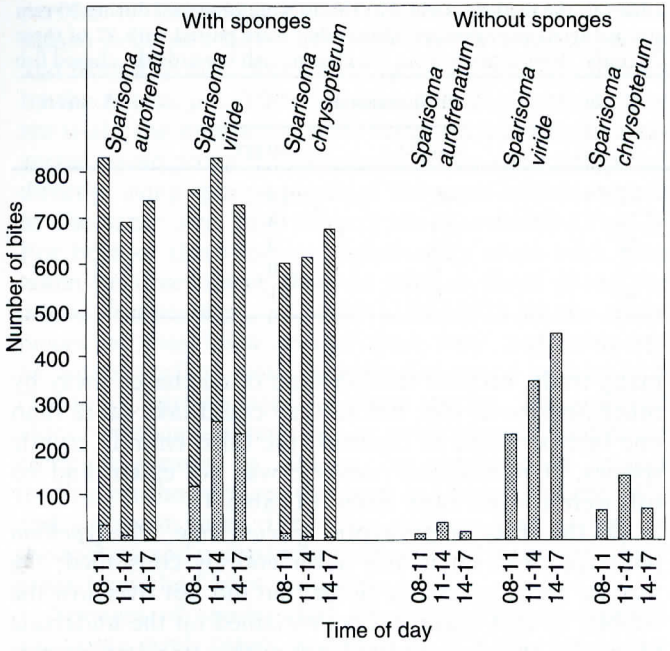

Fig. 2 *Sparisoma* spp. Time of day and feeding rates of three species. During each hour between 0800 and 1700 hrs, five trials, each consisting of 20 min with sponges and 20 min without sponges, were run (i.e., $n = 45$ trials). Data are grouped in three equal time intervals for graphical display. Total number of bites in a 0.125 m^2 feeding area taken by *Sparisoma* spp. at different times of day are given. Bites on sponges are indicated by *cross-hatching*. *Shaded bars* represent bites on everything else (algae)

the *G*-test, $p > 0.1$). One and a half years later, during which no experiments were made, the number of bites taken by these three species on sponges during the first trial that included edible sponges on 6 November 1987 was 106. Although there may have been some learning by the parrotfish that edible sponges might be available when I was on the reef, they were already attracted to the sponges during the first 20 min of experimental presentation. In addition, from the start of the experiments, the parrotfishes consistently fed on the same sponge species, and did not even sample species that, as data accumulated, were clearly unacceptable as food.

Sparisoma viride was the only one of these three species to forage extensively in circles without sponges, and also to feed on non-sponge foods when sponges were available. Nevertheless, 69.4% of bites taken by *S. viride* in sponge-spiked circles were on cryptic sponges. *S. aurofrenatum* and *S. chrysopterum* seemed to be attracted to feed in the circles only when cryptic sponges were offered (Table 1; Fig. 1) and took, respectively, 97.0 and 96.2% of their bites on sponges when foraging in circles with cryptic sponges added. Proportions of bites taken on sponges by these two species differed significantly from the proportion of bites taken on sponges by *S. viride* (*G*-test, $p < 0.001$ in both comparisons). Of the total number of bites observed, 95.9, 70.6, and 88.8% were in sponge-spiked circles for *S. aurofrenatum*, *S. viride*, and *S. chrysopterum*, respectively; and, of the total number of visits made to the circles, 96.7, 76.1, and 91.3% were to sponge circles for these three species, respectively. All of these proportions differ significantly (*G*-test, $p < 0.001$ in each case) from the 50:50 ratio of bites in or visits to sponge circles versus control circles that is predicted if *Sparisoma* species do not feed differently in the presence of cryptic sponges. In contrast, although *Scarus iserti* made slightly more visits to circles with sponges (56.6% of 1043 visits, significantly different from 50% by the *G*-test, $p < 0.001$), they did not take significantly more bites in sponge circles (51% of 9044 bites, *G*-test, $p > 0.05$). When the more conservative comparison is made, as described above, using only pairs of trials in which at least one *S. iserti* individual fed in the circles, again no significant difference in number of bites taken in circles with and without cryptic sponges available is found (*t*-test for paired comparisons, $p > 0.5$). Although *Scarus iserti* fed on sponges much less than the *Sparisoma* species, nevertheless 28.5% of the bites they took in sponge circles were on sponges.

When sponges were available in the circles, parrotfishes of larger size classes were more likely to concentrate their feeding on the sponges than were smaller individuals. For statistical analysis, size classes were grouped into four categories defined by equal standard length (SL) intervals of 2 to 5, 6 to 9, 10 to 13, and 14 to 17 cm. For all three *Sparisoma* species, fish of the smallest size category took significantly smaller proportions of their bites on sponges than fish of the next larger size category (proportion of sponge circle bites taken on sponges for fish of 2 to 5 vs 6 to 9 cm SL for, respectively, *S. aurofrenatum*, *S. viride*, and *S. chrysopterum*, were 88.5 vs 95.9%, 71.0 vs 77.4%, and 86.7 vs 99.1%; *G*-test, $p < 0.001$ in each case). For both *S. aurofrenatum* and *S. chrysopterum* all fish >6 cm SL took virtually all of their bites in experimental circles on cryptic or semi-cryptic sponges. For *S. viride*, however, the larger individuals of 14 to 17 cm SL fed on sponges significantly (*G*-test, $p < 0.001$) more than medium individuals of 10 to 13 cm SL (100 vs 76.2%); and *Scarus iserti* larger individuals, including terminal males, were the only ones that concentrated on eating sponges when they were available (proportions of sponge circle bites taken on sponges for fish of, respectively, 2 to 5, 6 to 9, and 10 to 13 cm were 13.3, 56.6, and 93.7%; differences between each pair of size classes are significant by the *G*-test, $p < 0.001$ in each case).

Interactions among the parrotfish were very different when cryptic sponges were available versus when they were absent, with the water directly over the sponge-spiked circle sometimes appearing to be boiling with *Sparisoma* spp. individuals chasing each other away. Feeding on cryptic sponges by *Sparisoma* spp. was terminated in 32% of the visits by a fish chasing away or being chased by another parrotfish (Table 2). Almost invariably (459 times out of 487 = 94.2%) the larger fish succeeded in chasing away the smaller one (Table 2). In spite of the many *Scarus iserti* always present (Table 1), only rarely did other parrotfishes chase them

Table 2 Parrotfishes and damselfishes. Census of chases of one fish by another that resulted in the fish leaving the feeding circle, along with sizes of both fish, for seventy-four 20-min trials, with sponges added to the feeding circle. No chases were observed during 20-min control trials (no sponges added) that were paired with 52 of these 74 trials. *Arrows* point from the chasing fish towards the chased fish

	S. aur.	*S. vir.*	*S. chr.*	all *Sparisoma*		*S. iserti*
				smaller	larger	
Sparisoma aurofrenatum →	230	32	92	340	14	1
Sparisoma viride →	17	21	24	48	14	1
Sparisoma chrysopterum →	13	26	32	71	0	3
Scarus iserti →	0	0	0	0	0	2
damselfishes →	30	21	40	0	91	21

away (Table 2). Only 1.4% (7/494) of the chases between parrotfishes involved this very common species which appears to be relatively uninterested in sponges (Fig. 1; Table 1). No chases between parrotfishes were observed in circles without cryptic sponges. The only other chases observed in circles included ten chases by damselfishes of surgeonfish, wrasses, and other damselfishes.

Sponges were not eaten indiscriminately by the parrotfishes. In 100% of the trials, *Halichondria* cf. *lutea* and *Geodia* cf. *gibberosa* were entirely consumed within 24 h, with the fish overturning the rubble pieces to which they were attached in order to remove every scrap of sponge tissue (Table 3). Because these sponges live so completely inside the cryptic spaces in the reef, bits of sponge tended to be somewhat hidden in between closely spaced coral branches, causing fish to return again and again, attempting to remove the remaining bits. Thus many bites were directed at relatively small volumes of sponge tissue. Some tissue remained after 20 min in many trials, because the fish were often chased away by other *Sparisoma* spp. before they could take more than one bite per visit. In contrast, the third entirely cryptic species, *Hymeniacidon caerulea*, was not eaten, and no fish were chased away from it (Table 3).

Of the three semi-cryptic species, one, *Pachypellina podatypa*, was eaten, but never entirely consumed; the fish ate easily accessible tissue, but did not overturn the rubble, so that tissue always remained on the underside (Table 3). Puzzling results for the other two semi-cryptic species, *Mycale laevis* and *Adocia* sp. (black), which were sometimes eaten quickly and at other times avoided, focused attention on what differed between trials with different results. The fish appeared to avoid these species when an unbroken surface was presented to them, but to feed vigorously when the inner tissue was exposed. When the inner tissue was exposed experimentally, by slicing off a few millimeters of the surface with a razor blade, the number of bites per trial increased, and the

Table 3 Parrotfish feeding on 18 species of sponges. Sponge-feeding evaluated by average number of bites per trial on each sponge species, percent of trials in which sponges were entirely consumed within 20 min, and percent of trials in which sponges were entirely consumed within 24 h. For each of a total of 74 trials, pieces of two to six species were offered. Independence of feeding on each sponge species was confirmed by complete correspondence among the last three columns in this table; i.e., sponge species from which many bites were taken were also entirely consumed within 20 min, and were the only ones entirely consumed in 24 h. Likewise, sponge species not eaten during the 20-min observation periods were never consumed within 24 h

Sponge species	Times offered	Bites per trial (mean)	Full consumption (% trials)	
			within 20 min	within 24 h
Cryptic				
Halichondria cf. *lutea*	71	97	44%	100%
Hymeniacidon caerulea	25	5	0	0
Geodia cf. *gibberosa*	30	42	23%	100%
Semi-cryptic				
Pachypellina podatypa	27	15	0	0
Adocia sp. (black)	13	31	8%	15%
inner tissue only	18	43	67%	100%
surface intact	10	1	0	0
Mycale laevis	29	25	0	0
inner tissue only	18	54	83%	100%
surface intact	10	2	0	0
Semi-exposed				
Lissodendoryx colombiensis	20	19	0	0
Spirastrella cf. *mollis*	8	0	0	0
Amphimedon erina	19	7	0	0
Pellina carbonaria	7	0	0	0
Exposed				
Iotrochota birotulata	12	0	0	0
Amphimedon rubens	12	0	0	0
Aplysina fulva	12	0	0	0
Niphates erecta	12	0	0	0
Callyspongia vaginalis	12	0	0	0
Desmapsamma anchorata	12	0	0	0
Ectyoplasia ferox	7	3	0	0
Verongula rigida	12	0	0	0

percent of times that these sponges were entirely consumed in 20 min increased from 0 to 83% for *M. laevis* and from 8 to 67% for *Adocia* sp. (significantly different by the *G*-test, $p < 0.001$ for each species, Table 3). For ten trials, the number of bites taken on inner tissue only versus tissue protected by intact surface were compared directly, using sponge pieces of the same individual, cut to the same size, and offered simultaneously (Fig. 3). For both of these species, significantly more bites were taken on inner tissue than on surface tissue (*t*-test for paired comparisons, $p < 0.001$). In 100% of the trials, pieces of these two species that were not protected by intact surface were entirely consumed within 24 h (Table 3). Surface layers of these species, when offered alone, were only bitten once or twice per trial and never completely eaten in 20 min. No evidence of further feeding on the surfaces was seen in the subsequent 24 h and, in most cases, the outer surfaces had curled on themselves and completely reconstituted a surface where inner tissue had been removed.

Sponges of species that are normally semi-exposed were only rarely bitten, and even in 24 h the entire piece of sponge was never eaten (Table 3). Completely exposed species were never bitten during the 20-min trials and never showed evidence of fish bites during the subsequent 24 h. Although the parrotfish could be seen to roll their eyes to look towards feeding circles whenever anything was offered, they were never observed to change direction to come to the circles when only exposed sponges were available.

In summary, an inverse relationship can be seen between the amount parrotfish feed on sponges and the relative availability of those sponges (Fig. 4). Two of three cryptic sponges, and inner tissue of semi-cryptic sponges, are highly attractive to the fish, whereas semi-exposed species and outer surfaces of semi-cryptic species are rarely eaten, and exposed sponges are never eaten. Valid comparisons among sponge species and among groups of sponge species depend upon the assumption that feeding on different sponge species is independent of the context, i.e., the other species made available simultaneously, in which they are offered. This is supported by the data in a variety of ways. First, the number of bites taken on a sponge species per trial consistently predicts whether or not a sponge will be consumed entirely during a trial or after 24 h (Table 3), i.e., sponge species from which the most bites were taken were also most frequently consumed within 20 min, and these species were always consumed within 24 h.

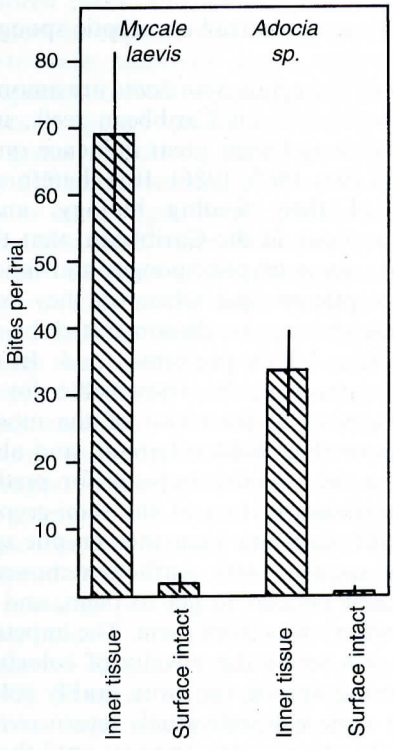

Fig. 3 *Sparisoma* spp. and *Scarus iserti*. Feeding on inner tissue versus surface tissue of two semi-cryptic sponge species. Mean (±SE) number of bites per 20-min trial ($n = 10$ trials per species) taken on the mostly cryptic species *Mycale laevis* and *Adocia* sp., comparing feeding on inner tissue only versus intact surface tissue. In each trial, sponge pieces differed only in whether or not surface tissue was removed or not, and were offered at the same time (i.e., exposed to the same fish individuals for the same time interval). Differences between feeding on inner tissue versus intact surface tissue were significant by the *t*-test for paired comparisons ($p < 0.001$ for both species)

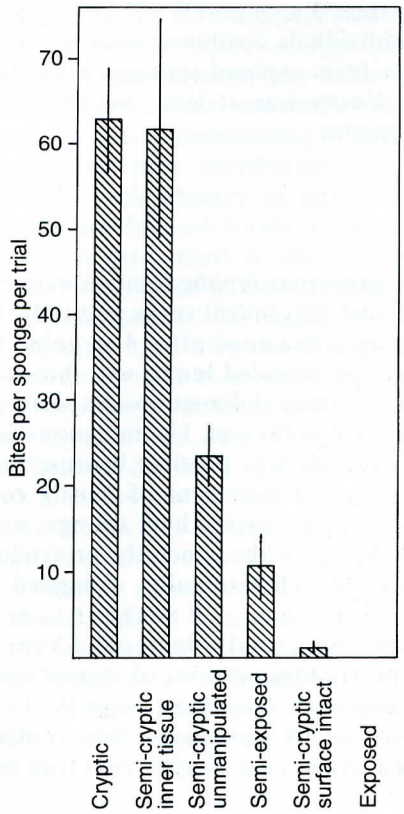

Fig. 4 *Sparisoma* spp. and *Scarus iserti*. Mean (±SE) number of bites per trial ($n = 74$ trials) per sponge type, comparing sponges that are unprotected and protected, to various degrees, by living within the reef frame or by concentrating defenses against predators in their surfaces

Sponges that were not fed on within 20 min were never consumed within 24 h (Table 3). Secondly, sample sizes are sufficiently large that variations among trials due to weather, and other causes of differences in fish abundance, are unlikely to have skewed the overall results. A total of 12 115 bites on sponges by the three *Sparisoma* species were observed over the course of 74 trials, and in the course of a trial, a mean of 144 bites (SE = 12) were taken in the circle by parrotfish. Many different fish visited the circles during a given trial (Table 1); and over the 70-m reef edge and the more than 2 years of accumulating these data, many different fish could come to the experiments. Thirdly, the clear separation among different categories of sponges (Fig. 4) demonstrates consistent reactions by parrotfishes to sponge species in each category. Fourth, these experiments do not represent a situation in which hungry, confined fish are allowed a limited selection of foods and must settle for those of poor quality after preferred foods are consumed. Instead, these experiments mimic a natural situation in which foods that are only rarely available are exposed to the fish, and the fish always have the alternative to eat the algae on which they normally feed.

Natural feeding by parrotfishes on exposed reef sponges is also extremely rare. During a 12-year period (1978 to 1990) of recording bites taken by fish on exposed reef sponges, all angelfishes, trunkfishes, and filefishes combined were observed to take a total of 4151 bites from exposed sponges (Wulff 1994), but all *Sparisoma* spp. individuals combined were observed to take only 18 bites from exposed sponges, even though their population density was at least one or two orders of magnitude greater.

Cages

Many of the cages over cryptic sponges were removed by children, so that no control cages and only 7 of 20 experimental cages remained after 4 months. In each of these seven cages rounded lumps and thin-walled tubes of from one to three different species were protruding above the surface of the reef. Unambiguous definition of protruding portions was possible because the reef surface is a nearly flat pavement of mostly consolidated rubble. The largest protruding sponge was a *Halichondria* cf. *lutea*, for the which the protruding portion consisted of two horizontally elongated tubes of $3.2 \times 2.1 \times 1.5$ cm and $3.9 \times 0.8 \times 1.1$ cm (length × width × height) for a total volume of 13.5 cm^3. The total number of protruding portions of cryptic sponges were nine *Halichondria* cf. *lutea* (size range 0.5 to 13.5 cm^3), eight *Hymeniacidon caerulea* (size range 0.2 to 5.2 cm^3), and five *Geodia* cf. *gibberosa* (size range 0.2 to 1.3 cm^3).

These results contrast with the complete absence of protruding portions of cryptic sponges before cages were installed, and the complete absence of protruding cryptic sponges anywhere on the reef except under the experimental cages. The protection afforded to the sponges by the cages was corroborated when, within 2 h of removal, all cryptic sponges except *Hymeniacidon caerulea* had been eaten by *Sparisoma* spp. so that the sponges no longer protruded above the surrounding rubble. Within a few days the surface of the protruding portions of *H. caerulea* was densely fouled with diatoms where the tissue seemed to have retracted from the edges of the skeleton.

During the dry season (January to April), a thick carpet of macroalgae, primarily *Dictyota divaricata*, blankets the top of Guigalatupo reef, and fish foraging on the reef top is curtailed because the shallow water can be too rough. Small tubes and thin arms were observed to grow from cryptic sponges, protruding from the reef and becoming entangled in the algae. These protruding parts were fragile, and although some were up to 10 cm in length, they rarely exceeded 2 to 5 mm in diameter. When clumps of algae were ripped off, as an experiment or by the waves, bits of the sponges were exposed, and parrotfishes were observed to eat the sponges within minutes.

Discussion

Can herbivorous fishes feed on cryptic sponges?

Parrotfishes of the genus *Sparisoma* are among the most important herbivores on Caribbean reefs, in terms of their abundance and their great influence on reef vegetation (e.g., Lewis 1985, 1986). It is therefore a surprising aspect of their feeding biology, and of reef community ecology in the Caribbean, that these herbivores feed on some cryptic sponges and inner tissue of some semi-cryptic sponges whenever they are available and that these sponges are demonstrated, by a variety of criteria, to be a highly preferred food. In turn, these parrotfishes appear to be responsible for restricting cryptic sponges of at least two of the most common three species to their hidden habitat, and also possibly for providing the selective impetus for predator-deterrent surface tissues in two of the semi-cryptic species. The fish readily consume excavated cryptic sponges and semi-cryptic sponges with surfaces removed, immediately alter their courses to get to them, and vigorously chase each other away from them. The impetus for these reactions is not solely the novelty of colorful bits suddenly appearing among the more drably colored algae, because the same fish individuals return over and over during a trial to bite cryptic sponges until they are gone. More compelling, the fish show none of these reactions when only exposed (i.e., inedible) sponges of the same size and similar colors are available. The fish chase away only those fish that compete with them for this resource, which appears and disappears quickly, and they do not chase fish of species that do not eat the sponges. They were not observed to chase each other away from their usual algal foods, or from normally exposed or semi-

exposed sponges, but only from cryptic sponges. In addition, the fish seemed to be already experienced about the relative edibility of the different sponge species even at the beginning of the experiments, not even sampling *Hymeniacidon caerulea* or normally exposed sponges when these were offered in the feeding circles. A final indication that cryptic sponges are preferred over other available foods comes from the temporal pattern of sponge-feeding. For at least some species of Caribbean macroalgae, susceptibility to herbivorous fish changes in tandem with a daily growth pattern (Hay et al. 1988; Polunin and Klumpp 1989; Bruggemann et al. 1994a). For *Sparisoma viride*, foraging rate has been demonstrated to change in a pattern reflecting diurnal variation in algal food quality (Bruggemann et al. 1994a). If this is a general pattern, fish might be expected to eat sponges only during times of day when palatability of their usual algal diet is lower, if the sponges are a less preferred food. This was not the case, however, and although *S. viride* fed on algae relatively less during the morning, just as reported by Bruggemann et al. (1994a), all three *Sparisoma* species ate sponges throughout the day, whenever they were offered.

All generalist herbivores considered in this study did not react to sponges in the same fashion. Surgeonfish entirely ignored them, and, among the scarids, significant differences in eagerness to eat sponges were clear. *Scarus iserti* were markedly less attracted than the *Sparisoma* species to feed on sponges, although 28.5% of their bites in sponge circles were on sponges. Even within the genus *Sparisoma*, feeding of *S. viride* was significantly different from that of the other two species, with less focus on sponges, by all criteria examined.

This is the first time, since Bakus's (1964, 1967) observations, that herbivores have been reported to consume sponges readily in the field, but previous studies have demonstrated that herbivorous fishes do not necessarily confine their eating to plants. Jones et al. (1991) give examples of flexibility in feeding exhibited by various reef fishes, and Choat (1991) has summarized studies of how various herbivorous fishes deal with the nutritional challenges, such as low protein content, presented by plants as primary food. These include fecal feeding by adults (Robertson 1982), and carnivory by recent recruits (Bellwood 1988; Horn 1989). Sponges are somewhat lower in energy per unit dry weight relative to most other animals because of their high ash content, much of it in the form of siliceous spicules (McClintock 1987; Meylan 1990). Even in terms of ash-free dry weight, sponges have a lower energy content, and the organic portion of sponges can, to various extents, consist of spongin or collagen fibers, which are not known to be digestible (Meylan 1990). Such sponge attributes, along with their unusual chemistry, may make them not worth the effort for wrasses and butterflyfishes, which ingest animals or parts of animals as a regular part of their diet (Randall 1983), and these fish were not observed to feed even on cryptic sponges in this study. Nevertheless, for exposed sponge species eaten by hawksbill turtles, Meylan (1990) demonstrated ash-free protein values of 25 to 59%, comparing favorably with values of 17.2 to 21% for algae eaten by *S. viride* (Bruggeman et al. 1994b). Thus, for Caribbean *Sparisoma* species, opportunistic feeding on cryptic sponges may be an effective solution to the problem of ingesting adequate nitrogen on a generally herbivorous diet. One partial test of this idea would be to compare details of algal feeding by the three species of *Sparisoma* to determine if *S. viride*, which feeds significantly less on sponges, ingests an algal diet relatively higher in nitrogen. Foraging on algae by *S. viride* has been studied in detail (Bruggemann et al. 1994a, b), but the other *Sparisoma* species in the present study have not been studied in a comparable way.

Whatever the physiological basis for the preference of *Sparisoma* spp. for cryptic sponges, these sponges appear to be sufficiently preferred over more generally available foods that, if they were not cryptic, the fish would surely exterminate them. Cryptic sponges and the inner tissue of semi-cryptic sponges are only available sporadically and unpredictably when physical disturbance rearranges the reef enough to expose them, when they grow above the reef surface, or when the dry season algal cover on top of the reef is lost. When cryptic sponges are exposed, the fish detect and devour them quickly, so that they are only available for a short time. Consequently, *Sparisoma* spp. seldom have opportunities to ingest cryptic sponges, and this is corroborated by Randall and Hartman's (1968) report that sponges are only a minor component (< 2%) of *Sparisoma* spp. gut contents. Although gut contents may reflect the average diet of the fish, they do not necessarily indicate food preferences or give an understanding of the control the fish may exert over prey distribution and abundance patterns. Despite their absence in gut contents, some cryptic sponges are favored foods of *Sparisoma* spp., and the fishes, in turn, exert a strong influence over distribution and abundance of these sponge species.

Randall and Hartman (1968) suggested that the trace amounts of sponges that they did find in the guts of *Sparisoma* spp. could have been accidentally ingested as the fishes fed on other organisms, such as algae, and the present study suggests that, on a regular daily basis, this is the case. During the brief occasions when cryptic sponges and inner tissues of semi-cryptic sponges are exposed, however, such as at the end of the dry season and after damage to the reef surface, individual fish may purposefully take as many bites as they can between being chased and chasing competitors away. When excavations were made in the reef to collect sponges for the experiments, the fish gathered quickly and attempted to consume the sponges, apparently unconcerned about people, digging tools, or cameras. Cages had to be immediately placed over excavations to prevent the parrotfishes from consuming all the sponges before they could be used in experiments. An average of 18 bites taken on cryptic sponges per *Sparisoma* spp. individual per 20-min trial suggests that, when cryptic sponges are available, individual fish might accumulate much sponge

material in their guts. These occasions may be too rare to be reflected in gut content data. Trace amounts of sponges found in parrotfish guts may help to explain their ability to supplement their diet opportunistically with these unusual foods. Effective coping with chemical and mechanical challenges presented by eating a sponge may have been selected for in these fishes by their constant low-level exposure as they accidentally ingest small bits of sponges entangled in algae.

Are biogeographic patterns in intensity of predation on sponges due to geography or habitat?

Are cryptic sponges confined to their habitat because they are susceptible to predation by herbivorous fishes, or have these sponges been confined to cryptic spaces for some other reason and have subsequently lost defenses against predators because these are too expensive to maintain when they are not continuously necessary? Advantages offered by the cryptic habitat, in addition to protection from swimming predators, include protection from ultraviolet radiation and from breakage by vigorous water movement. On the other hand, disadvantages of cryptic living are many. Cryptic spaces constrain the shape and the size to which an individual can grow. In addition, the lower flow rates inside the reef frame must make this habitat less than optimal for filter-feeding organisms, especially ones that process water as rapidly and efficiently as sponges (e.g., Reiswig 1971).

For a sponge to thrive in this habitat, several traits might be expected. Cavernous architecture, in which the bulk of the volume of the sponge consists of wide canals, might facilitate pumping in this reduced-flow environment. Modification of the surface for protection from predators, fouling organisms, and ultraviolet radiation at only those small points at which it does emerge through the reef surface might also be expected. Cryptic sponges might also be predicted to have lost the capacity to repel predators and to have lost the capacity to make large erect structures. Among the cryptic and semi-cryptic sponges in this study, these predicted traits are proportionately more common than among exposed sponges. Although some exposed sponges might also have traits such as cavernous architecture, surface modifications, and inability to make large erect structures, one trait that is not negotiable for exposed sponges is inherent defenses against common and abundant predators. Exposed sponges palatable to parrotfishes would presumably quickly disappear.

Data in the present study demonstrate that defenses against predation by generalist fishes are better developed in exposed sponges than in cryptic sponges. The avoidance of *Hymeniacidon caerulea* was a striking exception, suggesting something other than predation forces a cryptic habit on this species. This species was initially described (Pulitzer-Finali 1986) as small encrustations in 4 to 8 m depth, thus it is possible that it is confined to cryptic habitats in very shallow water because of inadequate inherent protections against ultraviolet radiation. Shading by the wide plastic strips forming the meshes in the cages may have also provided sufficient protection for the sponges to emerge from the reef. Whatever the basis for effective predator defenses in *H. caerulea*, it is also rejected consistently by other predators which would not normally have had any contact with it, including the starfish, *Oreaster reticulatus* (Wulff 1995), and the Pacific smooth pufferfish, *Arothron hispidus* (Wulff 1997); and *H. caerulea* was never consumed in the course of 4770 bites on 64 sponge species by unmanipulated Caribbean angelfish, trunkfish, and filefish species that specialize on sponges (Wulff 1994). The suggestion that cryptic sponges are, in general, confined to their hidden habitat because they lack inherent (i.e., within their tissue) protection from predation has been made previously (Green 1977; Bakus 1981; Bakus et al. 1986; Wulff 1988). In general, the means by which many species of these soft-bodied, sessile creatures are able to live exposed appear to be secondary compounds that deter predators, as sponges are rich sources of unusual secondary metabolites (e.g., Faulkner 1986, 1987, 1988, 1990), and several sponge secondary metabolites have been shown to deter feeding by generalist fishes (e.g., Rogers and Paul 1991; Duffy and Paul 1992; Paul 1992).

Sponge toxicity towards goldfish swimming in extracts of exposed and cryptic sponges was assayed by Bakus (1981) at Lizard Island (Great Barrier Reef). Of the ten exposed sponges he tested, six were toxic by this assay, whereas only two of six cryptic species were toxic. Toxicity of cryptic and exposed Caribbean sponges to goldfish was assayed by Green (1977) by evaluating their behavior when placed in a fingerbowl with sponge extracts. By this assay, a greater proportion of cryptic sponges were nontoxic. Some of the sponges he tested were congeners of, or conspecific with, the sponges in this study, but, in general, direct comparisons are difficult because of the lack of many species' identifications. Where comparisons are possible, the data do not match results of the present study closely. For example, in the present study *Sparisoma* spp. did not eat *Iotrochota birotulata*, which by Green's goldfish assay was nontoxic. In another study, Green et al. (1990) found *Iotrochota birotulata*, *Niphates erecta*, *Callyspongia vaginalis*, and *Desmapsamma anchorata* to be nontoxic to guppies swimming in diluted methanolic extracts. In my study, *Sparisoma* spp. avoided all of these sponges. It is possible that these sponges are unpalatable to parrotfishes, but not toxic (distinction discussed for sponges by Schulte and Bakus 1992, and for soft corals by Sammarco and Coll 1990), or not toxic unless ingested.

Accessible macroalgae have been determined to be resistant to grazing by *Sparisoma* spp. (Lewis 1985), whereas species living in habitats with low grazing pressure were susceptible to feeding by these fishes. Hay and Fenical (1988) and Hay (1991) review a number of other herbivore–algae studies in which this pattern has been found. A similar pattern has been demonstrated for

the Caribbean starfish *Oreaster reticulatus*, which rejects grassbed and rubble flat sponges with which it coexists, but which feeds readily on reef-dwelling sponges, although these are normally inaccessible because the starfish do not live on the reef (Wulff 1995). Eastern Pacific sponges living in cryptic habitats on coral reefs or under and between intertidal cobbles are also consumed by fish predators which normally have no access to these sponges (Wulff 1997). The present study shows that some cryptic Caribbean sponges are also preferred foods that are only rarely ingested because predators completely confine them to life in a generally inaccessible habitat.

The contrast between reports of fish predation on cryptic sponges in the Indo-West Pacific (Bakus 1964, 1967) and eastern Pacific (Glynn et al. 1972), where sponges are not a conspicuous part of the sessile fauna on many reefs, and evidence of sponge-feeding by only a few very highly specialized fishes in the Caribbean (Randall and Hartman 1968), where sponges frequently are the dominant sessile invertebrates, can only be understood by consideration of how the studies were done, the habitats of the sponges, and biogeographic differences. While gut content analysis provides a determination of the average diet of fishes, opportunistic feeding on generally unavailable but preferred prey may be missed by this method. It is these prey, hidden because of their extreme susceptibility to predation, that are most likely to have their distribution and abundance tightly controlled by predators. It is also clear that the habitat of the sponges studied is of primary importance in explaining these contrasting data, with many cryptic sponges evidently confined to their habitat by feeding of normally herbivorous fishes, and exposed sponges adequately defended against the great majority of reef fishes. These data do not directly address the possibility that biogeographic differences in predation intensity, or other biological, physical, or historical factors, explain the lack of exposed sponges in many areas of the tropical Pacific, but they do demonstrate an inverse relationship between availability and edibility of some sponges. This may provide an explanation for an apparent biogeographic difference in sponge-feeding by generalist fishes.

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