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Sponge feeding by Caribbean angelfishes, trunkfishes, and filefishes

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ABSTRACT: Sponges are conspicuous and abundant on most Caribbean coral reefs, but appear to be well defended from predators. Randall & Hartman (1968) found significant sponge remains in gut contents of only 11 of the 212 species of Caribbean reef fishes they examined. From 1978-1990, every time I saw one of these species in a shallow reef area of 30 m x 40 m, I followed it and recorded what it ate. All 1395 sponges within 16 m^2 in the center of the observation area were counted and measured so that relative abundance, in terms of number of individuals and also total biomass, of each sponge species could be compared to preferences of the feeding fish. Trunkfishes of the genus *Acanthostracion* took virtually all of the 2374 bites observed on sponges. They fed on 25 species, but took most (85.4 %) of their bites on *Aplysina fulva*. The French and gray angelfishes, *Pomacanthus paru* and *P. arcuatus*, took 75 % of the 2285 bites observed on sponges. These angelfishes fed on 64 sponge species, representing a variety of colors, growth forms, and most orders of Demospongiae, and including all but 6 of the 42 species in the censused area. Individual angelfish fed on many different species, moving to new prey individuals after an average of only 2.8 bites. In 92 % of the cases in which an angelfish feeding on a sponge fed next on another sponge, the two sponges were of different species. Although angelfish fed on sponge species in order of their relative abundance, they fed disproportionately more on rare species and less on common species than predicted by the relative abundances of the sponges, indicating active diversification of their diets.

1 INTRODUCTION

Significant sponge remains (> 6 % by volume) were discovered in gut contents of only 11 of the 212 Caribbean reef fish species analyzed by Randall & Hartman (1968), leading them to conclude that sponge distribution on Caribbean reefs is not significantly limited by fish predation. By analyzing characters of the sponge species consumed, they determined that physical characters, such as spicules and tough fibers, are not consistently deterrent to fish, suggesting that sponge chemistry is also important in mediating these predator-prey relationships.

Sponge chemistry has subsequently been implicated, either directly or by default, in influencing other predators besides fish. Some dorid nudibranchs are specialists, feeding on a single sponge species and also sequestering toxins from it (e.g., Faulkner & Ghiselin, 1983; Rogers & Paul, 1991). Other dorid nudibranchs are generalists, capable of feeding on a variety of sponge species, though not necessarily sequestering secondary metabolites from all of them (e.g., Pawlik et al., 1988; Anderson et al., 1993). Likewise, one sponge-feeding antarctic asteroid is a specialist, but four others are generalists (Dayton et al., 1974). Just as for the sponge-feeding fishes, no consistent relationship was found between the energy and spicule contents of sponge species and the amount of feeding by asteroids on those species (McClintock, 1987). Sponges fed on by hawksbill turtles are also not consistently higher or lower in energy, protein, or organic content than sponges not eaten by the turtles, although the turtles do concentrate their feeding on members of the Astrophorida and Hadromerida, which are typically abundantly endowed with siliceous spicules (Meylan, 1990).

Thus, some sponge-feeders are specialists, able to ingest large quantities of the secondary metabolites of a single sponge species without mortal consequences, and others are generalists, able to feed on many sponge species. However, it is clear from the above examples, that at least three types of predator-prey relationships must be distinguished within the category "generalist": (1) Some predators eat many different prey species because they are relatively unaffected by secondary metabolites. Generalist sponge-feeding nudibranchs, capable of detoxifying or sequestering ingested toxins, may fall into this category. (2) Some predators feed on many different sponge species, but confine their non-selectivity to species within certain higher taxa, as the hawksbill turtles do. (3) Some predators need to feed on a wide variety of species in order to avoid poisoning themselves or depriving themselves of necessary nutrients by feeding too much on a single toxic or low-nutrient sponge. This "smorgasbord" foraging strategy was the one proposed by Randall & Hartman (1968) to account for the high diversity of sponge species they identified in gut contents of individual fish. Distinguishing among these four ways of foraging is necessary for understanding the evolution of defenses in sponges and the roles predators play in structuring communities dominated by sponges.

To determine how the fish forage, they must be observed feeding in the field. Equally importantly, the relative abundance of sponge species must be documented, to be able to compare what the fish eat with what is available. These were my goals in this study.

2 METHODS

Species of reef fishes identified by Randall & Hartman (1968) as sponge feeders are, in general, relatively rare and wary. They do not feed continuously, and tend not to feed at all while being overtly observed. Consequently, diving expressly for observing sponge-feeding fishes was impractical. Instead, I designated a feeding observation area of 30 m x 40 m, where I was working on other experiments. Whenever I saw a fish of a sponge-feeding species in this area, I followed it, recording how many bites it took from each prey individual it visited until it bolted or hid. In this way, data were accumulated for 12 years (1978 - 1990). The feeding area consisted of a shallow flat plane and the adjacent slope on Guigalga tupo reef, near the San Blas Field Station of the Smithsonian Tropical Research Institute, Republic of Panama. The substratum was primarily rubble from ramose coral species, dotted with small to medium massive corals. Sponges were the most abundant and diverse sessile organisms and were homogeneously distributed throughout the observation area.

To compare sponge species eaten with those available, 16 m^2 (two 1 m x 8 m transects, perpendicular to each other) were completely censused. The censused area was in the center of the observation area, but any portion would have been as representative. Numbers of individuals of each sponge species were counted and the size of each sponge individual was measured by approximation to geometric volumes. The time required to do a complete re-census was prohibitive, but a census of the 3 most common species (constituting 80 % of the total sponge volume in the area) was repeated 4 years later to determine if the initial census was still representative.

3 RESULTS

3.1 *Amount of sponge feeding*

Over the course of 12 years, I observed 4770 bites by seven species of sponge-feeding fishes. A total of 87 % of those bites were on sponges. The percent of bites taken on sponges by each of the fish species observed are given in Table 1.

3.2 *Sponge species available*

In the census of 16 m^2, representatives of 42 species were found among the 1395 non-excavating sponge individuals. These 42 species are ranked by decreasing total volume in Table 2. Only three sponge species that were not represented in the censused area could be found in a five hour search of the entire feeding obser-

Table 1. Comparisons of gut content analyses (Randall & Hartman, 1968) with in situ feeding observations (this study). Percentages of bites taken on sponges by seven species of sponge-feeding reef fishes while they were being observed in the field are compared here with percentages of gut contents that were found to be sponges by Randall & Hartman (1968).

	Randall & Hartman, 1968		This study	
	# individuals examined	% of total volume of gut contents that were sponges	# bites observed	% of bites that were on sponges
Angelfish				
Pomacanthus arcuatus (Linnaeus)	26	70.2	465	89.7
Pomacanthus paru (Bloch)	24	74.8	1820	71.2
Holacanthus tricolor (Bloch)	22	97.1	11	100.0
Trunkfish				
Acanthostracion polygonius (Poey)	4	11.7	1185	98.5
Acanthostracion quadricornis (Linnaeus)	6	30.7	1189	100.0
Filefish				
Aluterus scriptus (Osbeck)	8	0.4	71	73.2
Cantherhines macrocerus (Hollard)	10	86.5	29	65.5

vation area. These species, *"Xestospong-ia" tierneyi* de Laubenfels, *Tethya crypta* (de Laubenfels), and *Spheciospongia vesparium* (Lamarck), were all resident in a 2 m x 2 m patch of *Thalassia* meadow on an edge of the feeding area.

The initial census was still representative of population sizes of the 3 most common species 4 years later. In the recensus, the numbers of individuals of *Iotrochota birotulata*, *Amphimedon rubens*, and *Aplysina fulva* were, respectively, 100.5 %, 94.3 %, and 106.4 % of those found in the initial census.

3.3 *Sponge species eaten*

The filefish species, *Aluterus scriptus* and *Cantherhines macrocerus*, fed on 5 and 4 species of sponges, respectively. In one long feeding sequence, an *A. scriptus* fed on five sponge species and on various algae, but in each of the other 7 sequences observed, filefish fed on only one prey species. These data demonstrate that the filefish are sponge-feeders and feed on a variety of species, but the 100 bites observed do not illuminate details of feeding behavior.

Table 2. Complete census of 16 m^2, San Blas Islands, Republic of Panama. Among the 1395 individuals of non-excavating sponges in 16 m^2, these 42 species were represented. The species are ranked in order of decreasing total volume, and total volume is given in cm^3. Columns labeled "A" and "P" give the ranks of these sponge species in order of decreasing numbers of bites take by two *Acanthostracion* species ("A") and two *Pomacanthus* species ("P"). In cases of equal numbers of bites taken on two or more sponge species, the species are all given average ranks. All sponges eaten were included in the ranking by number of bites taken, and so gaps in the ranks given are due to feeding on species not represented in the censused area.

Rank	Vol.	A	P	Species
1	9767.3	1	5	*Aplysina fulva* (Pallas)
2	6001.3	2	1	*Iotrochota birotulata* (Higgin)
3	3626.3	3	7	*Amphimedon rubens* (Pallas)
4	2939.6	5	10	thickly encrusting, brown
5	1843.2	16.5	27	*Ircinia* sp., brown rounded fistules
6	1710.6	7.5	3	*Niphates erecta* Duchassaing & Michelotti
7	1094.6	20.5	33.5	*Ircinia* sp., tall grey fistules
8	1011.0	12.5	6	*Verongula rigida* (Esper)
9	1006.9			*Ircinia campana* (Lamarck)
10	656.7	4	12	*Mycale laevis* (Carter)
11	651.0		60	*Ircinia strobilina* (Lamarck)
12	530.0		27	*Ircinia* sp., pale grey-brown
13	465.6	20.5	19	thickly encrusting, brownish yellow
14	442.0	20.5	54.5	*Ircinia felix* (Duchassaing & Michelotti)
15	274.6	16.5	22	*Callyspongia vaginalis* (Lamarck)
16	260.6			*Ircinia* sp., encrusting, brown
17	233.4		2	*Spirastrella* cf. *coccinea* (Duchassaing & Michelotti)
18	221.0		15	*Lissodendoryx colombiensis* Zea & van Soest
19	219.0		16.5	*Xestospongia proxima* (Duchassaing & Michelotti)
20	208.5	20.5	8	encrusting, purple
21	124.5		31	*Desmapsamma anchorata* (Carter)
22	96.0		29.5	cryptic, bright orange
23	80.0		41	*Adocia* sp., purple
24	48.3			small pointed fistules, red
25	42.4			encrusting, strawberry red
26	39.4		41	*Pellina carbonaria* (Lamarck)
27	38.7		4	cryptic, dark orange
28	28.7		37	*Chondrilla nucula* Schmidt
29	18.0		27	*Pachypellina podatypa* (de Laubenfels)
30	9.0		49.5	encrusting, smoothly connulose, red
31	6.8			encrusting, red
32	6.0		16.5	*Amphimedon erina* (de Laubenfels)
33	3.5		37	cryptic, yellow-grey
34	3.2		25	*Placospongia carinata* (Bowerbank)
35	3.1		49.5	encrusting, soft, black
36	2.6		54.5	*Monanchora unguifera* (de Laubenfels)
37	2.0	11	41	*Halichondria* sp., pale yellow-orange
38	2.0		60	encrusting, smooth, purple
39	1.5		33.5	encrusting, orange-red with white flecks
40	1.4	6	11	*Rhaphidophlus raraechelae* van Soest
41	0.3		49.5	*Dysidea etheria* de Laubenfels
42	0.2			encrusting, filmy white

The two trunkfish species, *A. polygonius* and *A. quadricornis*, fed on 15 sponge species represented in the censused area (ranked by number of bites taken on them in Table 2) and on 10 additional species during the 36 feeding sequences observed but they both appear to specialize on *A. fulva*, taking respectively 89.7 % and 81.1 % of their bites from this species. *Aplysina fulva* was the most abundant sponge species, constituting 29 % of the total sponge volume. By the G-test, 89.7 % and 81.1 % are both significantly ($p < .001$) greater proportions of total bites than predicted by the 29 % *A. fulva* abundance, indicating that these *Acanthostracion* are truly specialists on this species. Not all *A. fulva* individuals are equally attractive, however. After a trunkfish feeding session, some sponge individuals would be covered with bite marks, whereas other individuals would only have a few or no bites taken from them. When I determined which *A. fulva* individuals were likely to be clone-mates (Wulff, 1986), it was clear that *Acanthostracion* favored a few clones and rejected members of other clones, even though the physiologically independent members of different clones were well interspersed with each other. A trunkfish also fed on three physiologically independent members of one clone (Wulff, 1986) of *Amphimedon rubens* but rejected members of two other clones.

Another possible specialist is the rock beauty angelfish, *Holacanthus tricolor*, which was only observed to take bites from *Iotrochota birotulata*. This was the second most abundant sponge species, with respect to volume, in the observation area. Apparent specialization could be due, therefore, simply to a high probability that 11 randomly taken bites would be from *I. birotulata*.

Angelfishes of the genus *Pomacanthus* feed very differently, eating small amounts of each of many sponge species. In the course of 70 observed feeding sequences, the gray and French angelfishes, *P. arcuatus* and *P. paru*, fed on all but 6 of the 42 species represented in the censused area (ranked in Table 2) and also fed on an additional 28 species, for a total of 64 prey species. Virtually all of the 28 species not resident in the censused area were so rare that they were only found in the feeding area when a fish was observed biting them. The adults of the two angelfishes often fed together and in the same fashion, moving to a new prey individual after an average of only 2.8 bites. In 92 % of the cases in which an angelfish feeding on a sponge moved on to feed next on another sponge, the two sponges were of different species.

To determine if these angelfish simply feed on sponge species in proportion to their relative abundance, Kendall's coefficient of rank correlation was used to test association between sponge abundance and fish feeding in two ways. First, association of total sponge volume with number of fish bites was tested, because tissue volume determines how many bites can be taken from it. Second, association of total number of sponge individuals with number of fish visits was tested, because moving to a new prey individual defines a visit. In both cases, the ranks of sponge abundance and the ranks of fish feeding frequency are significantly correlated ($p < .05$ for volume vs. bites and $p < .01$ for number of individuals vs. visits).

The fish do not choose prey randomly, however. Feeding by *Pomacanthus* species appeared to be more evenly distributed among sponge species than predicted by the total volumes of tissue representing those spe-

Table 3. Sponge abundance and angelfish feeding. The 42 sponge species represented in the censused plot were divided, by number of individuals, into the 14 most abundant, 14 least abundant, and middle 14 species; and the total number of individuals represented by each group was used to predict the number of visits that would be made to sponges in that group if angelfish choose prey sponges randomly. The same analysis was done using total volume as the measure of sponge abundance and numbers of bites as the measure of fish feeding on a species. In both cases, the number of bites or visits predicted by the abundance measures were significantly different from those observed.

Ranks of sponge species by number of individuals	% of individual sponges in censused area	% of total feeding visits by angelfish
1 - 14	92.8	79.4
15 - 28	5.8	15.4
29 - 42	1.4	5.1

Significantly different by the G-test, $p < .001$

Ranks of sponge species by volume	% of total sponge volume in censused area	% of total bites taken by angelfish
1 - 14	94.1	63.8
15 - 28	5.7	29.1
29 - 42	0.2	7.1

Significantly different by the G-test, $p < .001$

cies. This was tested by dividing the 42 species into 3 equal groups based on number of individuals, and using the total number of individuals in each group to predict the number of visits that would be made to sponges in that group if angelfish choose prey sponges randomly (Table 3). The same analysis was done using volume as the measure of sponge abundance and numbers of bites as the measure of fish attention to a sponge species. In both cases the number of bites or visits predicted by the abundance measures were significantly different from those observed (G-test, $p < .001$ in both cases, Table 3). The fish fed more on rare species and less on common species than predicted by actual sponge abundances. Thus, the fish are not choosing prey randomly, but appear to be foraging to increase the evenness of their predation over the species available.

3.4 *Sponge color*

If angelfish feed on sponge species more evenly than predicted by sponge abundances, the fish must be able to distinguish sponge species from each other. Two types of observations suggested that the fish use color in deciding what sponges to eat. First, in 89 % of the times in which an angelfish feeding on a sponge fed next on another sponge, the second sponge was of a different color than the first. Second, in 27 % of the few cases in which an angelfish feeding on a sponge moved on to feed next on another sponge of the same species, the two conspecific sponges were of different color morphs.

To explore the possibility that color helps angelfish decide which sponges to eat, the feeding sequences were also analyzed by color. Nine color categories were erected (Fig. 1), and most sponge species fit unambiguously into one of these. A few species (*Niphates erecta, Iotrochota birotulata,* and *Mycale laevis*) were represented by more than one color morph, and they were separated accordingly. By Kendall's coefficient of rank correlation, the association between the number of bites taken on each color of sponge and the total volume of each color of sponge is significant ($p < .05$), indicating that the fish are taking bites from the color categories in order of their relative abundance (Fig. 1). However, the number of visits to sponges of each color category that are predicted if angelfish

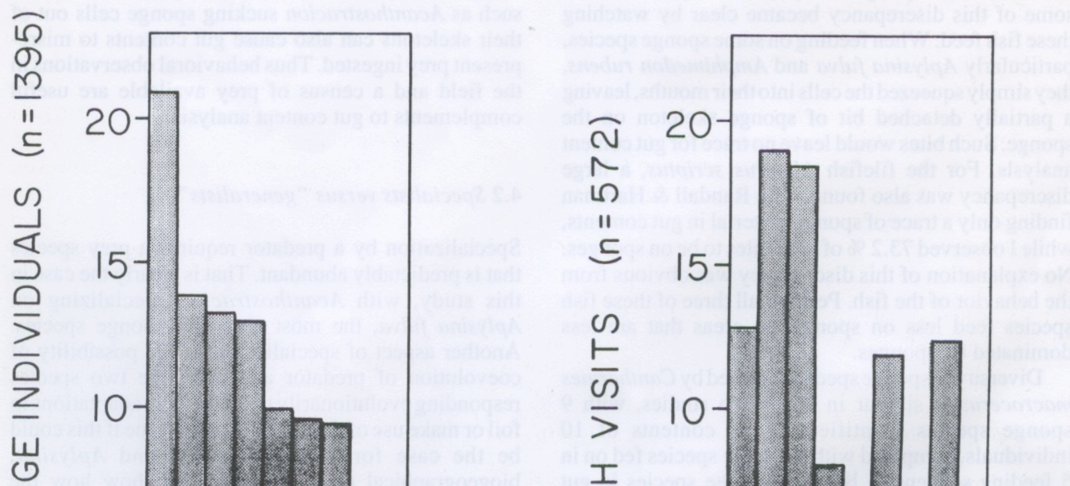

Figure 1: Relative abundances of sponges in different color categories compared with relative numbers of visits made to sponge species in those color categories by the angelfishes *Pomacanthus paru* and *P. arcuatus*. Sponges in the censused area were divided into 9 color categories: yellow-ochre (yo), brown (bn), green (gr), blue (bl), red (rd), black (bk), purple (pr), orange (or), and pale pink, grey (pg). Those species represented by more than one color morph were divided accordingly.

choose prey randomly are significantly different from those observed (G-test, $p < .001$), suggesting, again, that the angelfish are actively diversifying their diets (Fig. 1). The relatively even spread of bites taken among sponge colors gives no evidence for aposematism in these sponges.

4 DISCUSSION

4.1 *Comparison of gut contents with in situ feeding observations*

The percentages of bites observed in this study to be on sponges matched percentages of gut contents determined to be sponges by Randall & Hartman (1968) fairly closely for the three angelfish, *Pomacanthus arcuatus*, *P. paru*, and *Holacanthus tricolor*, and the filefish, *Cantherhines macrocerus* (Table 1). However, for the trunkfishes *Acanthostracion polygonius* and *A. quadricornis* virtually all the bites I observed were on sponges, whereas Randall & Hartman (1968) found only 11.7 % and 30.7 %, respectively, of their gut contents to be sponges. A possible explanation for some of this discrepancy became clear by watching these fish feed. When feeding on some sponge species, particularly *Aplysina fulva* and *Amphimedon rubens*, they simply squeezed the cells into their mouths, leaving a partially detached bit of sponge skeleton on the sponge. Such bites would leave no trace for gut content analysis. For the filefish *Aluterus scriptus*, a large discrepancy was also found, with Randall & Hartman finding only a trace of sponge material in gut contents, while I observed 73.2 % of total bites to be on sponges. No explanation of this discrepancy was obvious from the behavior of the fish. Perhaps all three of these fish species feed less on sponges in areas that are less dominated by sponges.

Diversity of sponge species ingested by *Cantherines macrocerus* is similar in these two studies, with 9 sponge species identified in gut contents of 10 individuals, compared with 4 sponge species fed on in 5 feeding sequences; but none of the species in gut contents were the same as those observed to be eaten. Diversity of species eaten is similar in the two studies for *Pomacanthus* also, with a total of 39 sponge species found in gut contents of 30 individuals, and a total of 64 species observed to be eaten in 70 feeding sequences. Many of the species and genera fed upon were the same in the two studies, although comparisons are hampered by difficulty in identifying many sponges to species in both studies. The relative amounts the species were fed on were sometimes strikingly similar in the two studies. *Gelliodes ramosa* (= *Niphates erecta*) was ranked 3rd and 4th in gut contents of the two *Pomacanthus* species, and ranked 3rd by feeding observations. Likewise, *Spirastrella* cf. *coccinea* was ranked 2nd and 8th in gut contents, and 2nd by feeding observations. However, *Callyspongia vaginalis* was ranked 1st by gut contents, and only 22nd by feeding observations. In combined gut contents of 22 *Holacanthus tricolor*, Randall & Hartman found 28 sponge species. Perhaps coincidentally, *Iotrochota birotulata* was the most abundant sponge in gut contents (15.6 % by volume) and also the only species observed to be eaten in the field. A total of 10 *Acanthostracion* individuals yielded only 5 sponge species in gut contents, contrasting with field observations of these fish eating small amounts of 24 species, and mostly eating *A. fulva*. Similarities in sponges ingested are more surprising than differences, given the great diversity of sponges on Caribbean reefs.

Randall & Hartman's assessment of *Pomacanthus* as smorgasbord feeders is fully supported by feeding observations and sponge census data in this study. In general, however, although gut content analysis can demonstrate that a sponge is eaten by a predator, more information is needed to conclusively distinguish specialists and the three types of generalists from each other. For example, a predator could appear to be a specialist because only one prey species is found in its gut, but this pattern could also result from that sponge being the only one available. Unexpected behaviors, such as *Acanthostracion* sucking sponge cells out of their skeletons can also cause gut contents to misrepresent prey ingested. Thus behavioral observations in the field and a census of prey available are useful complements to gut content analysis.

4.2 *Specialists versus "generalists"*

Specialization by a predator requires a prey species that is predictably abundant. That is clearly the case in this study, with *Acanthostracion* specializing on *Aplysina fulva*, the most abundant sponge species. Another aspect of specialization is the possibility of coevolution of predator and prey, the two species responding evolutionarily to each others adaptations to foil or make use of the other. To determine if this could be the case for *Acanthostracion* and *Aplysina*, biogeographical data are needed to show how the trunkfish feed where *Aplysina fulva* is not so abundant, i.e., if the fish feed on related species, or eat whatever the most common species is locally, or if the fish are absent altogether.

In contrast to the fine-tuning of chemistry demonstrated between specialist predators and their prey, and the ability to cope with a variety of secondary metabolites required of some types of "generalists", specifics of sponge chemistry may be irrelevant to smorgasbord feeders. A fish that always digests small bits of many sponge species simultaneously is not able to evaluate the food quality of each species and to respond in either an ecological or evolutionary sense. In addition, whereas specialists need only distinguish their single prey species from everything else, smorgasbord feeders require sensory equipment that allows distinction among all prey species and also brain development that allows for relatively complex behavioral sequences and memory of what has been recently eaten. Herbivorous primates are classic examples of smorgasbord feeding (e.g., Milton, 1979; Glander, 1982). Angelfishes of the genus *Pomacanthus* evidently also have what is needed to use this strategy for feeding on chemically defended prey.

That color plays a role in prey choice by sponge-feeding angelfishes is suggested by experiments on sponges with symbiotic zoanthids. West (1976) demonstrated that *H. tricolor* avoid *I. birotulata* colonized by *Parazoanthus swiftii*, a bright yellow zoanthid that contrasts dramatically with the dark green of the host sponge. Complementing these data, Lewis (1982) demonstrated that *P. arcuatus* do not distinguish between *Callyspongia vaginalis* with and without *Parazoanthus parasiticus* in their feeding. This sponge-zoanthid pair is monochromatic.

More information on color vision in angelfishes is needed to be certain that they choose their prey by color, but visual information clearly influences prey choices. These fishes appear to decide to feed on a sponge while some distance from it. The trunkfishes sometimes blow sediment off of a sponge and look at it again before taking a bite, but they do not generally spit out sponges they have tasted. The angelfishes look around, head straight for a sponge, and take bites, which are ingested entirely. In addition, when several sponge species are intertwined with and adherent to each other, fish can be observed to deftly take several bites from only one of the participating species. These fish clearly choose what to eat with care; but their goal is not to avoid particular species, but to eat a variety of species. This may partly explain the lack of evidence for aposematism in sponges in this study as well as in Randall & Hartman (1968) and Bakus & Thun (1979).

It is in the interests of both the predators and the chemically defended prey that a predator move on, after a few bites, to feed on another sponge species. For a smorgasbord-feeding predator to be able to tell all of the prey species apart visually is advantageous, then, to both predator and prey. If color is the means by which fish distinguish sponge species, then it is possible that predation by visually oriented smorgasbord predators has influenced the evolution of the striking diversity of color in coral reef sponges.

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REFERENCES

Anderson, R.J., J. Pika, E. Dumdei & D. Burgoyne 1993. Novel terpenoid metabolites from the northeastern Pacific nudibranch *Cadlina luteomarginata* and three sponges in its diet. In: *Book of abstracts 4th Int. Porifera Congr.* Amsterdam: University of Amsterdam.

Bakus, G.J. & M.A. Thun 1979. Bioassays on the toxicity of Caribbean sponges. In: C. Lévi & N. Boury-Esnault (eds.), *Biologie des spongiares. Colloq. Int. C.N.R.S. 291*:417-422. Paris: CNRS.

Dayton, P.K., G.A. Robilliard, R.T. Paine & L.B. Dayton. 1974. Biological accomodation in the benthic community at McMurdo Sound, Antarctica. *Ecol. Monogr.* 44:105-128.

Faulkner, D.J. & M.T. Ghiselin. 1983. Chemical defense and evolutionary ecology of dorid nudibranchs and some other opisthobranch gastropods. *Mar. Ecol. Prog. Ser.* 13:295-310.

Glander, K.E. 1982. The impact of plant secondary compounds on primate feeding behavior. *Yearbook of Physical Anthropology* 25:1-18.

Lewis, S.M. 1982. Sponge-zoanthid associations: Functional interactions. In: K. Rützler & I.G. Macintyre (eds.), *The Atlantic Barrier Reef ecosystem at Carrie Bow Cay, Belize*: 465-474. Washington, D.C.: Smithsonian Institution Press.

Meylan, A. 1990. Nutritional characteristics of sponges in the diet of the hawksbill turtle, *Eretmochelys imbricata*. In: K. Rützler (ed.), *New perspectives in sponge biology. Proc.3rd Int. Conf. Biol. Sponges:* 472-477. Washington, D.C.: Smithsonian Institution Press.

McClintock, J.B. 1987. Investigation of the relationship between invertebrate predation and biochemical composition, energy content, spicule armament and toxicity of benthic sponges at McMurdo Sound, Antarctic. *Mar. Biol.* 94:479-487.

Milton, K. 1979. Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. *Amer. Nat.* 114:362-378.

Pawlik, J.R., M.R. Kernan, T.F. Molinski, M.K. Harper & D.J. Faulkner 1988. Defensive chemicals of the Spanish dancer nudibranch *Hexabranchus sanguineus* and its egg ribbons: macrolides derived from a sponge diet. *J. exp. mar. Biol. Ecol.* 119:99-109.

Randall, J.E. & W.D. Hartman 1968. Sponge-feeding fishes of the West Indies. *Mar. Biol.* 1:216-225.

Rogers, S.D. & V.J. Paul 1991. Chemical defenses of three *Glossodoris* nudibranchs and their dietary *Hyrtios* sponges. *Mar. Ecol. Prog. Ser.* 77:221-232.

West, D.A. 1976. Aposematic coloration and mutualism in sponge-dwelling tropical zoanthids. In: G.O. Mackie (ed.), *Coelenterate ecology and behavior:* 433-452 New York: Plenum Press..

Wulff, J.L. 1986. Variation in clone structure of fragmenting coral reef sponges. *Biol. J. Linn. Soc.* 27:311-330.