

**CAUSES AND CONSEQUENCES OF DIFFERENCES IN SPONGE DIVERSITY AND  
ABUNDANCE BETWEEN THE CARIBBEAN AND EASTERN PACIFIC OF PANAMA**

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**ABSTRACT**

Sponges are diverse and abundant on Caribbean reefs, but low in diversity and generally small and cryptic in the eastern Pacific at Panama. If the sponge faunas were the same prior to closure of the Isthmus, present differences must be due to differential extinction and colonization, probably resulting from different physical, chemical, or biological conditions. In this study, Caribbean sponges thrived in tanks of running Pacific seawater, suggesting that physical/chemical conditions are not limiting to adult sponges. When cryptic habitats on eastern Pacific reefs were broken open, sponges inhabiting these spaces were consumed opportunistically by several fishes, indicating that cryptic species are confined by predators. However, when *Arothron hispidus*, the eastern Pacific fish determined by previous studies to be most likely able to cope with sponge defenses, was offered sponges from both the Caribbean and Pacific in tanks, it ate most cryptic and semi-cryptic species, but entirely rejected half of the exposed and semi-exposed species. Although the dearth of exposed sponges on eastern Pacific reefs is therefore probably not due entirely to predation, loss of some sponges from the Caribbean could result if these fish were able to cross the Isthmus.

**INTRODUCTION**

Coral reef sponge faunas of the Caribbean and eastern Pacific are strikingly different in diversity and abundance. In the Caribbean 640 sponge species have been reported, compared with only 134 from the tropical eastern Pacific (van Soest 1994). At Panama the contrast is extreme between Caribbean reefs, where, for example, in a small area of only 16 m<sup>2</sup> in the San Blas Islands, 42 species of exposed sponges are found, and the sponge volume of 2077.7 cm<sup>3</sup>/m<sup>2</sup> exceeds that of the corals (Wulff 1994); and Pacific reefs, on which virtually no sponges can be seen, except by close inspection of the bases of corals or by breaking open the reef frame to reveal cryptic and excavating sponges. Such great differences in sponge faunas might have consequences for coral reef structure and dynamics, reflecting the variety of ways sponges influence reefs. Sponges can affect the nutrient balance of reefs (e.g., Reiswig 1971, 1974; Pile in press), cause significant rearrangements of solid carbonate (e.g., Goreau and Hartman 1963, Hartman 1977, Wilkinson 1983), and outcompete corals for space (e.g., Aerts 1996). Sponges have also been demonstrated to increase survival of live corals by binding them to the reef (Goreau and Hartman 1966; Wulff and Buss 1979), and to facilitate regeneration of damaged reefs by interim binding of coral rubble (Wulff 1984).

Reefs on opposite sides of the Isthmus of Panama differ in more than the richness of their sponge faunas. Relative to Caribbean reefs, eastern Pacific reefs are also impoverished with respect to gorgonians, zoanths, calcareous green algae, and other sessile groups (Glynn 1972, Glynn et al. 1972). The diversity of scleractinian corals is lower in the eastern Pacific, and the abundance and diversity of predators is greater (Glynn 1982). The structure and dynamics of the reefs also differ, with eastern Pacific reefs being relatively less vertically developed, less consolidated, smaller in extent, and lacking biotic cementing and binding agents (Glynn 1982). It is possible that some of these other differences, in particular unconsolidated reefs and more effective sponge predators (Glynn 1982), are causally related to the dearth of large exposed sponges on eastern Pacific reefs. This possibility provides impetus for studies of the factors underlying sponge biogeography, lest these factors could be transmitted from the eastern Pacific and eliminate sponges from the Caribbean.

Panama is not the only place where ecological comparisons have been made between the Atlantic and Pacific oceans. Prominent among the explanations advanced to explain biogeographic patterns is the observation that predation seems to have been, and still is, a more important force in shaping distribution patterns and evolution of marine animals in the Pacific than in the Atlantic (e.g., Glynn 1982, Vermeij 1978, 1991). Sponges, as soft-bodied sessile animals, have no doubt undergone significant evolutionary change due to predation, and at least some distribution and abundance patterns of coral reef sponges are presently controlled by predator preferences (e.g., Bakus 1964, Wulff 1988, 1995). This study explored the possibility that differences in sponge diversity and abundance between the Caribbean and eastern Pacific are caused by predators. Two approaches were taken to investigate how predators might cause the lack of large exposed sponges on Pacific reefs at Panama. The possibility that some of the small sponges inhabiting eastern Pacific reefs are confined to cryptic habitats by predators was tested by exposing these sponges to potential predators in the field. To determine if predation could be responsible for the lack of large exposed sponges on eastern Pacific reefs, Caribbean sponges were offered in tanks to the smooth pufferfish, *Arothron hispidus*, the most likely eastern Pacific fish predator of exposed sponges. Because many physical and chemical factors differ between the Caribbean and Pacific at Panama, the possibility that non-biotic factors prevent large exposed sponges from thriving in the eastern Pacific was also explored by attempting to grow Caribbean sponges in tanks of running Pacific seawater.

**MATERIALS AND METHODS**

**Caribbean sponges and eastern Pacific water**

Small pieces, 2-4 cm in largest dimension, of 8 common species of Caribbean sponges [Order Verongida: *Aplysina cauliformis* (Carter); Order Haplosclerida: *Niphates erecta* Duchassaing and Michelotti, *Callyspongia vaginalis* (Lamarck), *Amphimedon rubens* (Pallas); Order Poecilosclerida: *Totrochota birotulata* (Higgin), *Mycale laevis* (Carter), *Desmapsamma anchorata* (Carter), and *Ectyoplasia ferox* (Duchassaing and Michelotti)] were collected in shallow water, less than 3 m deep, at Isla Grande, Panama, in July, 1986. A total of 40 sponges (5 of each species) were transported in coolers of seawater to the Naos Marine Lab of the Smithsonian Tropical Research Institute on the Pacific side of Panama, where they were attached to flat clay tiles using cotton twine,

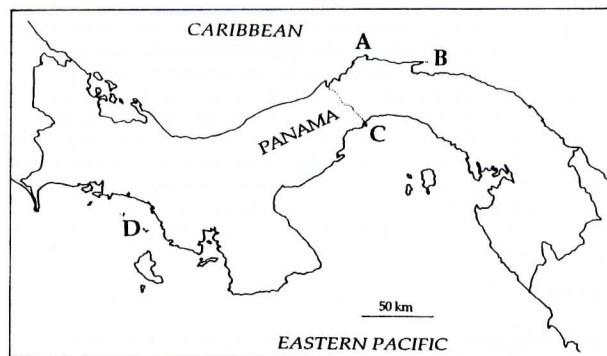


Fig. 1: Map of the Republic of Panama, with locations of field experiments and collections indicated by A = Isla Grande, B = San Blas Islands, C = Perico Island, D = Gulf of Chiriqui

and grown for up to 10 months in tables of running sea water from the Bay of Panama. The excurrent flow was chlorinated to prevent escape of propagules to the Pacific. The sponges were photographed after 2 months to document short-term growth rates, and those that weren't used in feeding experiments were observed for 10 months.

#### Eastern Pacific coral reef sponges and eastern Pacific fishes

Experiments to determine if eastern Pacific predators are able to consume normally unavailable eastern Pacific sponges were made on reefs composed primarily of the densely branching coral *Pocillopora damicornis* at Uva Island and in the Secas Islands in the Gulf of Chiriqui, Panama (Fig. 1). A feeding observation area was demarcated by placing a wire hoop, enclosing a 0.125 m<sup>2</sup> circle, on patches of coral rubble that were interspersed among stands of live *Pocillopora*. Observers hovered a few meters away and recorded all bites taken by fish on unmanipulated substrata inside this circle for 20 minutes, after which pieces of sponges that had been extracted from their usual habitats were added to the circle, and all bites taken were recorded for another 20 minutes (Wulff in press b, for details of identical experiments in the Caribbean). For each trial a selection of 2-6 sponge species was offered by laying small pieces of coral, rubble, or rock to which sponges were attached on the substratum within the circle. Two sponge species, *Halichondria* cf. *lutea* Alcolado and *Geodia* sp. live entirely within the reef frame of densely interlocking coral branches, and were found only by making small excavations. Individuals of *Haliclona caerulea* (Hechtel) were growing as low mounds or runners within the bases of *Pocillopora* colonies and tended to be densely perfused with branching algae, especially articulated coralline reds. One unidentified black haplosclerid species was thinly encrusting *Pocillopora* branches, and a purple haplosclerid was growing in low mounds and runners tucked into the bases of coral colonies. An encrusting species, *Spirastrella* cf. *mollis* Verrill, was found on rock walls adjacent to the reefs and on the sides of coral mounds. Small individuals of a bright blue, thinly encrusting keratose species were also found on the sides of coral mounds. Other cryptic and excavating species also inhabit these reefs, but the ones used in these experiments were the most common.

#### Caribbean and eastern Pacific sponges and an eastern Pacific pufferfish

Individuals of the large smooth pufferfish *Arothron hispidus* were captured in the Bay of Panama, using West Indian Z-style fish traps, and maintained on clams or shrimp in individual tanks (85 x 85 cm x 25 cm deep) of running sea water. Once a day, small pieces of several sponge species, tied to clay tiles with cotton string, were offered to the fish for 1 hour. Each set of offerings included Caribbean species, collected from shallow reefs at Isla Grande or in the San Blas Islands, and eastern Pacific species, collected under and among very low intertidal cobbles at Perico Island, near where the fish were captured in the Bay of Panama. A total of 18 Caribbean species and 7 Pacific species were offered for 22 - 62 trials each. Two controls were included in each trial: 1) a clam or piece of shrimp of the same size as the sponge pieces, to determine if the fish would eat at all; and 2) a piece of cellulose sponge, to determine if the fish would exhibit selectivity at all. A total of 16 fish individuals, ranging in standard length from 6.5 - 27 cm, were used in these experiments from October 1986 to August 1988.

#### RESULTS

##### Caribbean sponges and eastern Pacific water

All 8 species of Caribbean sponges thrived in the tanks of running seawater from the Bay of Panama. Individuals of *Aplysina cauliformis* grew at the tips. Two of the species of Haplosclerida, *Niphates erecta* and

*Callyspongia vaginalis*, generated narrow processes into the water column and along the surface of the tile. *Mycale laevis* and *Desmapsamma anchorata*, which have relatively open skeletal construction, grew long wide processes along the tile, but the other 2 species of Poecilosclerida, *Iotrochota birotulata* and *Ectyoplasia ferox*, which are more densely constructed, merely extended wide lobes. Growth was rapid for some species, with increases of size in the first 2 months of up to 42% and 115% by the more rapidly growing *M. laevis* and *D. anchorata*, respectively; and the Haplosclerid species increased by up to 19%. Growth rates were not measured after the first 2 months because the very low flow environment of the sea tables induced growth forms, especially narrow processes, that were not normal for the field and because the purpose was simply to determine if physical and chemical characteristics of eastern Pacific seawater precluded habitation by sponge species that grow to large sizes, fully exposed, in the Caribbean. All but a few individuals of each species were used in feeding preference experiments, but no sponge individuals developed necrotic tissue, died, or decreased in size, except by my razor blade, during 10 months in Bay of Panama water. Several individuals of each of an additional 10 species of Caribbean sponges (complete list of species in Table 4) were also maintained in the seawater tables for periods of one week to several months, while awaiting use in feeding preference experiments, and none of these sponges died or decreased in size except in the service of the experiments.

#### Eastern Pacific sponges and eastern Pacific fishes

Of the 6 sponge species that were used in more than 20 field trials, 3 were entirely consumed by fish during the 20 minute observation period in 21-34% of the trials (Table 1). A fourth species, *Haliclona caerulea*, was entirely consumed within 20 minutes in 20% of the trials when it was presented without its symbiotic macroalgae, but was never entirely consumed when the sponges offered were perfused with algae (Table 1). The two encrusting

Table 1: Percent of trials in which sponges of 6 species (one offered with and without symbiotic macroalgae) were entirely consumed by a natural assemblage of reef fishes, in the field, during trials lasting 20 minutes

	Number of trials	Percent of trials in which the sponge was entirely consumed
PACIFIC CORAL REEF SPONGES		
<i>Haliclona caerulea</i> (Hechtel) without algae	10	20.0
with algae	17	0
black haplosclerid encrusting	21	28.6
<i>Halichondria</i> cf. <i>lutea</i> Alcolado	52	21.1
<i>Spirastrella</i> cf. <i>mollis</i> Verrill	25	0
<i>Geodia</i> sp.	23	30.4
blue keratose encrusting	23	0

species that live exposed on the sides of coral mounds were never entirely consumed (Table 1), and means of only 1.2 bites per trial were taken on the blue keratose species and 3.1 bites per trial on *Spirastrella* cf. *mollis*, more than an order of magnitude less than the 49.3 - 82.6 bites per trial taken on the other 4 species (Table 1). *Haliclona caerulea* was consumed at a rate of only 3.1 bites per trial when perfused with algae, compared to 61 bites per trial without algae.

No bites were taken in the control circles, but fish of five species were frequently attracted to feed on the excavated sponges in experimental circles: an angelfish, the Moorish idol, a triggerfish, a sharpnose puffer, and a parrotfish (Table 2). Individuals of the angelfish

**Table 2:** Mean number of bites taken per 20 minute trial on 6 species of sponges by the 5 fish species that fed on the sponges most frequently. Hc = *Haliclona caerulea* (without symbiotic macroalgae), blk = thinly encrusting black haplosclerid, Hl = *Halichondria* cf. *lutea*, Sp = *Spirastrella* cf. *mollis*, Ge = *Geodia* sp., bl = thinly encrusting bright blue keratose sponge.

FISHES	Bites per trial on PACIFIC REEF SPONGES					
	Hc	blk	Hl	Sp	Ge	bl
<i>H. passer</i>	52.3	78.5	50.1	1.5	31.1	0.4
<i>Z. cornutus</i>	7.8	0.6	13.7	0.4	6.9	0
<i>S. verres</i>	0	0.8	1.6	0.7	1.7	0
<i>C. punctatissima</i>	0.5	2.1	1.9	0	0.1	0.8
<i>S. ghobban</i>	0.4	0.5	0.6	0.5	9.6	0
TOTAL	61.0	82.6	67.9	3.1	49.3	1.2

*Holocanthus passer* made more than twice as many visits and took more than 3 times as many bites on sponges as all other species combined (433 vs 196 visits and 5590 vs 1579 bites), even though angelfish were normally feeding on plankton, high above the reef. Typically one individual would notice the sponges, and drop straight down to feed on them, with other angelfish individuals following and continuing to take bites from the sponges until the preferred species were gone. In 10/56 trials the angelfish took so long to notice the sponge offerings that the 20 minute observation period had already ended. These trials coincided with the tide just starting to rise, flushing abundant plankton out of the reef and into the water column, where the angelfish were feeding. Of the fish species that fed frequently in circles with sponges, the only ones observed to feed on anything but sponges in the circles were the parrotfish, although only 6.7% of the bites taken by *Scarus ghobban* individuals in the circles were on food items other than the sponges offered. A second parrotfish species, *Scarus rubroviolaceus*, took a total of only 44 bites in the circles, half of which were on sponges, and this minor contribution was not included in the analysis. Likewise, damselfish took a total of only 48 bites from the experimental sponges, and were not included in the analysis. The smooth puffer *Arothron hispidus* also inhabits these reefs, but 10 individuals that were followed in the field for 30 to 60 minutes each were conspicuous in never feeding while observed, though one individual made vigorous attempts to bite the observer.

Fish species reacted differently to the sponge species. The angelfish spread their attention fairly evenly among the 4 acceptable sponge species (Table 2), as did the Moorish idols, with the exception that they appeared to avoid the black haplosclerid. The long snout of this fish distinguishes it as the only fish able to gain access to this sponge species through the densely packed *Pocillopora* branches without the intervention of an investigator. The 2 exposed encrusting species were definitely avoided by the angelfish and Moorish idol, but didn't appear to be so repugnant to less frequent sponge feeders. Although a total of only 28 bites were taken on the blue keratose species, 67.9% of those bites were taken by the gold-spotted pufferfish. Likewise, of the

77 bites taken on *Spirastrella*, cf. *mollis* 22% were taken by the triggerfish, although this fish species was responsible for only 2.1% of the total number of bites on sponges. The parrotfish *Scarus ghobban* took 79.3% of their bites on sponges on *Geodia* sp.

An additional indication of the desirability of some of these sponges as food is the vigorous chasing behavior among sponge feeding fish at the experimental circles. Depending on the fish species, between 5% and 24% of the sponge-feeding bouts were terminated by a fish chasing or being chased by another fish (Table 3). Fish only chased

**Table 3:** Percent of sponge-feeding visits to experimental circles in which a fish of the 5 most common sponge-feeding species left the experimental circle because it was chased or it chased another fish.

PACIFIC FISHES	Number of visits to eat sponges	Percent of visits terminated by chases
<i>Holocanthus passer</i> Valenciennes "King angelfish"	433	15.0
<i>Zanclus cornutus</i> (Linnaeus) "Moorish idol"	86	19.8
<i>Sufflamen verres</i> (Gilbert & Starks) "orangeside triggerfish"	37	24.3
<i>Canthigaster punctatissima</i> (Günther) "spotted sharpnose puffer"	20	5.0
<i>Scarus ghobban</i> Forsskål "bluechin parrotfish"	53	5.7

each other away from edible sponge species in the experimental circles, and this behavior was never observed in control circles.

#### Caribbean and eastern Pacific sponges and an eastern Pacific pufferfish

The pufferfish became quickly acclimate<sup>d</sup> when placed in individual tanks, and swam over to observers when they approached the tanks. The fish ate the clam or shrimp piece first in 188 of 203 trials (92.6%). In 10 of those 15 trials (67%), the species fed on before the clam or shrimp were *Geodia* cf. *gibberosa*, *Tethya taboga*, or *Pachypellina podatypa*, which together made up only 136/904 (15%) of the total number of sponge pieces offered. In 3 trials the clam or shrimp were not eaten, and those fish died the next day, possibly as a result of a dinoflagellate bloom. Results from those trials were not included in the analysis. Some individuals bit the cellulose sponge into dozens of tiny pieces on their first experience with it, but the artificial sponge was ignored after the first 2 trials in all but 15 trials (7.4%). In those 15 trials the artificial sponge was never sampled by the fish until they had sampled the other simultaneous offerings, and a mean of 21.9 bites (SD = 6.1) were taken on other items before the artificial sponge was bitten. Even after 2 months with no experiments, during which the fish were maintained on clams or shrimp, the fish individuals that had participated in experiments ignored the cellulose sponge. Fish individuals differed in sponge-feeding behavior, with some appearing to suck in an entire sponge piece and others taking many small bites. However, once an individual had experienced a particular sponge species, subsequent decisions about rejecting that species were made without touching the sponges (i.e., apparently using visual or olfactory information).

Sponge species collected in the Pacific, near where the fish were collected, were entirely consumed in from 76% to 97% of the trials (Table 4). The 2 species consumed

**Table 4:** Percent of trials, each 1 hour long, in which captive *Arothron hispidus* individuals entirely consumed pieces of 7 species of Pacific sponges collected in the very low intertidal of Perico Island and 18 species of Caribbean sponges collected in various habitats at Isla Grande or the San Blas Islands.

	Number of trials	Percent of trials in which the sponge was entirely consumed
<b>PACIFIC SPONGES</b>		
<u>cryptic</u>		
<i>Haliclona</i> cf. <i>coerulescens</i> (Topsent)	35	80.0
<i>Haliclona</i> sp.	25	76.0
<i>Lissodendoryx</i> <i>zonea</i> (de Laubenfels)	32	78.0
<i>Hymeniacion</i> sp.	33	75.8
<i>Haliclondria</i> cf. <i>magniconulosa</i> Hechtel	44	79.5
<i>Geodia</i> sp.	38	81.6
<i>Tethya</i> <i>taboga</i> (de Laubenfels)	62	96.9
<b>CARIBBEAN SPONGES</b>		
<u>cryptic</u>		
<i>Haliclondria</i> cf. <i>lutea</i> Alcolado	36	88.9
<i>Hymeniacion</i> <i>caerulea</i> Pulitzer-Finali	34	0
<i>Geodia</i> cf. <i>gibberosa</i> Lamarck	32	93.7
<u>semi-cryptic</u>		
<i>Adocia</i> sp.	43	62.8
<i>Pachypodia</i> <i>podatypa</i> (de Laubenfels)	42	73.8
<i>Mycale</i> <i>laevis</i> Carter	38	60.5
<u>semi-exposed</u>		
<i>Amphimedon</i> <i>erina</i> (de Laubenfels)	34	0
<i>Xestospongia</i> <i>carbonaria</i> (Lamarck)	31	0
<i>Lissodendoryx</i> <i>colombiensis</i> Zea & van Soest	38	28.9
<i>Spirastrella</i> cf. <i>mollis</i> Verrill	42	47.6
<u>exposed</u>		
<i>Amphimedon</i> <i>rubens</i> (Pallas)	22	0
<i>Niphates</i> <i>erecta</i> Duchassaing & Michelotti	52	23.1
<i>Callyspongia</i> <i>vaginalis</i> (Lamarck)	44	22.7
<i>Iotrochota</i> <i>birotulata</i> (Higgin)	31	22.6
<i>Desmapsamma</i> <i>anchorata</i> (Carter)	27	51.8
<i>Ectyoplasia</i> <i>ferox</i> Duchassaing & Michelotti	32	0
<i>Aplysina</i> <i>fulva</i> (Pallas)	25	0
<i>Verongula</i> <i>rigida</i> (Esper)	32	0

most frequently, *Tethya taboga* and *Geodia* sp., are also the 2 species that live completely cryptically, with no tissues exposed between the cobbles. Two of the 3 completely cryptic Caribbean species were entirely consumed in 89% and 94% of the trials, and the third was never eaten (Table 4). The Caribbean semi-cryptic (live with more than 1/2 of their bodies in cryptic spaces) species were consumed in from 60% to 74% of the trials, and the Caribbean semi-exposed (live with some, but less than 1/2 of their bodies in cryptic spaces) and fully exposed species were consumed in from 23% to 52% of the trials, if they were consumed at all; but 6 of these 12 species were never consumed (Table 4).

## DISCUSSION

### *Arothron* and sponges

Previous studies of feeding habits of eastern Pacific fishes suggest the genus *Arothron* as the most likely

group for finding differences in fish predation on sponges between the Caribbean and eastern Pacific. Hiatt and Strasburg (1960, p111) remark that fish of the genus *Arothron* "appear to feed predominantly as opportunists, and virtually nothing alive on the reefs is beyond their capacity for utilization". This genus is not represented in the Caribbean, where the only reef inhabiting tetraodontid puffer is the small sharpnose puffer *Canthigaster rostrata* (Randall 1983). A literature survey of the food habits of fishes of the tropical eastern Pacific consistently reveals evidence of sponge-feeding by *Arothron*. Both specimens of the large puffer *Arothron mappa* examined by Hiatt and Strasburg (1960) were notable for having their entire digestive tracts packed with sponge fragments. Three individuals of the smaller congener *A. meleagris* had fed exclusively on live corals, but the one specimen of *A. hispidus* had fed on a variety of animals and plants, including sponges (Hiatt and Strasburg 1960). The only *Arothron* species examined by Dawson, et al (1955) was *A. hispidus*, and 5 of their 8 specimens contained sponges or sponge spicules. Although *A. mappa* has not been reported from the eastern Pacific (Allen and Robertson 1994), *A. meleagris* and *A. hispidus* are abundant on Pacific reefs at Panama, where *A. meleagris* is known to feed almost exclusively on corals (Glynn, et al. 1972). *A. hispidus*, which is abundant over rocky or rubble bottoms as well as on reefs, appears to be an omnivore, with sponges figuring prominently (69.5% of total dry mass) in gut contents of 7 individuals caught in the Bay of Panama (Glynn, et al. 1972). Feeding studies of this fish in the field were discontinued when placing more than one in the same cage led to fighting with severe injuries (H. Guzman pers. comm.), and the fish were also singularly uncooperative in the field in the present study.

Rather than being an uninhibited sponge-feeder that prevents exposed sponges from living on eastern Pacific reefs, *Arothron hispidus* appears to be opportunistic in its sponge-feeding and demonstrates the sensory, memory, and behavioral capacity necessary for consistent selective feeding on only certain sponges. *Arothron hispidus* preferences for feeding on the Caribbean sponge species offered are very similar to the preferences of 4 species of Caribbean parrotfishes when these same sponge species were exposed to them in the field (Wulff 1988, in press b). Puffers were somewhat less particular than the parrotfishes, perhaps in part because they were tested in tanks instead of in the field. For both the puffers and the parrotfishes rates of consumption of the sponge species tested decreased as their degree of normal availability in the field increased, even though the puffers had no prior experience with these sponges. Sponges that coexist with *Arothron hispidus* in the Bay of Panama, but are not necessarily accessible to them unless cobbles are disturbed, were readily consumed in the tank experiments. Some of these sponges live entirely cryptically and others occur between cobbles, binding the cobbles tightly together. Just as with the Caribbean reef sponges, increased rates of consumption coincided with decreased accessibility, with the only two sponge species that live entirely cryptically, *Geodia* sp. and *Tethya taboga*, also being most readily consumed. This pattern of selective feeding on sponges that have less impetus for development of inherent defenses against fish predators is compatible with viewing *Arothron hispidus* as an opportunistic feeder on sponges that only occasionally become available, and also as an agent of confining these sponges to cryptic spaces, but not as the excluder of all exposed sponges from eastern Pacific reefs.

### Other sponge-feeding fishes in the Caribbean and eastern Pacific

The small assortment of fish families feeding on sponges in the eastern Pacific is similar to that in the Caribbean, where gut content analysis of reef fishes by Randall and Hartman (1968) revealed significant sponge remains (>6% by volume) in only 11 of 212 species. Angelfishes and smooth pufferfishes are sponge-feeders in both oceans. The triggerfish *Sufflamen verres* consumed

sponges in this study, and Glynn et al. (1972) found sponge remains in gut contents of this species, but sponges were not found in triggerfish gut contents by Randall and Hartman. However, some of the closely related file fishes are sponge feeders in the Caribbean (Randall and Hartman 1968, Wulff 1994). Trunkfishes and spadefishes are also sponge-feeders in the Caribbean (Randall and Hartman 1968, Wulff 1994), and although I did not observe these fish in the Pacific at Panama, the eastern Pacific representatives are designated as sponge feeders by Allen and Robertson (1994). The Moorish Idol, sole member of the family Zaclidae, does not inhabit the Caribbean. Randall and Hartman (1968) found less than 2% sponge material in gut contents of parrotfishes and damselfishes, coinciding with my field observations and gut content analyses by Glynn et al. (1972) that eastern Pacific representatives of these families feed on sponges, but far less than the other fishes.

In the Caribbean, angelfishes appear to be especially committed to feeding on sponges (Randall and Hartman 1968; Wulff 1994). Angelfish are abundant on the eastern Pacific reefs, but dedicated spongivores could not support themselves on these reefs devoid of large accessible sponges. In the Gulf of Chiriqui, *Holacanthus passer* feeds on plankton in the water column above the reef, as it does in the Gulf of California (Strand 1977), where it is primarily a grazer on sessile organisms, including sponges, (Reynolds and Reynolds 1977). Individuals of this species consistently died in seatables before their reactions to exposed Caribbean sponges could be tested, so it is not known if this species could be responsible for eliminating exposed sponges from eastern Pacific reefs. However, in the Caribbean, both gut content analysis and field observations have demonstrated that angelfish feed in a smorgasbord manner, taking small amounts of many species (Randall and Hartman 1968; Wulff 1994). Thus Caribbean angelfish coexist with dense and diverse populations of exposed reef sponges and do not appear to control reef sponge distribution and abundance. *Holacanthus passer* did not exhibit smorgasbord feeding on normally cryptic sponges in the Gulf of Chiriqui, but this is not surprising since feeding on these sponges by generalist fishes indicates that the cryptic sponges may lack inherent defenses that provide impetus for smorgasbord feeding by specialists. A large *Haliclona caerulea* individual grew exposed inside a predator-exclusion cage that had been left for some months on Uva reef by Peter Glynn (pers. observ, pers. comm.), corroborating results of the feeding experiments, in which this sponge species was consumed, especially by angelfish, when not associated with macroalgae. *Haliclona caerulea* may also inhabit the Caribbean (Wulff in press a), where, consistent with its apparent lack of adequate defenses against angelfish, it occurs without its algal symbionts only on mangrove roots and reef flats, i.e., habitats that are generally inaccessible to angelfish. Another indication that *H. passer*, while abundant and eager to feed on some sponges, is not responsible for the dearth of exposed sponges on Pacific reefs at Panama, is that it virtually ignored experimental presentation of the 2 encrusting sponge species that normally live exposed.

#### Why are so few sponges on eastern Pacific reefs?

These results do not answer the question of why there are no large exposed sponges on Pacific reefs at Panama. Previous studies of geographic differences in sponge abundance have frequently implicated nutrients (Wilkinson 1987, Wilkinson and Cheshire 1990, Zea 1994), but nutrients are not likely to be limiting, in the sense of insufficient food, in the eastern Pacific. Birkeland (1977) demonstrated that biomass accumulation on settling plates was 11.7 times greater on the Pacific side of Panama than on the Caribbean side after 148 days, reflecting dramatically greater nutrient supply in the Pacific during the upwelling season. Coral recruits on lower surfaces of his recruitment blocks and panels survived better than those on the tops, in spite of decreased growth rates due to low light levels, because

smothering by sediment or rapid growth of algae decreased survival. Birkeland (1977) concluded that such problems with settlement and recruitment have a greater influence than adult survival on differences in sessile macrofauna between the two oceans. Birkeland focused on coral recruits, but rapid growth of filamentous algae in response to high nutrient levels in the eastern Pacific could also smother sponge recruits. Perhaps sponges that live in cryptic spaces are disproportionately represented in the eastern Pacific because their larvae, but not those of exposed sponges, are equipped with habitat selection mechanisms for settling on surfaces devoid of light, where they avoid being overgrown by algae. In a comparison of a variety of habitats in the Colombian Caribbean, Zea (1993) found significantly greater rates of sponge recruitment in darker habitats, such as under overhangs on the rocky shore, reef slope, and reef base.

Sponge recruitment also was demonstrated by Zea (1993) to be greater near dense populations of adult sponges, corroborating conclusions of many previous studies of limited dispersal of sponge larvae (refs in Zea 1993). If a shared Caribbean and eastern Pacific reef sponge fauna was largely extinguished in the eastern Pacific as the Isthmus closed, replenishment of eastern Pacific reefs from the central and western Pacific would therefore be a considerable challenge, given the great distance. Such re-colonization seems still less likely with the additional problems of relatively sparse sponge faunas due to low nutrient levels on central Pacific oceanic islands and atolls, and possible smothering of recruits by rapidly growing algae in the eastern Pacific. Extinction in the eastern Pacific of most species from a once shared fauna, combined with virtually no colonization from the west, would be compatible with a curious pattern of similarity of some of the most common eastern Pacific sponge species to Caribbean sponge species (de Laubenfels 1938, Wulff in press a).

#### Consequences of so few sponges

Shallow reefs of ramose corals in the eastern Pacific are less consolidated, relative to those in the Caribbean, and appear to lack a mechanism for regeneration once they are damaged by physical or physiological disasters. Encrusting coralline algae capable of permanent binding of loose pieces of carbonate into a stable framework suitable for coral recruitment are abundant. However, they tend to grow only around individual pieces of coral rubble because of high rates of bioturbation that disrupt rubble too frequently for individual pieces to become bound to each other (Glynn et al. 1972, Glynn 1982). In the Caribbean, sponges can serve this role of rapid temporary binders, holding rubble until the slower-growing coralline algae can bind adjacent rubble pieces permanently and solidly (Wulff 1984). Dating of rubble from an eastern Pacific reef in Costa Rica indicates that the reef had been dead for 3-400 yr (Glynn pers comm). Lack of sponges may eliminate this key step in the regeneration of shallow reefs of branching corals.

Results reported here do not provide support to a scenario of complete exclusion of exposed sponges from the eastern Pacific because eastern Pacific predators are better able to cope with sponge physical or chemical defenses than are Caribbean predators. However, even consumption of some sponge species could have important consequences. For example, the semi-cryptic species *Mycale laevis*, that was consumed by *A. hispidus*, has an intimate relationship with corals and is particularly effective at binding live corals to the reef frame and providing protection from boring sponge colonization (Goreau and Hartman 1966, Wulff and Buss 1979). Thus, consumption of some exposed and semi-exposed Caribbean species by *A. hispidus* sounds a note of caution regarding the possible consequences of allowing mingling of the eastern Pacific and Caribbean faunas, as through a sea-level canal.

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