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**SPONGE PREDATORS MAY DETERMINE DIFFERENCES IN SPONGE
FAUNA BETWEEN TWO SETS OF MANGROVE CAYS,
BELIZE BARRIER REEF**

BY

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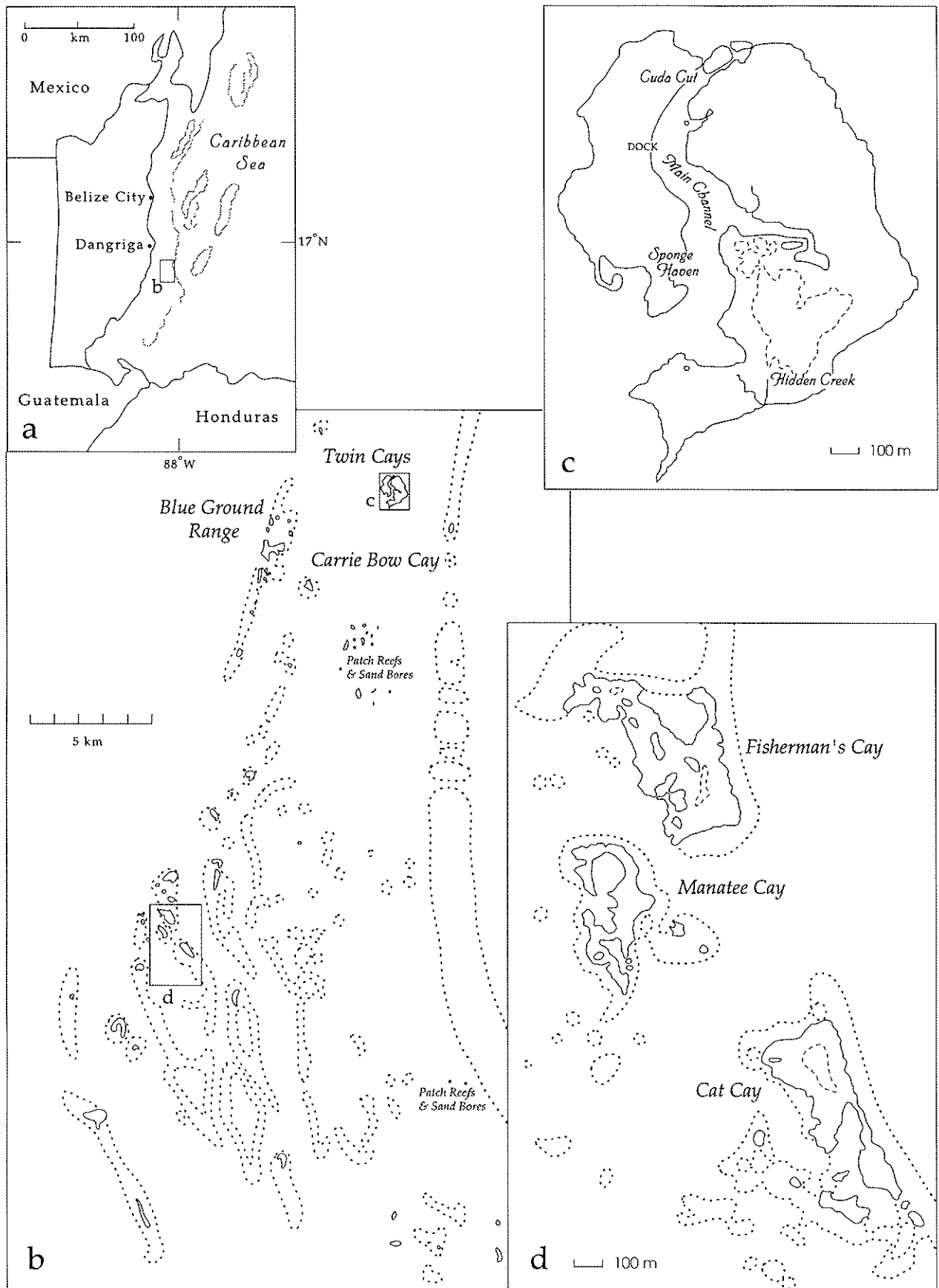


Figure 1. Map of Belize (a) with enlarged research areas: southern barrier reef lagoon (b), Twin Cays (c), and portion of Pelican Cays (d).

SPONGE PREDATORS MAY DETERMINE DIFFERENCES IN SPONGE FAUNA BETWEEN TWO SETS OF MANGROVE CAYS, BELIZE BARRIER REEF

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ABSTRACT

Mangrove roots in the well-protected channels and ponds among dense mangrove stands provide very similar habitats for sponges in the Twin Cays and Pelican Cays and harbor extraordinarily dense and diverse sponge communities in both locations. The species of sponges are very different, however, possibly because of an important difference in context: the Twin Cays mangrove roots are embedded in peat banks, whereas the Pelican Cays mangrove roots are embedded in coral reefs, which may provide habitat for sponge-feeding fishes. Current and previous observations of feeding preferences and habitat requirements of potential sponge predators suggest that sponge predators play a key role in determining substantial differences in the sponge faunas, both in species composition and in species diversity, of Twin Cays and Pelican Cays.

INTRODUCTION

Mangrove cays on the Belize Barrier Reef appear to be close to an ideal habitat for many filter-feeding animals, among them an extraordinary diversity and density of sponges (Rützler and Feller, 1996). Physical and chemical factors are highly favorable, with the mangroves providing protection from physical disturbances, such as storm waves, and also providing an organically enriched environment favoring organisms that filter their food out of the water column. These factors are important determinants of the distribution and abundance patterns of tropical sponges. For example, areas that are relatively protected from physical disturbance, either geographically (i.e., out of the hurricane belt) or in lagoons and on leeward sides of islands, are the only areas in the Caribbean in which significant sponge abundance has been reported in very shallow (< 2-m depth) water (e.g., Alcolado, 1979; Alvarez et al., 1990; Wulff, 1995a, and additional references therein). Nutrient availability has also been related to sponge abundance on geographic spatial scales (e.g., Wilkinson and Evans, 1989; Zea, 1994).

Differences in sponge distribution among adjacent habitats with similar nutrient levels and protection from adverse physical factors have been recently shown to depend on the interactions of sponges with other organisms, especially predators. For example, the community of sponges found in seagrass meadows and rubble beds inhabited by the large starfish *Oreaster reticulatus* (Fig. 2) is limited to those sponge species with inherent defenses against predation by this starfish (Wulff, 1995b); and the starfishes are efficient at finding and consuming undefended sponge species that stray into their habitat from adjacent reefs. Similarly, some species of cryptic

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Figure 2. Starfish, *Oreaster reticulatus*, feeding on sponge, *Mycale laevis*.

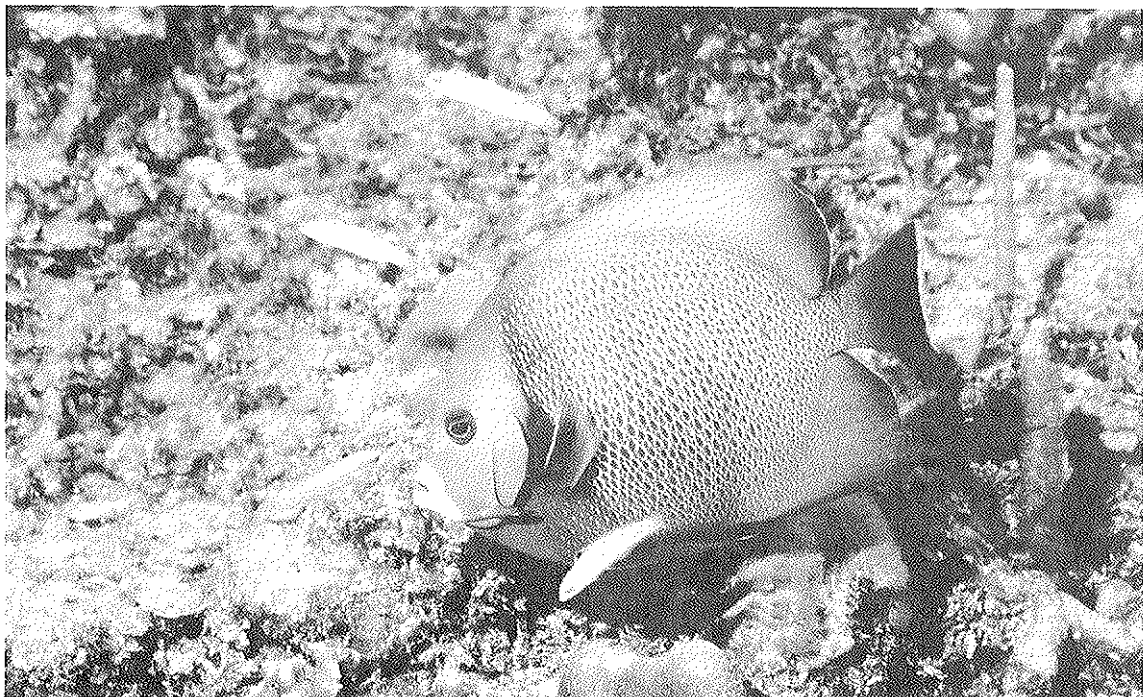


Figure 3. Gray angelfish, *Pomacanthus arcuatus*, looking for prey (photo: Carl Hansen).

sponges inhabit crevices in the reef because they are refuges from the attentions of generalist herbivores, such as parrotfish of the genus *Sparisoma* in the Caribbean (Wulff, 1997a) and of the genus *Scarus*, and from omnivores such as large smooth pufferfish of the genus *Arothron* in the tropical eastern Pacific (Wulff, 1997b). A very different relationship exists between exposed reef sponges and spongivorous fishes. A large percentage of exposed reef sponge species is consumed by angelfishes of the genera *Holocanthus* and *Pomacanthus* (Fig. 3), the most important sponge specialist fishes in the Caribbean (Randall and Hartman, 1968; Wulff, 1994). Unmanipulated angelfishes in a natural reef sponge community were observed to feed on 36 of the 42 species present (Wulff, 1994). Exposed reef sponges continue to coexist with the angelfishes because the fishes take only small amounts of each species, possibly to avoid being poisoned by defensive chemistry (Randall and Hartman, 1968; Wulff, 1994). Even though the angelfishes do not consume reef sponges to the point of eliminating them, they do exhibit preferences such that the rate at which sponge species are consumed is inverse to their abundance (Wulff, 1994). This suggests that the angelfishes may exert some control over the relative abundance of sponge species. That control would be expected to be extreme in the case of sponge species that have not been selected to develop and maintain inherent defenses because they do not live in habitats with specialist sponge predators. This expectation appears to be corroborated by the findings of Dunlap and Pawlik (1996), who made four species of mangrove sponge species available to angelfishes, which rapidly consumed one of them.

The reputation of sponges as inedible therefore appears to derive from a consistent pattern of being adequately defended against predators with which they coexist. Membership in sponge faunas typical of habitats such as coral reef, seagrass meadows, rubble beds, sediment plains, and mangrove roots, may at least in part be determined by which predators have access to these habitats. Any departure from the normal complement of sponge species in a habitat may therefore reflect unusual circumstances with respect to predator access. In the Pelican Cays, the mangroves are rooted in coral reefs instead of in peat banks (as in the Twin Cays) or in terrestrial sediments (as on the mainland). In the complex microtopography provided by the corals, sponge-feeding fishes may find shelter from their predators and thus gain access to mangrove root sponge assemblages that are normally off limits because of risk of predation.

METHODS

During late summer of 1997, intensive collecting activity focused on three sites in the Twin Cays (Hidden Creek, Cuda Cut, and Sponge Haven), as well as three sites in the Pelican Cays (Cat Cay, Manatee Cay, and Fisherman's Cay). The field team was made up of Caribbean sponge biologists Belinda Alvarez, Cristina Diaz, Rob van Soest, Kate Smith, Janie Wulff, and Sven Zea. All sponge species observed were listed, collected, and their relative abundance noted (see Rützler et al., this volume). In addition, I recorded microhabitat distributions, associations, evidence of predation, and presence of potential predators. Direct evidence of predation consisted of actual feeding on sponges and, also in the case of starfishes, the typical rounded feeding scars left by the extruded stomachs of *Oreaster reticulatus* (Wulff, 1995b). The potential for predation on sponges was assessed from qualitative surveys of the relative abundances of known sponge predators, including starfishes, parrotfishes, spadefishes, angelfishes, trunkfishes, and filefishes. These include all Caribbean species that have been observed to feed on sponges (Wulff, 1994, 1995b, 1997b) or to have sponge remains in their gut contents (Randall and Hartman, 1968).

RESULTS

Sponges

Sponges were qualitatively ranked according to increasing relative abundance (see Rützler et al., this volume) on a scale of 1 to 3, by consensus of the field team after each field trip. Of the 23 species judged to be the most common sponges at Twin Cays (Table 1), 6 were even more abundant in the Pelican Cays, and the other 17 species were as common or more common at Twin Cays than in the Pelicans. Of those 17 species, 5 (*Biemna caribea*, *Mycale* aff. *magniraphidifera*, *Halichondria* ?*poa*, *Haliclona pseudomolitba*, and *Haliclona mucifibrosa*) were not reported at all from the Pelicans. By contrast, of the 30 most common sponge species in the Pelicans, only 3 were also common at Twin Cays, and 16 were not reported at all from Twin Cays (Table 2). The majority of the species on mangrove roots in the Pelicans were not recorded at Twin Cays. This reflects a dramatic difference in overall diversity, with 2.6 times as many sponge species found in the Pelicans (147 species and distinct forms recorded in the Pelicans, versus 57 species and forms at Twin Cays; Table 2).

Potential Sponge Predators

Although potential sponge predators were observed at five of the six sites, their abundance, and the degree to which different groups were represented, differed (Table 3). No individuals of fish groups that are known to specialize on sponges (i.e., angelfishes, trunkfishes, filefishes, and spadefishes) were observed in the Twin Cays; by contrast, large individuals representing all of these groups were observed in the Pelicans. Especially striking in Fisherman's Cay Pond E were many large grey angelfishes, *Pomacanthus arcuatus*, and a few enormous French angelfishes, *P. paru*, as well as two large spadefishes, *Chaetodipterus faber*. In Manatee and Cat Cays, large angelfishes were positioned at intervals under overhanging peat banks. No sponge specialist species were observed at Twin Cays. In Twin Cays, small parrotfishes of the species *Scarus isertii* and *Sparisoma radians* were seen among seagrass at Cuda Cut, but heavy epiphytization on the especially dense *Thalassia testudinum* blades may provide evidence of their relative scarcity. Medium-large individuals of several species of the parrotfishes genus *Sparisoma* were seen in all of the ponds in the Pelicans, but the parrotfishes were more common on the reefs. The large starfish *Oreaster reticulatus* was found in Twin Cays, in areas of less dense seagrass and occasionally on the peat banks into which mangrove roots were embedded. However, this starfish was far more abundant in the Pelicans, where individuals are especially concentrated directly under the mangrove roots in areas with patches of hard substrate or in which sediment is stabilized by seagrasses.

Observed Predation on Sponges

Individual *Oreaster reticulatus* were observed to be feeding on, or had left unambiguous scars from recent feeding (nearly round areas, 8–16 cm in diameter, from which live tissue had been recently removed) on 11 species of sponges (Table 4). In several cases, sponges appeared to have very recently fallen off mangrove roots and up to 3 starfishes were observed to be feeding on one of these large windfalls at a time. In one case, a chunk of the highly edible (Wulff, 1995b)

Table 1. The most abundant 23 sponge species on mangrove roots in Twin Cays, Belize, and all species reported from mangroves in at least 3 other Caribbean locations.

Sponge species	Locations							
	Bel	Bah	Jam	Cub	VeM	VeB	PaS	PaG
<i>Plakortis halichondrioides?</i>	x							
<i>Cinachyrella apion</i>	x							
<i>Geodia gibberosa</i>			x		x	x		x
<i>Geodia papyracea</i>	xx		x					
<i>Chondrilla nucula</i>	x	x			x			
<i>Suberites zeteki</i>			x		x			x
<i>Lissodendoryx isodictyalis</i>	xx			xx	x	x	xx	
<i>Biemna</i> spp.		xx					x	x
<i>Clathria schoenus</i>	p		x		x		x	
<i>Clathria venosa</i>	x						x	
<i>Mycale laevis</i>	p		x			x	x	
<i>Mycale</i> aff. <i>magniraphidifera</i>		xx						
<i>Mycale microsigmatosa</i>	x		x	x		x	x	
<i>Tedania ignis</i>	xx	x	x	xx	x	x	xx	x
<i>Scopalina ruetzleri</i>	x		x	x	x			
<i>Amorphinopsis</i> sp.1	xx							
<i>Halichondria magnicomulosa?</i>	xx		x	x		x	x	
<i>Halichondria melanodocia</i>			x	x		x	xx	
<i>Halichondria poa?</i>	xx							
<i>Haliclona caerulea</i>		x	x		x		x	x
<i>Haliclona curacaoensis</i>	x							
<i>Haliclona implexiformis</i>	xx		x	x				
<i>Haliclona manglaris</i>	xx			x			xx	
<i>Haliclona mucifibrosa</i>	xx							
<i>Haliclona pseudomolitba</i>	xx							
<i>Haliclona tubifera</i>	xx		x				x	
<i>Amphimedon erina</i>	p		x		x		x	
<i>Calyx podatypa</i>	x							
<i>Hyrtios proteus</i>	x			xx				
<i>Spongia tubulifera</i>	x						x	
<i>Dysidea etheria</i>	p	x	x	xx	x		x	

Relative abundance at Twin Cays is expressed as: xx = more common in Twin Cays than in the Pelicans; x = as common, or more common, in the Pelican Cays; p = present in Twin Cays, but not common. Relative abundance at other Caribbean locations, if indicated by the cited author, is expressed as: xx = very common, x = common.

Key to locations: Bel = Twin Cays, Belize (this study); Bah = Bimini, Bahamas (Rützler, 1969); Cub = Cuba (Alcolado, 1980); Jam = Port Royal, Jamaica (Hechtel, 1965); PaG = Galeta, Panama (Wulff, personal observation); PaS = San Blas, Panama (Wulff, personal observation); VeM = Parque Nacional Morrocoy, Venezuela (Diaz et al., 1985); VeB = Bahía de Buche, Venezuela (Sutherland, 1985).

Table 2. The most abundant 30 sponge species on mangrove roots in the Pelican Cays, Belize.

Most abundant mangrove sponges in Pelican Cays	Also found in Twin Cays	Also found on very shallow reefs in Panama
<i>Cinachyrella apion</i>	xx	x
<i>Chondrilla nucula</i>	x	xx
<i>Anthosigmella varians</i>	p	xx
<i>Placospongia intermedia</i>		x
<i>Spirastrella mollis</i>		xx
<i>Terpios manglaris</i>		
<i>Tethya actini</i>		x
<i>Monanchora arbuscula</i>		xx
<i>Desmapsamma anchorata</i>		xx
<i>Artemisina melana</i>		x
<i>Clathria schoenus</i>	p	x
<i>Clathria venosa</i>	x	x
<i>Mycale laevis</i>	p	xx
<i>Mycale microsigmatosa</i>	x	x
<i>Iotrochota birotulata</i>		xx
<i>Scopalina ruetzleri</i>	x	x
<i>Haliclona curacaoensis</i>	xx	
<i>Amphimedon compressa</i>		xx
<i>Amphimedon erina</i>	p	x
<i>Xestospongia carbonaria</i>		xx
<i>Xestospongia proxima</i>		x
<i>Hirtios proteus</i>	xx	x
<i>Ircinia felix</i>		xx
<i>Spongia obscura</i>	p	
<i>Spongia tubulifera</i>	x	x
<i>Dysidea etheria</i>	p	x
<i>Chelonaplysilla</i> aff. <i>erecta</i>		
<i>Halisarca caerulea</i>		x
<i>Aplysina fulva</i>		xx
<i>Verongula rigida</i>		xx

Note: Relative abundance of these species in Twin Cays, Belize, is indicated by: xx = very common in Twin Cays as well as in the Pelicans; x = more common in the Pelican Cays than in Twin Cays; p = present, but not common in Twin Cays. Indication is provided of which species are also common (x) or very common (xx) on very shallow reefs (less than 3 m) in San Blas, Panama (Wulff, 1984; Clifton, et al., 1996; personal observation).

Table 3. Relative abundances of facultative and specialist sponge feeders and their predators in three locations in each of the Twin Cays and Pelican Cays, Belize

Sponge feeders and predators	Twin Cays			Pelican Cays		
	HID	CUD	SPO	CAT	MAN	FIS
Potential Sponge Predators						
Angelfish, <i>Pomacanthus</i> spp.				xx	xx	xx
Trunkfish, <i>Acanthostracion</i> spp.					x	x
Filefish, <i>Aluterus scriptus</i>				x		
Spadefish, <i>Chaetodipterus faber</i>						
Parrotfish, <i>Sparisoma</i> spp.		x		x	x	x
<i>Scarus isertii</i>					xx	x
Starfish, <i>Oreaster reticulatus</i>		x	x	xx	xx	xx
Potential Predators of Sponge Predators						
Barracuda, <i>Sphyaena barracuda</i>	x	xx	xx			

Note: xx = very abundant, x = present and readily seen without extensive searching, but not especially abundant. Key to locations within Twin Cays and Pelican Cays: HID = Hidden Creek, CUD = Cuda Cut, SPO = Sponge Haven, CAT = Cat Cay, MAN = Manatee, FIS = Fishermans Cay.

Table 4. Number of times individuals of the starfish *Oreaster reticulatus* were observed to be feeding on 11 species of sponges and various other foods in Twin Cays and Pelican Cays, Belize.

Sponges and other starfish food	Twin Cays	Pelican Cays
Sponges		
<i>Chondrilla nucula</i>		2
<i>Lissodendorxy isodictyalis</i>	1	
<i>Clathria echinata</i>		1
<i>Mycale laevis</i>	2	10
<i>Iotrochota birotulata</i>		6
<i>Tedania ignis</i>		3
<i>Amorphinopsis</i> sp.	2	2
<i>Xestospongia carbonaria</i>		3
<i>Oceanapia</i> sp.		1
<i>Ircinia</i> spp.		5
<i>Aplysina fulva</i>		1
Other invertebrates		
Compound ascidian		1
Zoanthid		1
<i>Agaricia tenuifolia</i>		12
Plant material		
Heavily epiphytized <i>Halimeda</i> sp.	1	4
Filamentous mangrove root epiphytes		1
Filamentous algae on peat	1	
Microalgae in sediments	9	

Note: Three of the observations on *Mycale laevis* were in the form of unambiguous scars from recent (i.e., within the previous couple of days) feeding, rather than direct feeding observations, and 7 of the observations on *Agaricia tenuifolia* were in the form of feeding scars.

Mycale laevis had fallen among a dense community of sponges that are not among those preferred by these large starfishes (primarily *Chondrilla nucula*), and this sponge, evidently protected by these inedible species completely surrounding it, was one of the few fallen individuals of edible sponge species that were not consumed by the starfishes. Sponge species represented among individuals that had fallen off the mangrove roots or that were growing on substrates under the roots, but had not been consumed by starfishes, included *Spongia tubulifera*, *Amphimedon erina*, *Chondrilla nucula*, *Placospongia intermedia*, and *Ircinia strobilina*. In the Pelicans, I observed several starfishes with broken spines indicating that they had recently strayed into areas in which parrotfishes forage (Wulff, 1995b).

Three bites were observed as they were being taken, all by sponge-feeding grey angelfishes. *Chondrilla nucula* suffered two of these bites and the other was on *Aiolochoia crassa*.

DISCUSSION

What Is a "Typical Caribbean Mangrove Sponge Community"?

The more common species at Twin Cays appear to coincide with the more or less typical mangrove-associated sponge fauna (Table 1) described in the literature (Alcolado, 1990; Hechtel, 1965; Sutherland, 1980; Rützler, 1969; Diaz et al., 1985) or personally observed (Galeta and San Blas, Panama). There are some exceptions (de Weerd et al., 1991), however: *Haliclona caerulea* is not present, but the Twin Cays fauna include several other Chalinid sponges that are absent from other mangrove faunas. Also lacking are *Halichondria melanodocia*, *Suberites zeteki*, and *Geodia gibberosa*, which have been reported to live on mangrove roots in at least three other places in the Caribbean (Table 1). Another six species (*Clathria schoenus*, *Mycale laevis*, *Amphimedon erina*, *Dysidea etheria*, *Mycale microsigmatosa*, and *Scopalina ruetzleri*) reported on mangrove roots in at least three other Caribbean locations are present at Twin Cays, but are more common in the Pelicans. An additional nine species that are common at Twin Cays but have not been reported from other locations outside Belieze, may in large part reflect the intensity of the collecting at Twin Cays, as well as the fact that some team members recently revised important groups of mangrove sponges. In any case, the Twin Cays mangrove-root sponge community easily falls within the range of variation in membership reported among other Caribbean mangrove root sponge communities (see references in Table 1).

In contrast, all but 4 of the 30 most common species in the Pelicans are closer in composition to the species inhabiting very shallow reef areas in San Blas, Panama, which are characteristic of reef habitats (Table 2). However, 16 of these 30 species appear to be absent from the nearby mangroves in Twin Cays (i.e., 80% of the species in common with a shallow reef, but fewer than 50% of the species in common with a nearby set of mangrove cays). Although several other excellent species lists of Caribbean coral reef sponge assemblages have been published (e.g., Alcolado, 1979, 1990; Alvarez et al., 1990; Schmahl, 1990), I compared the Pelicans only with Panama, in large part because of the flux in Caribbean sponge systematics in the past 10 years and thus the possible inconsistency in the names applied to the same sponges species. Because the data from Panama are my own (Wulff, 1994; Clifton et al., 1996), this at least

provides a consistent interpretation of the systematics and a consistent intensity of surveying. The Panama reef sponge assemblages are also in much shallower water than reef sponges reported in other studies, and this depth range makes the habitat more comparable to the mangrove habitat in at least that variable. In the San Blas Islands in Panama, coral reef sponges live in dense communities in as little as 2 m (e.g., Wulff, 1994, 1995a). On the Pelican Cays mangrove roots, these sponges can also occur in shallower water, even within the top 1 m. Exposure during extreme low tides demonstrates how shallow these sponges are and indicates one constraint on sponge distribution on mangrove roots (Rützler, 1995). Another important constraint on sponge distribution in mangroves is sediment. Alcolado (1990) mentioned complete lack of sponges on mangrove roots in areas of high sediment, for example, near rivers and within estuaries, and this is also the pattern in San Blas, Panama (personal observation). Wulff (1995a) suggested that the distribution of sponges in shallow water is prevented by rough water movement, whereas in Panama hurricanes virtually never occur, and during the single recorded hurricane, sponge populations were more protected on the leeward sides of reefs. The occurrence of dense communities of reef sponges in very shallow water in the Pelican Cays corroborates that shallow water per se does not restrict reef sponge distribution.

Demonstrated Predator-Imposed Constraints on Habitat Distribution of Caribbean Benthic Organisms

Experiments and observations of herbivorous grazers on reefs have repeatedly confirmed that herbivores influence the abundance and also the species composition of algal communities (e.g., reviews in Lubchenko and Gaines, 1981; Hay, 1997). Halos around patch reefs in seagrass meadows are one obvious indication of the importance of shelter to herbivorous fishes and sea urchins (e.g., Ogden et al., 1973) in the context of safe access to feeding areas. Many studies have also demonstrated that plant community composition can be influenced by nearby habitats in which the microtopography is complex enough to allow herbivorous fishes to find shelter from their predators, although topographic relief is not the sole important factor in some cases (e.g., Lewis, 1985).

That predators exert similarly profound effects on distribution and abundance of sponge species is a relatively new idea. Although sponges have been reputed to be inedible, and in fact demonstrated to be largely inedible for potential predators that have continuous access to them, sponge predators can effectively prevent edible sponges from sharing their habitat (Wulff, 1994, 1995b, 1997a, 1997b). Sponges that do not have adequate inherent defenses against a particular predator are absent from habitats frequented by those predators. As previous studies of predation on sponges have demonstrated, some sponge species that are normally entirely hidden in crevices in the reef (e.g., *Halichondria* cf. *lutea* [possibly = *Amophinopsis* sp. 1 in this study] and *Geodia* cf. *gibberosa*) are readily consumed by herbivorous parrotfishes when experimentally removed from their refuges (Wulff, 1988, 1997a). These cryptic species were able to grow beyond the confines of their cryptic spaces when protected by small cages. Two sponge species that live partially hidden (*Adocia* sp. and *Mycale laevis*) are also readily consumed by these herbivores when their surfaces are removed, indicating that defenses in these species are concentrated in their surfaces (Wulff, 1997a). If defenses are expensive to produce, concentration of defenses in surface tissue would be particularly adaptive for species that are also somewhat protected by their partly hidden habitat. Sponges living on mangrove roots are not normally challenged by sponge-

feeding fishes because these fishes are consistently associated with coral reefs, possibly because of the availability of shelter from their predators, which is lacking among the mangrove roots. When a *Halichondria* species, *Geodia gibberosa*, *Tedania ignis*, and *Chondrosia collectrix* were removed from mangroves and placed in a reef-fish habitat, they were also consumed, with angelfishes preferring *C. collectrix* and parrotfishes preferring *G. gibberosa* (Dunlap and Pawlik, 1996). In this study, large chunks of sponge were presented in the open on racks, however, and it is not clear that the results can be applied to the natural situation of many dozens of species growing together in dense multispecies clusters.

Transplantation experiments will be required to determine if fish predators are indeed excluding the more typical mangrove sponge fauna from Pelican Cay mangroves because fishes can consume an entire edible sponge within minutes, and even removal of a single bite can leave barely a trace because the sponges heal so quickly.

The influence of starfishes on sponge distribution is more readily observed. The large starfish *Oreaster reticulatus* extrudes its stomach and digests the sponge tissue, leaving behind distinctive feeding scars providing evidence of its meal for some days afterward (depending on the amount of spongin in the skeleton). The effect of starfish predation on sponge distribution was obvious in the Pelicans, where sponges demonstrated to be edible to *O. reticulatus* (Wulff, 1995b) were abundant on mangrove roots only 0.5 m or less above hard substrate, on which a very different sponge community, composed solely of species demonstrated to be rejected by the starfishes, was thriving; that is, the distribution pattern appeared to be enforced by starfish predation, because the only factor that differed between the substrates was accessibility to starfish grazing.

Are Predators the Primary Influence on Sponge Community Structure in the Twin Cays and Pelican Cays?

If sponge predators are restricting sponges without inherent defenses from living in the Pelicans, why is the fauna there not merely a depauperate version of the Twin Cays sponge fauna? That is, why is it not the same typical mangrove root fauna, but lacking the undefended sponge species? The far more diverse sponge fauna of the Pelicans is reminiscent of other, less complex, situations in which predators have been demonstrated to increase diversity by feeding on organisms that otherwise are capable of outcompeting many of the species in the system (e.g., Paine, 1966). Although little is known of sponge energetics, recent work by Uriz et al. (1995) suggests that allocations to secondary chemistry used in predator defense could decrease growth rates or reproductive rates. It is possible that this is the key, and decreased growth and reproduction rates may be the trade-off for increased predator resistance. Reef sponges, which would be extinguished without inherent defenses against predators, may be outcompeted on mangrove roots because they divert resources to predator defenses and thus have lower growth rates. The observation of many sponges brooding abundant larvae in populations in which recruitment by sexually generated larvae is too low to be observed (Wulff, 1991), except after a hurricane scoured the substrate (Wulff, 1995a), suggests that the limiting step in successful recruitment is not availability of larvae, but rather availability of suitable substrate. The usual mangrove sponge fauna may even be selected for increased allocation to reproduction in response to the finite nature of individual mangrove roots and the need to colonize fresh roots because expansion to adjacent space is not possible by vegetative means of propagation, as it is on the

reef.

In his study of sponge community dynamics on mangrove roots in Venezuela, Sutherland (1980) concluded that, at least for the Venezuelan mangrove sponge fauna he studied, recruitment was a relatively rare event, followed by long periods of relative stasis. Recruitment of reef sponges has also been demonstrated to be relatively rare, except after a storm cleared the substrate (Wulff, 1995a) or in cryptic spaces near adult sponges (Zea, 1993).

Growth has been demonstrated to be relatively slow and highly variable for most reef sponges (e.g., Hoppe, 1988; Wulff, 1990, 1991) and relatively rapid for at least a couple of mangrove sponge species (Ellison et al., 1996). When apparent competition between sponges has been investigated over long periods or experimentally, the intimate associations have actually been shown to be of mutual benefit to participating species in some cases (e.g., Sarà, 1970; Rützler, 1970; Wulff, 1996). Examples of mutual benefit have all come from sponge species that consistently coexist. It is possible that the distinct separation of Caribbean sponges into a typical mangrove root fauna and a typical reef fauna results in part from competitive exclusion of reef sponges from mangroves by faster-growing mangrove sponge species, except in unusual circumstances, as when the habitat context favors residence of spongivores.

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REFERENCES

- Alcolado, P. M.
 1979. Ecological structure of the sponge fauna in a reef profile of Cuba. In *Biologie des Spongiaires*, edited by C. Levi and N. Boury-Esnault, 297–302. Colloq Int CNRS, Paris, v. 291.
1990. General features of Cuban sponge communities. In *New Perspectives in Sponge Biology*, edited by K. Rützler, 351–357. Washington, DC: Smithsonian Institution Press.
- Alvarez, B., M. C. Diaz, and R. A. Laughlin
 1990. The sponge fauna on a fringing reef in Venezuela, II: Composition, distribution and abundance. In *New Perspectives in Sponge Biology*, edited by K. Rützler, 358–366. Washington, DC: Smithsonian Institution Press.
- Clifton, K. E., K. Kim, and J. L. Wulff
 1996. A Field Guide to the Reefs of Caribbean Panama with an Emphasis on Western San Blas. *Proceedings of the 8th International Coral Reef Symposium*, Panama.
- Diaz, H., M. Bevilacqua, and D. Bone
 1985. *Esponjas en Manglares del Parque Nacional Morrocoy*. Fondo Editorial, Acta Científica Venezolana.

- Dunlap, M., and J. Pawlick
1996. Video-monitored predation by Caribbean reef fishes on an array of mangrove and reef sponges. *Marine Biology* 126:117–123.
- Ellison, A. M., E. J. Farnsworth, and R. R. Tilley
1996. Facultative mutualism between red mangroves and root-fouling sponges in Belizean mangroves. *Ecology* 77:2431–2444.
- Hay, M. E.
1997. The ecology and evolution of seaweed-herbivore interactions on coral reefs. *Proceedings of the 8th International Coral Reef Symposium, Panama*, 1:23–32.
- Hechtel, G. J.
1965. *A Systematic Study of the Demospongiae of Port Royal, Jamaica*. Peabody Museum of Natural History, Yale University, Bulletin 20.
- Hoppe, W. F.
1988. Growth, regeneration, and predation in three species of large coral reef sponges. *Marine Ecology Progress Series* 50:117–125.
- Lewis, S. M.
1985. Herbivore abundance and grazing intensity on a Caribbean coral reef. *Journal of Experimental Marine Biology and Ecology* 87:215–228.
- Lubchenco, J., and S. D. Gaines
1981. A unified approach to marine plant-herbivore interactions. I. Populations and communities. *Annual Review of Ecology and Systematics* 12:405–437.
- Ogden, J. C., R. A. Brown, and N. Salesky
1973. Grazing by the echinoid *Diadema antillarum* Philippi: Formation of halos around West Indian patch reefs. *Science* 182:715–717.
- Paine, R. T.
1966. Food web complexity and species diversity. *American Naturalist* 100:65–76.
- Randall, J. E. and W. D. Hartman
1968. Sponge-feeding fishes of the West Indies. *Marine Biology* 1:216–225.
- Rützler, K.
1969. The mangrove community, aspects of its structure, faunistics and ecology. In *Lagunas Costeras*, 515–536. UNAM-UNESCO, Mexico, DF.
1970. Spatial competition among Porifera: Solution by epizoism. *Oecologia* 5:85–95.
1995. Low-tide exposure of sponges in a Caribbean mangrove community: P.Z.N.I. *Marine Ecology* 16:165–179.
- Rützler, K., and I. C. Feller
1996. Caribbean mangrove swamps. *Scientific American* 274:94–99.
- Sarà, M.
1970. Competition and cooperation in sponge populations. *Symposium of the Zoological Society of London* 25:273–284.
- Schmahl, G. P.
1990. Community structure and ecology of sponges associated with four Southern Florida coral reefs. In *New Perspectives in Sponge Biology*, edited by K. Rützler, 376–383. Washington, DC: Smithsonian Institution Press

Sutherland, J.

1980. Dynamics of the epibenthic community on roots of the mangrove *Rhizophora mangle*, at Bahia de Buche, Venezuela. *Marine Biology* 58:75–84.

Uriz, M. J., X. Turon, M. A. Becerro, J. Galera, and J. Lozano

1995. Patterns of resource allocation to somatic, defensive, and reproductive functions in the Mediterranean encrusting sponge *Crambe crambe* (Demospongiae, Poeciloscerida). *Marine Ecology Progress Series* 124:159–170.

Weerdt, W. H. de, K. Rützler, and K. P. Smith

1991. The Chalinidae (Porifera) of Twin Cays, Belize, and adjacent waters. *Proceedings of the Biological Society of Washington* 104:189–205.

Wilkinson, C. R., and E. Evans

1989. Sponge distribution and abundance across Davies Reef, Great Barrier Reef, relative to location, depth, and water movement. *Coral Reefs* 8:1–7.

Wulff, J. L.

1988. Fish predation on cryptic sponges of Caribbean coral reefs. *American Zoologist* 28:166.
1990. Patterns and processes of size change in Caribbean demosponges of branching morphology. In *New Perspectives in Sponge Biology*, edited by K. Rützler, 351–357. Washington, DC: Smithsonian Institution Press.
1991. Asexual fragmentation, genotype success, and population dynamics of erect branching sponges. *Journal of Experimental Marine Biology and Ecology* 149:227–247.
1994. Sponge-feeding by Caribbean angelfishes, trunkfishes, and filefishes. In *Sponges in Time and Space: Biology, Chemistry, Paleontology*, edited by R. W. M. van Soest, T. M. G. van Kempen, and J-C Braekman, 265–271. Rotterdam: A. A. Balkema.
- 1995a. Effects of a hurricane on survival and orientation of large, erect coral reef sponges. *Coral Reefs* 14:55–61.
- 1995b. Sponge-feeding by the Caribbean starfish *Oreaster reticulatus*. *Marine Biology* 123:313–325.
1996. Mutualisms among species of coral reef sponges. *Ecology* 78:146–159.
- 1997a. Parrotfish predation on cryptic sponges of Caribbean coral reefs. *Marine Biology* 129:41–52.
- 1997b. Causes and consequences of differences in sponge diversity and abundance between the Caribbean and eastern Pacific at Panama. *Proceedings of the 8th International Coral Reef Symposium*, Panama, 2:1377–1382.

Zea, S.

1993. Recruitment of demosponges (Porifera, Demospongiae) in rocky and coral reef habitats of Santa Marta, Colombian Caribbean: P.Z.N.I. *Marine Ecology* 14:1–21.
1994. Patterns of coral and sponge abundance in degraded versus still healthy reefs at Santa Marta, Colombian Caribbean. In *Sponges in Time and Space*, edited by R. W. M. van Soest, T. M. G. van Kempen, and J-C Brakeman, 257–264. Rotterdam: Balkema.