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Effects of a hurricane on survival and orientation of large erect coral reef sponges

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Abstract. In October 1988, Hurricane Joan struck reefs in the San Blas Islands, Panama, where hurricanes had never been recorded. Effects on large erect sponges were dramatic. For several years before the hurricane, the three most common sponges had been studied, providing pre-storm data on population structure and dynamics. Nearly half the individuals and biomass of three species were lost in the storm. The species were not affected in the same way, even though they are all of erect branching growth forms. *Iotrochota birotulata* lost significantly more individuals than *Amphimedon rubens* (57.6% vs 42.9%), which lost significantly more individuals than *Aplysina fulva* (31.6%). Patterns of biomass loss were very different, with both *Iotrochota* and *Aplysina* suffering losses of about 50%, but *Amphimedon* losing only 4.9%. Patterns of loss appear to be related to differences between species in the relative proportions of spicules (siliceous) and spongin (protein) in skeletal fibers and by differences in the speed and success rate of fragment reattachment. The incidence of toppling due to base failure varied among the six most common large erect sponge species, with significantly less toppling of the two species with skeletons composed solely of spongin. Clones of *Iotrochota birotulata* characterized by narrow branches suffered disproportionately greater losses than clones with more robust branches. The abundance of very small sponges, possibly developed from sexually produced larvae, was an order of magnitude higher after the storm than before.

Introduction

The relative influence of various physical and biological factors on distribution and abundance of Caribbean coral reef sponges is poorly known. This represents an important gap in knowledge of reef dynamics because of the great abundance and diversity of sponges on Caribbean reefs (e.g., Reiswig 1973; Hartman 1977; Bonem and Stanley 1977; Rützler 1978; Suchanek et al. 1983; Wilkinson 1987a; Alcolado 1990; Alvarez et al. 1990; Wulff 1994). Caribbean sponges play key roles in the nutrient balance of reefs (Reiswig 1971, 1974, 1981; Wilkinson 1987a), in bioerosion (e.g., Goreau and Hartman 1963; Hartman 1977; Wilkinson 1983a), and in recovery from disturbance and maintenance of reef integrity (Goreau and Hartman 1963; Wulff and Buss 1979; Wulff 1984). Thus, determinants of sponge abundance may be as critical to reef health as the better-studied determinants of coral abundance. Predators, sunlight, chronic turbulence, sedimentation, and nutrients all affect sponge distribution and abundance, both in the tropical Pacific (e.g., Bakus 1964, 1969, 1983; Jokiel 1980; Wilkinson 1983b, 1987b; Wilkinson and Trott 1985; Wilkinson and Evans 1989) and in the Caribbean (e.g., de Laubenfels 1950; Reiswig 1973; Alcolado 1979; Wilkinson 1987a; Wulff 1988; Diaz et al. 1990; Schmahl 1990; Zea 1994). Disturbances, such as hurricanes, also influence sponge distribution and abundance. Hurricane Allen, in August 1980, severely damaged (> 1/3 of tissue lost or killed) 32% of sponge individuals at 12–15 m on the fore-reef at Discovery Bay, Jamaica, as estimated from surviving portions (Woodley et al. 1981; Wulff, unpubl. data). However effects of hurricanes have not been reported for sponges for which prior population dynamics and census data are available.

The San Blas Islands, Republic of Panama, at 9° N latitude, lie outside of the western Atlantic hurricane belt. Hurricane Joan, which struck the San Blas reefs in mid October 1988, was the first to be recorded there. These reefs regularly experience a dry season swell that is the largest recorded in the Caribbean (Glynn 1973), with the direction of heavy seas strongly influenced by the northeast tradewinds. Hurricane Joan, however, arrived from the south, striking reefs on what is normally their undisturbed leeward side. This provided an opportunity to study the influence of a hurricane on sponge distribution and abundance in a community that was not already disturbance-adapted by previous exposure to hurricanes.

Common large erect sponges were the subject of this investigation. The three erect branching species on which most post-hurricane attention was focused had been the subjects of an extensive, long-term investigation of population structure and dynamics of asexually fragmenting sponges (Wulff 1985, 1986b, 1988, 1990, 1991), allowing comparisons of these populations before and after the hurricane. The skeletons of these species differ in materials and construction, and the resulting differences in biomechanical properties make a comparison of hurricane effects between these species biologically informative.

Specific questions are addressed: Were sponge species affected differently by the hurricane? Were different clones within a species affected differently? Were very small sponges, possibly developed from larvae, more abundant after the hurricane? What proportion of surviving sponges were reoriented by being toppled onto their sides or off stable solid substrata? More generally: what attributes appear to help sponges resist or recover from severe physical disturbance?

Materials and methods

Species and study site

Post-hurricane data collection was primarily focused on three sponge species: *Iotrochota birotulata* (Higgin), *Amphimedon rubens* (Pallas) [*Amphimedon compressa* D & M, *sensu* Wiedenmayer (1977)], and *Aplysina* (*Verongia*) *fulva* (Pallas) [see systematic discussions by de Laubenfels (1936) and van Soest (1978)]. All three are erect branching species, resembling trees, bushes, or vines in overall morphology. However, their skeletons differ sufficiently in composition and organization that each of these species is placed in a different order of the class Demospongiae.

Population dynamics of these three species are dominated by asexual propagation by fragmentation; therefore individuals can be defined either physiologically or genetically. "Individual" is defined as physiologically confluent tissue enclosed within an unbroken surface pinacoderm. "Clone" is defined as physiologically independent individuals representing a single genotype. Sponges lack unambiguously defined repeating units and are therefore not referred to as colonies (Hartman and Reiswig 1973).

The populations studied are on a shallow plain (−2.1 to −3 m below MLW) and on the slopes of a channel (−3 to −12 m below MLW) that wraps around what is normally the leeward side of Guigalatupo, an island near the San Blas Field Station of the Smithsonian Tropical Research Institute in Panama (map in Robertson 1987). The substratum on this southwest-facing portion of Guigalatupo reef is a homogeneous mixture of rubble from ramose coral species, dotted with small to medium sized massive corals, primarily of *Montastrea*, *Siderastrea*, and *Diploria*. The sponge community is dense, both in numbers of individuals ($87.2\,\mathrm{m}^{-2}$) and total volume ($2107.6\,\mathrm{cm}^3\,\mathrm{m}^{-2}$). It is also relatively diverse (42 species/16 m^2). The three species studied are the most abundant, with respect to both biomass and numbers of individuals, and together constitute 57.5% of the total sponge volume in this community (Wulff 1994). These species are also common on shallow to mid-depth reefs throughout the Caribbean.

Rates of survival

Four weeks after Hurricane Joan, an area that had been censused in August, 1988, just three months earlier, and also in February, 1984, 4.7 years earlier, was censused again. The 24 m^2 censused are in the center of a homogeneously populated area. Numbers of individuals were counted at all three censuses. In addition, in 1984 and after the hurricane, sizes (as total volume) of all sponges (except excavating species) were measured by detailed approximation to geometric solids.

On a different part of Guigalgatupo reef, seven large individuals of each species were monitored. Before the hurricane, these 21 individuals constituted all of the sponges greater than 30 cm in height and with at least 2 branches in a 20 m strip, 2 to 4 m deep, on the south-facing side of the reef.

Because storm effects were expected to differ between these three species due to differences in skeletal materials, an estimate was made of the relative proportions of spongin (protein) and spicules (siliceous) in their skeletal fibers. On camera lucida drawings of fibers from which tissue had been removed, the number of tips of millimeter marks on a ruler that fell directly on spicules versus spongin were counted. The ruler was positioned by sets of randomly placed points. A total of 80 points were counted for each species.

Rates of survival of clones differing in branch width

Tissue compatibility and morphological analyses had been used to determine probable clone membership of the 60 largest individuals of *Iotrochota* on a shallow slope adjacent to the censused area (Wulff 1986b). Within the probable clones of *Iotrochota*, branch width was found to be invariant, but branch width differed between clones (Wulff 1986b). After the storm, survival of the 60 *Iotrochota* individuals was recorded, in order to determine if the storm had altered the representation of narrow-branched individuals relative to wide-branched individuals.

The influence of branch width on the ease with which an individual is fragmented was evaluated experimentally by stretching branches until they broke. A total of 25 branches, ranging from 0.7 to 2.2 cm in diameter, were attached to a spring scale at one end and grasped by an assistant at the other end. Each branch was pulled until it broke, and the force exerted at breakage was recorded.

Reorientation of surviving large sponges

Hurricane effects were also studied in other sponge-dominated communities for which prior census data were not available. Reefs that lie leeward of Ulagsukun, Mamitupo, Korbiski, Tiantupo, and Aguadargana were visited (map in Robertson 1987). All sponge individuals of 30 cm in height or greater, and with at least two branches, in the case of branching species, were evaluated. Data recorded for each sponge included orientation (upright versus toppled onto its side), substratum type (unconsolidated rubble versus coral heads and patch reefs), and depth. Sponges that had been toppled in the hurricane were readily distinguished by the upwards reorientation of the tips of their prone branches or tubes.

Abundance of very small sponges

Special care was taken in the censusing to look for very small sponges (i.e., less than 0.5 cm in every dimension). It is possible that these developed from larvae that had settled in the few weeks after the storm, but there was no way to prove this non-destructively. Abundance of very small sponges after the hurricane was then compared with earlier data from 20 quadrats, each 1 m^2, which had been censused four times in one year, with special attention to recruitment (Wulff 1991). All of these recruitment quadrats were within a few meters of the censused area.

Results

Rates of survival

Hurricane Joan (October, 1988) had a dramatic effect on population sizes of *Iotrochota birotulata*, *Amphimedon* *rubens*, and *Aplysina fulva* (Fig. 1), reducing their combined populations by nearly half in terms of both numbers of individuals (45% lost) and biomass (44.7% lost), when compared with abundances before the hurricane. This contrasts with the remarkable congruence in numbers of individuals between the census made in August, 1988 and the one made in February, 1984, 4.5 years earlier. Between these censuses, the greatest difference in numbers of individuals for a species was only 6.4%, and combined numbers of individuals of these 3 species differed by only 0.8% (Fig. 1).

The sponge species were not affected equally by the storm. *Iotrochota* suffered nearly twice the loss of individuals as *Aplysina* (57.6% versus 31.6%; G-test, $P < 0.001$), and losses of *Amphimedon* were intermediate (42.9%; significantly different from losses in both of the other species, $P < 0.001$). Patterns of biomass loss were very different, with both *Iotrochota* and *Aplysina* losing half of their biomass (51.9% and 50.2%, respectively), but with the total biomass of *Amphimedon* remaining virtually unaltered (4.9% lost; significantly different from losses in each of the other species, $P \ll 0.001$). Relative abundance of the three species was shifted by the storm from 42.7%, 20.1%, and 37.2% to 33.0%, 20.8%, and 46.2% of total number of individuals for *Iotrochota*, *Amphimedon* and *Aplysina* respectively. Relative volume for the three species was shifted from 31.9%, 13.3%, and 54.0% of total volume before the storm to 27.7%, 22.9%, and 49.4% afterwards. Thus, *Aplysina* gained in proportional representation of number of individuals, and *Iotrochota* lost; but, in proportional representation of volume, *Amphimedon* gained and the other two species lost.

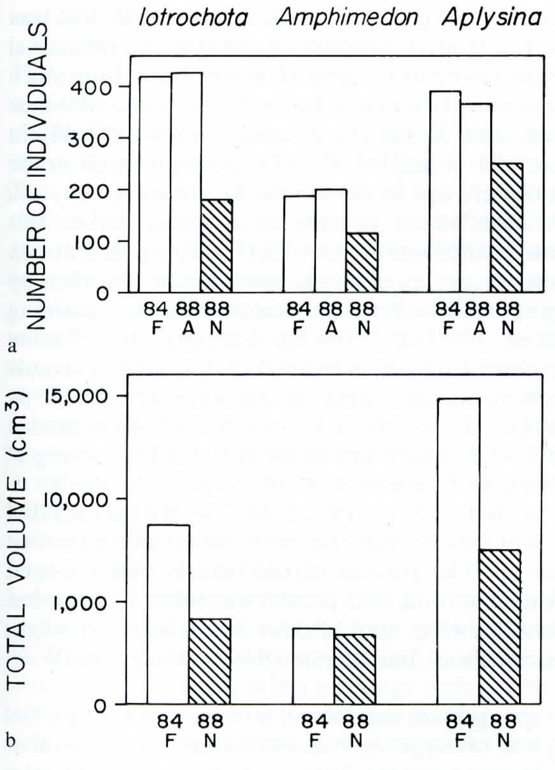

Fig. 1a, b. Abundance, **a** in terms of numbers of individuals and **b** in terms of total volume, for the three most common sponge species in 24 m^2 for three census dates. The years are indicated along the x-axis by 84, 1984; 88, 1988. The months are indicated by F, February; A, August, N, November. The cross-hatched bars represent abundances 4 weeks after Hurricane Joan

Elsewhere, on the south-facing edge of the reef, where storm waves impinged more directly, destruction of sponges was even greater. Not one of the 21 large, shallow, individuals of *Iotrochota*, *Amphimedon*, and *Aplysina* that had been monitored before the hurricane remained in recognizable form after the hurricane.

These three species differ significantly in the relative abundance of spongin and silica in their skeletons. The proportion of skeletal fiber cross sections composed of siliceous spicules was 82.5% (66/80 points) for *Iotrochota*, and 40% (32/80 points) for *Amphimedon* (G-test, $P < 0.001$). *Aplysina* fibers do not include any spicules.

Over half (33/60) of the *Iotrochota* individuals for which probable clone membership was identified were lost in the storm. Although fragments may have remained, the lost sponges were no longer recognizable on their original bases. Narrow-branched individuals were lost disproportionately more than wide-branched individuals. After Hurricane Joan, the relative abundance of the narrow-branched *Iotrochota* morph was 37% (10/27 individuals), significantly smaller than the 60% (36/60 individuals) of the population represented by this morph before the hurricane (G-test, $P < 0.025$).

Narrow branches of *Iotrochota* broke with significantly less experimentally-applied force than wide branches. The mean force required to break branches 0.7–1.4 cm in diameter was 2.4 kg (95% confidence interval: 2.0–2.7 kg, $n = 14$). For branches 1.5–2.2 cm in diameter, the mean force required for breakage was 3.9 kg (95% confidence interval: 2.9–4.9 kg, $n = 11$).

On shallow portions (top 9 m) of south-facing slopes of five reefs (normally protected) 50.6% of the surviving large erect sponges (i.e., trees, bushes, vases or clusters of tubes) were reoriented by toppling onto their sides in the storm (Table 1). More may have been toppled or fragmented and then transported elsewhere, or even pulverized, but in the absence of data from a prior census, conclusions must be drawn solely from those individuals that survived the storm.

Sufficient numbers of large individuals were observed in six species for statistical comparisons to be made between different depths and substratum types. These six species included the three most common species referred to already, as well as the next three most common (Wulff 1994) large erect species. One of these species, *Niphates erecta* D & M, is also an erect branching species, but *Ircinia campana* (Lamarck) is a large open tube or cup, and *Callyspongia vaginalis* (Lamarck) grows as a cluster of tall, narrow tubes. The relative abundance of spongin to spicule in skeletal fibers differs among these species, but all six species are characterized by small basal attachment to volume ratios. Proportionately more surviving sponges were toppled in shallow (1–5 m) than in deep (5–9 m) water (57.2% versus 39.1%; G-test, $P < 0.001$). Also, proportionately more surviving sponges were found in toppled position on the unconsolidated rubble and sediments than on patch reefs or coral bluffs (74.9% versus 27.9%; G-test,

Table 1. Numbers of surviving large (i.e., greater than 30 cm in height and, in the case of branching species, with at least 2 branches) sponges that were left in erect position versus toppled onto their sides by the hurricane in deep versus shallow water, and in total, and on stable solid reef substrata versus on unconsolidated rubble or sediments. Ib, *Iotrochota birotulata*; Ar, *Amphimedon rubens*; Af, *Aplysina fulva*; Ne, *Niphates erecta*; Cv, *Callyspongia vaginalis*; Ic, *Ircinia campana*

	Deep (5–9 m)		Shallow (1–5 m)		Total		Reef		Rubble	
	Total number	toppled [%]	Total number	toppled [%]	Total number	toppled [%]	Total number	toppled [%]	Total number	toppled [%]
Ib	26	30.8	43	74.4	69	58.0	35	31.4	34	85.3
Ar	67	50.7	101	65.3	168	59.5	76	30.3	92	83.7
Af	22	4.5	47	29.8	69	21.7	36	11.1	33	33.3
Ne	12	41.7	17	52.9	29	48.3	18	33.3	11	72.7
Cv	26	46.1	55	63.6	81	58.0	44	40.9	37	78.4
Ic	8	37.5	13	15.4	21	23.8	17	5.9	4	100.0
Total	161	39.1	276	57.2	437	50.6	226	27.9	211	74.9

$P \ll 0.001$). Surviving large individuals of two of these six erect sponge species were found toppled at a significantly lower incidence than the other four species. Incidences of toppling for *Aplysina fulva* and *Ircinia campana* (the two keratose species) were, respectively, 21.7% and 23.8%, whereas for the other four species toppling incidences ranged from 48.3% to 59.5% (Table 1; G-test, $P < 0.001$).

A total of 25 small sponges (less than 0.5 cm in every dimension) were found in the 24 m^2 censused area. All of these small sponges were of *Iotrochota birotulata*, *Amphimedon rubens*, and *Aplysina fulva*. The number of very small individuals of each species was compared with the number of recruits before the hurricane (Table 2). Numbers of very small sponges found per square meter per census differed by nearly an order of magnitude, with 1.04 individuals m^{-2}/census found after the storm, but only 0.11 individuals m^{-2}/census found before.

Very small sponges in the pre-hurricane recruitment experiments were considered, with some confidence, to have settled as larvae, because all sponges in each quadrat were mapped to scale at each census, and it was clear that none had regenerated from a base of a fragmented large sponge. It was not certain, however, that the very small sponges found after the hurricane were derived from larvae. A case for recent larval origin is supported by their extremely smooth surface, encrusting morphology, and delicate appearance, all of which contrasted with the robust appearance of small sponges that were clearly regenerating basal portions, left on the substratum when the remainder of the sponge was broken off. The regenerating sponges were 3-dimensional and their surfaces were not smooth, due to the slight protrusion of broken skeletal fibers.

Table 2. Numbers of small sponges before and after the hurricane

	Numbers of small sponges	
	Number/20 m^2 before the hurricane (4 censuses)	Number/24 m^2 after the hurricane (1 census)
Iotrochota birotulata	1	9
Amphimedon rubens	0	3
Aplysina fulva	8	13
Total	9	25
Number of very small sponges per m^2 per census	0.11	1.04

Discussion

Losses from these sponge populations due to Hurricane Joan were dramatic, reducing combined density of the three most common species by nearly half. Differences among these three species in terms of individuals lost was related to the relative proportions of spicules (siliceous) and spongin (protein) in their skeletal fibers. *Iotrochota birotulata* is relatively brittle because of a preponderance of spicules, and is therefore easily broken (Wulff, in preparation). Over half (57.6%) of these individuals in the shallow site were lost in the storm. By contrast, *Aplysina fulva*'s skeleton, made entirely of spongin, makes this sponge flexible and highly extensible (Wulff, in preparation). For this species, energy of storm waves can be absorbed by stretching sponges rather than snapping them, explaining a loss rate of only 31.6%. The third species, *Amphimedon rubens*, is intermediate between the other two in its spicule to spongin ratio, and also in extensibility (Wulff, in preparation). An intermediate number of *Amphimedon* individuals (42.9%) were lost in the storm. This ranking of susceptibility to fragmentation of these three species is identical to that demonstrated by 140 unmanipulated individuals of these species that were observed over a nine month period. The percent of individuals that changed size by fragmentation and partial mortality during that time were 62%, 43%, and 32% for *Iotrochota birotulata*, *Amphimedon rubens*, and *Aplysina fulva*, respectively (Wulff 1990).

Many sponges are capable of surviving severe partial mortality and undergoing frequent fragmentation, so that patterns in loss of individuals cannot be used to infer patterns of loss of biomass. A lack of concordance between loss of biomass and loss of individuals is especially illustrated by *Amphimedon*, which lost little biomass (4.9%), but many individuals (42.9%). This reflects a strong size-dependence in loss, with disproportionately heavy losses of small individuals. Size-frequency distributions of all three of these species were strongly dominated by smaller size classes before the hurricane, with 54% of the *Amphimedon* individuals being smaller than 20 cm^3, but all of these individuals combined accounted for only 13.3% of the total *Amphimedon* biomass (Wulff 1991).

Although *Aplysina* survived significantly better than the other two species, in terms of numbers of individuals, *Amphimedon* survived far better than the others in terms of biomass. *Iotrochota* and *Aplysina* may have suffered similar high rates of biomass loss for very different reasons. Survival after a storm depends on both resisting damage during the storm and recovering from damage afterwards. For fragmenting sponges, this constitutes prevention of fragmentation and toppling, coupled with the ability of fragments and detached whole individuals to survive rolling and to reattach to stable solid substrata. *Iotrochota* fragments survive significantly better than those of the other two species, especially under conditions of vigorous water movement, because they are able to reattach to stable substrata more quickly (Wulff 1985). However, the relative brittleness of the *Iotrochota* skeleton makes it more susceptible to fragmentation (Wulff, in preparation). Under less severe conditions, the ability to reattach rapidly to solid substrata may compensate for the ease with which *Iotrochota* is fragmented, but during the hurricane, the fragmentation rate may have been so high that many individuals in this shallow site were fragmented to the point of pulverization. In contrast, although the flexibility and extensibility of *Aplysina* decrease the rate at which it is fragmented, *Aplysina* fragments survive relatively poorly. They do not reattach as easily and do not survive dispersal well (Wulff 1985). In summary, *Iotrochota* is easily fragmented, but the fragments survive well; whereas *Aplysina* resists fragmentation, but the fragments survive poorly. The compromise strategy, represented by *Amphimedon rubens*, which is intermediate in extensibility and in reattachment success, was most successful in preventing biomass loss in the hurricane.

Surviving sponges with skeletons differing in spongin to spicule ratios also exhibited different incidences of toppling. The two species that were toppled the least, *Aplysina fulva* and *Ircinia campana*, are both keratose species with extensible skeletons composed solely of spongin. Spongin fiber skeletons of *Ircinia* are augmented by abundant fine spongin filaments (Bergquist 1978), making sponges of this genus extremely resistant to tearing, breaking, or other physical damage. The shape of *Ircinia campana*, a large open cup on a very small base, is a viable morphology in shallow water only because of this highly resistant skeleton. Toppling increases vulnerability to substratum-associated sources of mortality and fragmentation, especially when a sponge ends up on unstable substrata, such as unconsolidated rubble or sediment. Even on stable substrata, partial mortality is disproportionately heavy on basal and repent portions of these species (Wulff 1990). Thus, the full consequences of toppling are not evident directly after a hurricane, even if the sponges have physiologically recovered and reattached.

Clones, within a species, that differ in susceptibility to fragmentation, were also affected differently by the hurricane. *Iotrochota* individuals with narrow branches had been predicted to be more susceptible to breakage because, prior to the hurricane, the narrow-branched morph was disproportionately represented by clones with greater numbers of physiologically independent individuals (i.e., resulting from more fragmentation; Wulff 1986). This prediction is supported by the demonstration that greater experimentally-applied forces were required to break wider branches. Whereas the ability to be easily fragmented may be advantageous in general for these branching species (Wulff 1991), the vigorous water movement during the hurricane shifted relative representation of morphs in the population in favor of the more robust ones.

Have hurricanes influenced sponge distribution and abundance in the Caribbean?

How the patterns of distribution and abundance have been influenced by severe disturbances of short duration is difficult to evaluate in communities of organisms that live longer than the interval between disturbances, because the history of previous disturbances may never be completely erased. Such communities have become essentially disturbance-adapted by elimination of organisms that are incapable of surviving disturbance, and their undisturbed state cannot be regained when most space is already occupied by individuals that have survived and recovered from previous disturbances. How such communities have been shaped by hurricanes can best be determined from the natural experiment of a hurricane hitting a previously undisturbed community.

Do the effects of Hurricane Joan on the previously undisturbed sponge communities of San Blas provide evidence that hurricanes may have limited sponges elsewhere in the Caribbean? One striking difference between the San Blas reefs and those described elsewhere in the Caribbean is that especially rich sponge communities, both dense and diverse, are common in very shallow water in San Blas, whereas the reported minimum depth for significant sponge populations elsewhere has been 10 m. In Jamaica, Reiswig (1973) estimated a volume of 3000 cm^2 m^{-2} on the fore-reef slope at Discovery Bay and reported that this zone, from 23 m to 50 or 60 m was the center of distribution of the sponge fauna. The greatest sponge biomass reported by Wilkinson (1987b) was 2.5 kg m^{-2} in Barbados, at 20 m. At Los Roques, in Venezuela, Diaz et al. (1990) reported maximum density of sponge individuals at 28–35 m and maximum surface area occupied at 18 m and deeper; and also that "sponges were practically absent between 0 and 2 m in open reef habitats". Alcolado (1979) reported greatest numbers of individual sponges between 11 and 16 m and "exceedingly few sponges" at 2 m or less in Cuba. Schmahl (1990) also reported maximum abundance, in numbers of individuals, from 12–20 m in southern Florida.

Although comparisons are hampered somewhat by the variety of ways in which sponge abundance has been measured, it is clear that abundance, whether measured by number of individuals, area, volume, or weight, is very low in shallow (<2 m) water and greatest somewhere between

10 and 50 m. In San Blas, abundance is also higher in deeper water, with a sponge volume of $5783\,\mathrm{cm}^3\,\mathrm{m}^{-2}$ removed from patch reefs between 13 and 20 m for an experiment on Marsagantupo reef (Wulff and Buss 1979). However, in contrast to the other Caribbean sites, sponges can be abundant in shallow water in San Blas, with a pre-storm sponge volume of $2107.6\,\mathrm{cm}^3\,\mathrm{m}^{-2}$ in the censused area, which is less than 3 m deep.

Since the three species studied in detail together constituted 57.5% of this total volume, and 44.7% of their biomass was lost in the storm, even in the unlikely case that all 39 other species in the censused area were unaffected by the storm, Hurricane Joan eliminated 1/4 of the total sponge biomass (25.7%). Whether or not this would be sufficient damage to explain the lack of significant sponge populations in shallow water in areas regularly hit by hurricanes would depend on the speed of recovery to pre-storm population sizes relative to intervals between storms. From what has been demonstrated of the population dynamics of these branching species (Wulff 1985, 1986b, 1990, 1991), recovery of their populations after disturbance, which is primarily by asexual fragmentation, can be rapid. Ten cleared 1 m^2 quadrats were repopulated within a year by fragments to population levels about half of those before clearing (Wulff 1991). Post-hurricane repopulation would not be expected to be this rapid because the experimentally cleared quadrats were in the midst of an otherwise intact sponge community. However, it is possible that, although Hurricane Joan caused large losses from these three species, their recovery will be complete. On the other hand, Hurricane Joan was a relatively minor storm causing only minimal damage to coast and island villages in San Blas. A more severe storm might have eliminated branching species altogether from shallow water, as Hurricane Joan did on the south-facing side of Guigalatupo reef. Unfortunately, the other sponge species in the community could not be included in the post-hurricane census, and it is the forms that are not adapted for propagation by fragmentation that might recover less readily, if at all.

The normally very low success rate of recruitment by larvae of branching sponges was predicted to be greater after major storms because hard substrata would be cleared of sediment and algae that can smother small filter feeders (Wulff 1986a). The relatively high abundance of small sponges after the hurricane suggests survival is enhanced after a major storm. For nonfragmenting sponges that rely on larvae for propagation, enhanced survival of small sponges after a hurricane is critical for population recovery. For fragmenting sponges, the possibility of post-storm additions of new genotypes to their populations is of interest from an evolutionary viewpoint even if the actual contribution of new genotypes to reconstitution of the pre-storm biomass is minimal. If recruitment by larvae is greater after major storms, genetic variation within populations would be predicted to be greater in areas with frequent hurricanes.

If the case for hurricanes causing the dearth of sponges in very shallow water in other Caribbean sites is equivocal, other factors that might differ between the San Blas and the other sites must be considered. Factors that have been invoked to explain sponge distribution and abundance patterns include UV-B light, predators, nutrients and turbulence. Some sponges have been demonstrated experimentally to be killed by exposure to UV light (Jokiel 1980). However, many of the sponge species that are most abundant in shallow water in San Blas (Wulff 1994) are the same as those reported from deeper water elsewhere in the Caribbean (e.g., Alcolado 1979, 1990; Alvarez et al. 1990; Schmahl 1990; Zea 1994), demonstrating that UV-B is not a factor inhibiting their proliferation in shallow water at the other sites. Although cryptic sponges may be restricted to their hidden habitats by fish predators (Wulff 1988), predation by fish is probably not an important factor in limiting distribution and abundance of exposed sponges in the Caribbean (Randall and Hartman 1968; Wulff 1994). Coral reef fish are more abundant in San Blas than in areas, such as Jamaica, where fish stocks have been severely depleted by fishing. Hawksbill turtles can consume large volumes of sponges, but they appear to specialize (95% of gut contents by volume) on members of the orders Choristida and Hadromerida (Meylan 1990) rather than the Haplosclerida, Poecilosclerida, and Keratosa that dominate shallow reef areas. The influence of nutrient levels on sponge abundance has recently been discussed by Zea (1994), who concluded that higher nutrient levels favor sponges, primarily when turbidity is sufficiently high to inhibit the algae that are also favored by high nutrient levels. On the Great Barrier Reef, Wilkinson and Evans (1989) found sponge abundance to be greater with higher nutrient levels, unless constrained by turbulence. In San Blas, steep topography and high precipitation during the rainy season cause seasonally high run-off. However, the influx of nutrients and sediment might be reduced, in comparison to other Caribbean sites, by largely intact mangrove forests and terrestrial forests. Turbulence was suggested to be an important cause of low sponge abundance in shallow water in all of the published accounts referred to above. In San Blas, the especially rich sponge communities are on the leeward sides of reefs, as expected if turbulence is an important constraint on distribution and abundance. Significant differences in the incidence of toppling between depths of 1–5 m and 5–9 m suggest an important effect of depth on protection from storm waves, even in ranges of a few meters. Likewise, the total loss of sponges on the south-facing side of Guigalatupo, compared to losses of 50% of sponges on the south-west facing side, at the same depth, suggests an important effect of slight differences in reef orientation relative to storm waves. In conclusion, of the environmental factors that have been demonstrated to influence coral reef sponge distribution and abundance, exposure to chronic turbulence and acute physical disturbances seem especially important in limiting sponge proliferation on shallow Caribbean reefs.

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