MUTUALISMS AMONG SPECIES OF CORAL REEF SPONGES

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Abstract. Intimate associations among individuals of three common species of Caribbean coral reef sponges can be mutually beneficial. Both growth rate and survival are enhanced when heterospecific sponges adhere to each other, as demonstrated by experiments in which sponges of the same size and genotype were grown (1) in intimate association with conspecific vs. heterospecific sponges, (2) alone vs. in intimate association with conspecific sponges, and (3) alone on the primary substratum vs. attached to an intact branch of a conspecific or heterospecific sponge. Natural development and long-term dynamics of these associations were observed in unmanipulated individuals and also modeled by an experiment in which branches were exchanged between neighboring sponges. The three species studied (*Iotrochota birotulata, Amphimedon rubens,* and *Aplysina fulva*) share an erect branching growth form but differ in tissue and skeletal characteristics sufficiently that they are in different orders of the Class Demospongiae. Reflecting these differences, the species are demonstrated to differ from each other in their susceptibility to a variety of environmental hazards, including predation by angelfishes and trunkfishes, predation by starfish, smothering by sediment, breakage by storm waves, pulverization by storm waves, toppling by storm waves, fragment mortality, and pathogens. Although the mechanisms by which growth rate is enhanced by adhering to a heterospecific sponge are unknown, these sponges appear to be able to decrease their loss rate by adhering tightly to sponges of species that differ from them in chemistry, tissue density, and skeletal construction, thereby increasing survival of hazards to which they would succumb when growing alone.

Key words: coral reefs; diffuse mutualism; direct mutualism; facultative mutualism; sponge extensibility; sponge strength.

Introduction

As study of mutualism has been taken more seriously in the last decade or so (e.g., May 1982, Boucher et al. 1984, Boucher 1985), patterns in occurrence of mutualism are being discovered. One of the most consistent patterns is that the great majority of documented mutualisms are between partners that are quite different from each other, frequently from different kingdoms (e.g., Hutchinson 1965, Wulff 1985b, Saffo 1992). Examples are photosynthetic protists endosymbiotic in cnidaria, insect pollinators of flowering plants, mychorrhizae of vascular plants, and protistan gut flora of mammals and arthropods. Because partners from different kingdoms may differ from each other in size, mobility, sensory equipment, and biochemical capability, they can make significant contributions to each other's needs without having to share the same resources. In contrast, when interacting organisms are very similar, competition for common resource needs can outweigh benefits offered by close association. Examples of similar species demonstrated or inferred to be interacting in a mutually beneficial fashion are cich-

lids, eagles, squirrels, flocks of foraging birds, and herds of grazing ungulates (e.g., Hutchinson 1965, McNaughton 1976, Dickman 1992 and references therein, Nakai 1993). Mobile organisms, such as these, can readily abandon the association whenever competitive effects outweigh mutualistic effects, but sessile organisms do not have this option. Thus, a reasonable prediction could be made that intimate associations between sessile organisms with similar resource requirements would be less likely to be mutually beneficial.

Associational resistance of sessile plants to predators or harsh physical conditions has been demonstrated for macroalgae (Hay 1986, Littler et al. 1986), fruiting vines (Atsatt and O'Dowd 1976), and salt marsh plants (Bertness and Shumway 1993, Bertness and Hacker 1994). However, it is notable that, in these plant–plant examples, the benefit from the association has not been demonstrated to be mutual, and, in the absence of predators or harsh physical conditions, these associations may not be beneficial to any of the participants (e.g., Bertness and Shumway 1993, Bertness and Hacker 1994).

In light of the foregoing, mutual benefit for all participants in intimate associations among sponges seems unlikely. Sponges are sessile filter feeders that are extremely efficient at removing organic particles, such as the bacterioplankton that serve as food for most species in the group, from water (e.g., Reiswig 1971). Intimate

association among sponges may therefore decrease access to resources for participating individuals. Nevertheless, statements regarding the possibility that intimate associations among sponge species are beneficial for all participants have been published before. Dense and diverse assemblages of sponges in caves and on cobbles in the Mediterranean and Adriatic were independently suggested to be of mutual benefit to participating sponges by Sarà (1970) and by Rützler (1970). By monitoring community dynamics, Sarà discovered no evidence for competitive elimination of one sponge species by another; and by using histological techniques to evaluate the health of overgrown sponges and to understand the relationships of sponges growing in intimate association, Rützler demonstrated that overgrown sponges were unharmed and also appeared to have adaptations allowing them to be overgrown. The positive nature of these associations might be mediated by a need for substratum space by the overgrowing species and a need for protection from predators and ultraviolet light for overgrown species.

In dense and diverse assemblages of Caribbean coral reef sponges, many individuals can be found to be intimately intertwined with each other in multi-species associations. Participating individuals adhere tightly to each other, and sometimes even appear to be overgrowing or smothering each other. However, these associations persist without either species being eliminated.

This is a study of intimate pairwise associations among three species of sponges that are among the most common sponges on shallow and mid-depth Caribbean coral reefs. They can frequently be seen growing with their branches adherent to sponges of other species. Often a sponge that has become disengaged from the substratum by failure of its basal attachment is still held upright and in place by its attachment to a neighboring sponge of another species, suggesting that environmental hazards that cause significant partial mortality to one sponge do not necessarily affect a neighboring sponge of a different species. If these species are differentially susceptible to various environmental hazards, adhering to a sponge of a different species could be an effective mechanism for prolonging the life of a genotype.

Are these associations of mutual benefit? These specific questions are asked. (1) Is growth enhanced when sponges grow in intimate association with each other? (2) Is mortality decreased when sponges grow in intimate association? (3) Are growth and mortality influenced differently when two associated sponges are of the same species vs. of different species? (4) What role does the tight adherence of associated sponges to each other play? i.e., is the close association the key to the interaction or is the actual adhesion important? (5) If a positive effect of intimate association is found, what physical and biological environmental factors mediate it? (6) Do sponges growing attached to the sub-

stratum benefit from becoming adherent to a neighboring sponge as much as sponges that are attached solely to that neighbor, and are held in its branches up off the solid or sedimentary carbonate substratum? (7) How do these associations develop naturally? (8) What is the incidence of these associations in natural populations, and under what circumstances are they found?

METHODS

Species and study site

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)] are among the most common sponges on shallow to mid-depth coral reefs in the Caribbean (e.g., Wulff 1994). All three species are of an erect, branching morphology, resembling trees, bushes, and vines, but they are sufficiently different in other ways that they are in different orders of Demospongiae: the Poecilosclerida, Haplosclerida, and Verongida, respectively. Individual sponges range from 1 to 150 cm in maximum dimension, and from <1 to at least 770 cm^3 in total tissue volume (Wulff 1991). Asexual propagation dominates the life histories and population structures and dynamics of these species; fragmentation, fusion, and partial mortality cause far more change in biomass within a defined area than do growth or mortality (Wulff 1990, 1991), in part because fragments can be dispersed some distance before reattaching to hard substrata. Because sponges are not composed of unambiguously defined repeating units, they are not referred to as colonies (Hartman and Reiswig 1973). Following Hartman and Reiswig, an "individual" is defined as the tissue bounded by an unbroken surface pinacoderm. A genetically defined individual, i.e., a "clone," is not easy to identify because of the possibility that the various physiologically independent individuals of the same genotype, derived from each other by fragmentation, have dispersed far from each other (Wulff 1986). Although fragmentation may enhance overall growth rate of a genotype due to size dependence of growth rate (Wulff 1990, 1991), and recruitment into these populations is almost entirely by successful reestablishment of fragments generated from individuals already in the populations, fragmentation is not without risk. Two independent measures of fragment survival suggest that ≈30% of fragments are alive and reattached a year after they are generated (Wulff 1985a, 1991).

The site at which interactions among these sponges were studied is a shallow reef to the leeward of Guigalatupo, an island near the San Blas Field Station of the Smithsonian Tropical Research Institute in Panamá (map in Robertson 1987). The substratum consists of homogeneously distributed rubble from ramose coral species, dotted with small to medium-sized coral heads.

Sponges are by far the most abundant sessile organisms on this reef, and are densely and homogeneously distributed over the study area. The fauna is characteristic of lagoon channels, shallow back-reef areas, steep slopes within bays, and mid-depth fore-reef habitats, throughout the San Blas Islands and elsewhere in the Caribbean (Bonem and Stanley 1977, Alcolado 1979, 1990, Alvarez et al. 1990, Diaz et al. 1990, Schmahl 1990, J. Wulff, personal observation in Jamaica, Belize, the Bahamas, and Panamá), with the one difference that sponge communities are denser and more diverse in quite shallow water in San Blas than in other sites described in the literature (Wulff 1994, 1995a). A complete census of 16 m² yielded 1395 nonexcavating sponges in 42 species, representing all colors, sizes, and morphologies of sponges (Wulff 1991, 1994). The three species studied here are the most abundant, with respect to both biomass and numbers of individuals, and constitute 57.5% of the total volume of sponges.

Experimental investigation of intimate associations among sponges

Four different experiments were designed to test if growth and survival of sponges are influenced by intimate association with other sponges of the same or different species. For all experiments, stainless steel razor blades were used to cut sponge branches to the same length, generally 8 cm. Using small nylon cable ties, these experimental sponges were attached either to intact branches of other sponges or to stakes that were stuck into the reef. The stakes were made of 1.29 mm (16-gauge) stainless steel (Number 304, a seawater-resistant alloy) wire, covered with biologically inert Tygon tubing, and bent at one end to grip a piece of dead, clean coral rubble. Once a sponge was attached to the stake, the stake was pushed into the reef until the coral rubble rested on the substratum. The sponges adhered to the coral rubble within a few days. Thus these sponges were grown on stable natural carbonate substrata, in normal upright growth position. The experimental sponges were arranged in a grid pattern to facilitate finding them for subsequent monitoring. Genotype was controlled in some experiments, and initial size was controlled in all experiments. The supply of sponges large enough to provide several 8 cm branches of the same genotype placed a limit on the number of replicates of each experiment and also on the number of parameters that could be tested simultaneously. The total number of experimental sponge individuals was 666 (Table 1).

Detailed drawings of all experimental sponges were made in time series, at intervals ranging from 1 mo to 2 yr, and for total times ranging from 9 to 51 mo. The variation in time intervals was due to imperfect control over timing of field work and also to an initial ignorance about the appropriate time scale on which significant changes would occur. Length, diameter, and orientation of all branch segments were recorded on

TABLE 1. Number of individual sponges of *Iotrochota birotulata* (Ib), *Amphimedon compressa*, and *Aplysina fulva* (Af) manipulated in the four experiments designed to test whether growth and survival of sponges is enhanced by intimate association with other sponges of the same or different species, on stakes or on intact branches.

Growth treatment	Number of individuals		
	Ib	Ar	Af
Experiment 1			
With Ib (on stake)	14	14	14
With Ar (on stake)	14	14	14
With Af (on stake)	14	14	14
Experiment 2			
Alone (on stake)	16	16	16
With Ib (on stake)		16	16
With Ar (on stake)	16		16
With Af (on stake)	16	16	
Experiment 3			
Alone (on stake)	18	18	18
With Ib (on branch)	18	18	18
Alone (on stake)	18	18	18
With Ar (on branch)	18	18	18
Alone (on stake)	18	18	18
With Af (on branch)	18	18	18
Experiment 4			
With Ib (on branch)	8	8	8
With Ar (on branch)	8	8	8
With Af (on branch)	8	8	8

Note: Size was controlled in all experiments, and genotype was also controlled for all comparisons in Experiments 2 and 3.

detailed drawings. The anastomosing three-dimensional forms generated by these sponges as they grow are too complex to be adequately captured using photography. Detailed drawings allow the three-dimensional forms to be rendered into two dimensions with all the parts in correct scale and position relative to each other, and all branching points brought into view. The time-consuming drawing limited the frequency with which each experiment could be monitored, but growth rates of these sponges turned out to be sufficiently slow that this was not a problem.

Experiment 1.—Experiment 1 compared growth and loss of sponges grown in intra-specific pairs vs. interspecific pairs (Fig. 1). All sponges were grown on stakes and were cut to 8 cm in length for the start of the experiment. For each of the 3 species, 14 individuals were grown in conspecific pairs and 14 individuals were grown paired with individuals of each of the other two species (Table 1). The pairs were established in January 1982 and monitored after 3, 5, 12 and 25 mo.

Experiment 2.—Experiment 2 compared growth and loss of sponges grown singly vs. paired with an individual of each of the other two species (Fig. 1). In this experiment, sponges were initially 8 cm long, and all pieces of sponge for each three-way comparison were of the same genotype, taken from the same sponge. Thus paired comparisons of growth and survival could be made between a sponge grown alone vs. a sponge of the same genotype paired with a sponge of a different
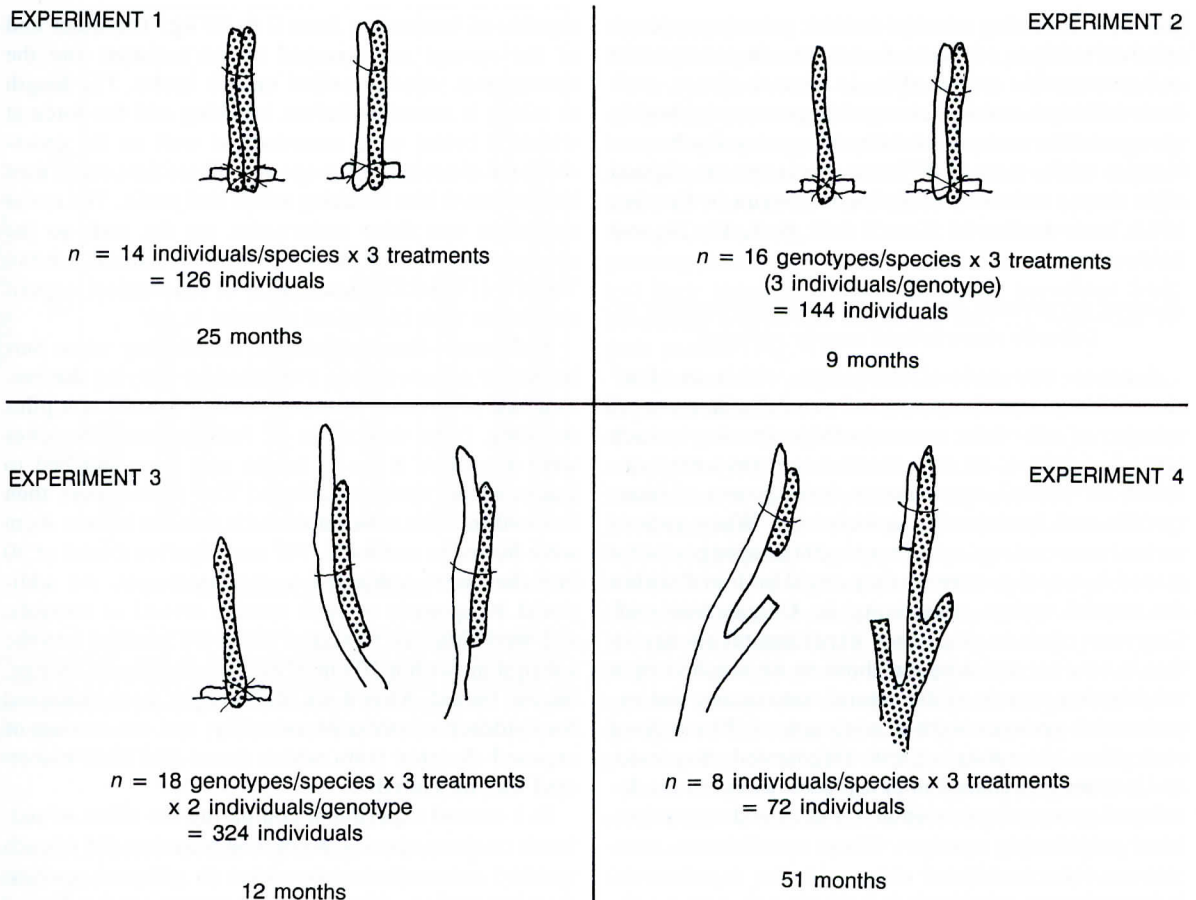
FIG. 1. Experimental design for four experiments based on the following hypotheses: *Experiment 1*: Null hypothesis = Growth and loss of sponges will not differ if they are grown in intimate association with a sponge of the same species vs. with a sponge of a different species (on stakes). *Experiment 2*: Null hypothesis a = Growth and loss of sponges will not differ if they are grown alone vs. in intimate association with a sponge of another species (on stakes). Null hypothesis b = Growth and loss of sponges will not differ if they are grown in intimate association with a sponge of one different species vs. with a sponge of another different species (on stakes). *Experiment 3*: Null hypothesis a = Growth and loss of sponges will not differ if they grow alone on the substratum vs. attached to an intact branch of a sponge of the same species. Null hypothesis b = Growth and loss of sponges will not differ if they grow alone on the substratum vs. attached to an intact branch of a sponge of a different species. *Experiment 4*: Long-term dynamics of adherence, growth, and survival of sponges attached only to intact branches of other sponges. Null hypothesis a = Growth and survival of a branch of a sponge will not differ if the branch is severed and attached to an intact branch of a neighboring sponge vs. if it remains attached to, and physiologically confluent with, its parent sponge. Null hypothesis b = Survival of severed sponge branches attached to the intact branches of neighboring sponges will not differ if the guest and host sponges are of the same species vs. if they are of different species.

species, and also between a sponge paired with a sponge of one of the other two species vs. a sponge of the same genotype paired with a sponge of the third species. For each of the three species, 16 different genotypes were tested (Table 1). The experiment was begun in June 1983, and was monitored at 8 mo, and again at 9 mo after inception.

Experiment 3.—Experiment 3 compared growth and loss of sponges grown alone on a stake vs. attached to a branch of a sponge of each of the other two species, or to a branch of a sponge of the same species (Fig. 1). Initial size of all sponges was 8 cm in length. Genotype was controlled in this experiment, so that paired

comparisons are possible between each sponge grown alone and a sponge of the same size and genotype grown on a branch of another sponge, either conspecific or heterospecific. For each combination of each species, 18 different genotypes were tested (Table 1). Experiment 3 was begun in February–March 1983, and was monitored at 11 mo, and again at 12 mo, after inception.

Experiment 4.—Experiment 4 was designed to model the natural development and long-term dynamics of these associations, beginning with adherence of branches of adjacent sponges to each other; and also to compare adherence, growth, and survival of sponge

branches remaining attached to their parent sponge vs. attached solely to a branch of a neighboring conspecific or heterospecific sponge (Fig. 1). Branch pieces, each 4 cm in length, were exchanged between neighboring sponges of the same or of different species. Each combination of the same or different species was replicated eight times, and these experiments, begun in October 1981, were monitored after 1, 2, 3, 6, 8, 17, 28, and 51 mo.

Natural occurrence and spontaneous development of intimate associations among sponges

A census was made of all sponges within an 11 m² area to document frequency of natural adherence of sponges of all of the common large species to each other. In addition, all experimental sponges were monitored for natural, spontaneous development of interspecific and intraspecific associations. When experiments were set up, all experimental sponges were placed in a grid pattern so they could be found within the natural sponge community on Guigalatupo reef. Care was taken to place each experimental sponge so that it was not touching or about to be touched by a neighboring sponge of the natural community, and experimental sponges were a minimum of 30 cm from each other. As sponges grew, fragmented, dispersed, and became established in new places, associations developed among experimental sponges and unmanipulated neighboring sponges. These spontaneous associations were monitored along with the experiments. Information recorded included: whether sponges touching each other were adherent to each other, and if the basal attachment to the substratum of either sponge had failed, leaving that sponge attached only to the intimately associated neighboring sponge.

Evaluation of resistance to environmental hazards

Relative resistance of these three sponge species to predators, sediment, physical disturbance, and disease was tested using a variety of experimental and observational protocols, detailed in the following sections. Where possible, estimates were also made of the probabilities that sponges in these populations would encounter these hazards.

Violent water motion and other physical disturbances: biomechanical experiments.—Biomechanical properties relevant to breakage by storm waves and by foraging eagle rays were measured by stretching branches until they broke, and measuring the force exerted at failure. Twenty-five branches of 8 cm in length were cut from each species of sponge, taking care to sample branches of a range of widths from each species. Small nylon cable ties were fashioned into a harness into which a spring scale could be hooked, and one end of a sponge branch was wrapped in knitted cotton material to prevent the harness from digging into the sponge tissue. The sponge was then aligned along a plastic ruler with the harness hooked onto a spring scale

capable of measuring from 0 to 20 kg. The other end of the sponge was grasped by an assistant and the sponge was steadily pulled until it broke. The length to which it stretched before breaking and the force at which it broke were recorded, as well as the cross-sectional diameter of the sponge. These data could then be converted into breaking stress and strain. The entire operation was done underwater, on the reef, so the sponges were never moved from their natural habitat. Vogel's (1988:183) description of mechanical experimentation with biological material is apt.

Sediment.—Susceptibility to smothering when buried under sediment was evaluated by burying the bottom half of severed sponge branches in sediment piles resulting from defecation of holothurians. Branches were a total of 8 cm in length and were attached to stakes in an upright position. The stakes were then inserted into the substratum such that the bottom 4 cm were buried in sediment. For each species a total of 30 branches were subjected to this treatment. An additional 30 sponges of each species served as controls, and were attached to stakes that were inserted into the substratum within 10 cm of each experimental sponge, but not buried. After 4 wk, the sponges were examined for evidence of stress or mortality; and the amount of exposed skeleton from which tissue had been macerated was measured.

In a second experiment comparing the effect of sediment on these species, 8 cm long branches (16 of each species) were attached to stakes in a repent position (i.e., long axis parallel to the substratum) and sediment was mounded on the center 4 cm to a depth of approximately 2.5 cm. These sponges were monitored for 6 wk, and the sediment mounds were replenished throughout that time as needed.

The proportion of the study area covered by sediment mounds (i.e., the probability that a sponge would be affected by sediment), was estimated by counting and measuring all sediment mounds within a 20 × 20 m square in the center of the sponge community. These counts were made on 5 days, so the average proportion of the area covered by sediment each day could be estimated.

Disease.—Whenever a sponge appeared to be infected by a pathogen, the progress of the infection was recorded. When diseased sponges were observed to be adherent to other sponge individuals, a record was made of the species involved and whether only one sponge individual or both were infected. These data were used to determine if infection can be transmitted by physical contact between sponges of different species as well as by contact between sponges of the same species.

RESULTS

Growth and loss of experimental sponges

Experiment 1.—Growth was significantly greater for sponges growing in intimate association with sponges
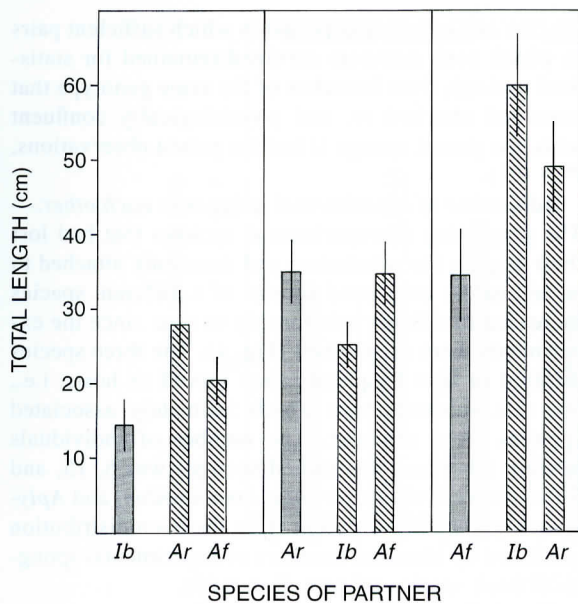
FIG. 2. Total branch length achieved by sponges grown in conspecific and in heterospecific pairs for 25 mo; Experiment 1. Cross-hatched bars represent growth of sponges in heterospecific pairs. *Ib = Iotrochota birotulata, Ar = Amphimedon rubens, Af = Aplysina fulva.* Vertical lines on bars are ±1 standard error.

of other species vs. those growing with sponges of the same species (Fig. 2) for *Iotrochota birotulata* (ANOVA, $P < 0.05$) and for *Aplysina fulva* (ANOVA, $P < 0.05$), but there was no difference for *Amphimedon rubens* (ANOVA, $P > 0.1$).

Loss from stakes was significantly greater for sponges growing in intra-specific combinations than for sponges in inter-specific combinations at the end of the experiment, after 25 mo (*G* test, $P < 0.01$, Fig. 3), and the percentage loss increased linearly with time between 5 and 24 mo (Fig. 3). Of those sponges still remaining on stakes after 12 mo, 10.1% (8 of 79) of those paired in intimate association with sponges of a different species had lost their own attachment and were prevented from becoming loose fragments only by being adherent to their intimate associates (Fig. 4). None of the sponges paired with other individuals of the same species were prevented from being lost in this way. After 25 mo, 25.7% (18 of 70) of the sponges paired with different species were prevented from becoming loose fragments only by being adherent to their intimate associates, whereas only 3.3% (1 of 30) of sponges paired with conspecific sponges were prevented from being lost in this way (*G* test, $P < 0.001$; Fig. 4).

Experiment 2.—Sponges grown in intimate association with a sponge of another species consistently grew more than individuals of the same genotype that were grown alone (Fig. 5), but these experiments could only be monitored for 9 mo, and the effect was only

significant for *Iotrochota* (repeated measures ANOVA, $P < 0.025$; for each of the other two species, $P > 0.1$).

For sponges of the same genotype, loss from stakes of sponges growing alone was significantly higher than loss of sponges growing in intimate association with sponges of different species at the end of the experiment, at 9 mo (6.25 vs. 2.08%; *G* test, $P = 0.05$). Of sponges remaining after 9 mo, 7.45% (7 of 94) of those growing paired with a sponge of a different species had lost their basal attachment and were prevented from becoming unattached fragments only by adherence to their partner (Fig. 4).

Experiment 3.—For each of the three species, sponges grown attached to a branch of a sponge of a different species grew significantly more than sponges of the same genotype grown alone, attached to stakes on the substratum (*t* test for paired comparisons, $P < 0.025$ for *Iotrochota*, $P < 0.05$ for *Amphimedon,* and $P < 0.05$ for *Aplysina*; Fig. 6). Sponges grown attached to a branch of a sponge of a different species generally elaborated more branches than those on stakes, and growth was dramatically greater for many genotypes (Fig. 7). Sponges grown attached to a branch of a conspecific sponge did not grow significantly more than sponges of the same genotype grown alone (*t* test for paired comparisons, $P > 0.1$ for each species; Fig. 6).

Loss of sponges of the same genotype grown alone on a stake vs. attached to a branch of a sponge of the same or a different species was not significantly different after 1 yr (*G* test, $P > 0.1$ for each species). It should be noted that, in this experiment, loss of a sponge that was growing attached to a branch of an-
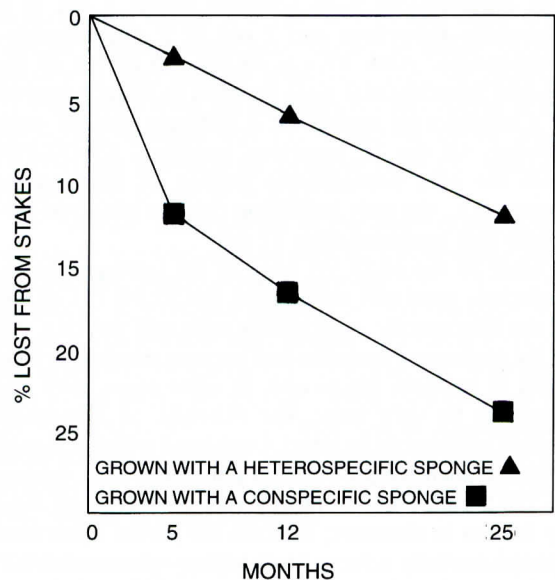

FIG. 3. Percentage loss from their stakes of experimental sponge individuals grown in intimate associations with a sponge of the same species or with a sponge of a different species in Experiment 1.
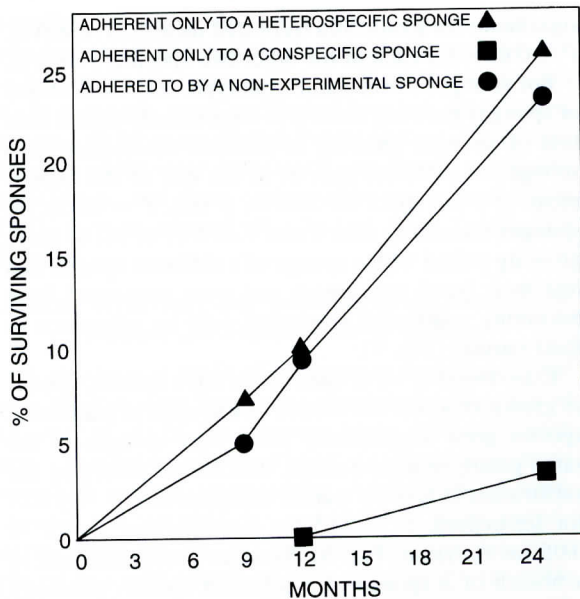
FIG. 4. Percentage of surviving sponges that had lost their attachment to carbonate substrata and become adherent only to a heterospecific sponge (▲), or only to a conspecific sponge (■); and percentage of surviving sponges that had become adhered to spontaneously by a nonexperimental sponge (●). Data are from Experiments 1 and 2.

other sponge could have resulted from loss of either or both the host branch and the guest sponge.

Experiment 4.—When these experiments were first monitored, after 1 mo, already all of the severed branches were adherent to intact host branches in the cases of inter-specific combinations, and all intra-specific combinations were adherent except 1 out of 8 *Iotrochota*–*Iotrochota* and 2 out of 8 *Amphimedon*–*Amphimedon*. After 17 mo, 48.6% (35 of 72) of the severed branches that were attached to intact branches of a neighboring sponge of a different species were thriving. Of the 35 surviving branches, 13 (37.1%) were the only recognizable portion of their parent sponge (i.e., the only indication that the genotype survived) that remained after 17 mo.

After 51 mo (4.25 yr) none of the intraspecific associations were still maintained, but 22.9% (11 of 48) of the interspecific associations were still thriving. All of the exchanged branches had become attached to their hosts in multiple places and, in some cases, they had grown to be very large. For example, an *Iotrochota* branch adherent to an intact *Amphimedon* had achieved a total branch length of 141.5 cm, and a total volume of 250.5 cm², from a starting size of only 4 cm long by 1.5 cm in diameter; whereas the parent *Iotrochota* sponge, initially a large bush with a volume of >600 cm³, was reduced to a small fragment of 30 cm in length and 19.2 cm³ in volume.

Growth of the severed branches adherent to neighboring sponges was not significantly different, after 17

mo (the last monitoring period in which sufficient pairs in which both members survived remained for statistical testing), from branches of the same genotype that remained attached to, and physiologically confluent with, the parent sponge (*t* test for paired observations, $P > 0.1$).

Adherence of experimental sponges to each other.— The proportion of experimental sponges that had lost their grip on the substratum and were only attached to an intimately associated sponge of a different species increased in a linear relationship to time since the experiments were established (Fig. 4). The three species differed in how frequently they served as hosts, i.e., the sole substratum to which intimately associated sponges were adherent. The number of individuals hosting otherwise unattached sponges was 6, 15, and 5 for, respectively *Iotrochota*, *Amphimedon*, and *Aplysina*; significantly different from the even distribution predicted by identical numbers of experimental sponges of each species (*G* test, $P < 0.05$).

The ability to become mutually adherent was greater among heterospecific pairs of sponges than among conspecific pairs. In experiments in which all sponges were initially attached to a stake, as well as to another sponge, significantly more sponges became adherent to intimately associated individuals of different species than of the same species for both *Iotrochota* and *Amphimedon* (*G* test, $P < 0.001$ for both species). In experiments in which sponges were attached by cable ties to branches of other sponges, this pattern of a significantly greater rate of adherence between intimately associated sponges of different species than of the same species was also seen (85 of 86 vs. 33 of 36, after 1 yr; *G* test, $P < 0.01$). In addition, a significantly greater proportion of sponges became adherent to intimately
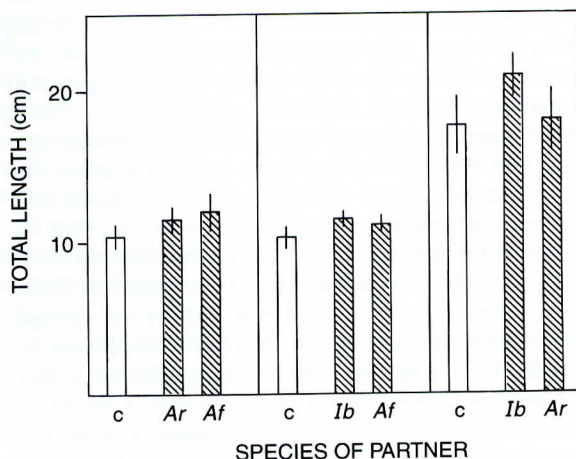

FIG. 5. Total branch length achieved in 9 mo by sponges grown alone on the substratum (C) vs. in intimate association with a sponge of a different species; Experiment 2. All sponges were 8 cm long at the start of the experiment, and control and experimental sponges were of the same genotype. *Ib* = *Iotrochota birotulata*, *Ar* = *Amphimedon rubens*, *Af* = *Aplysina fulva*. Vertical lines on bars are ± 1 standard error.
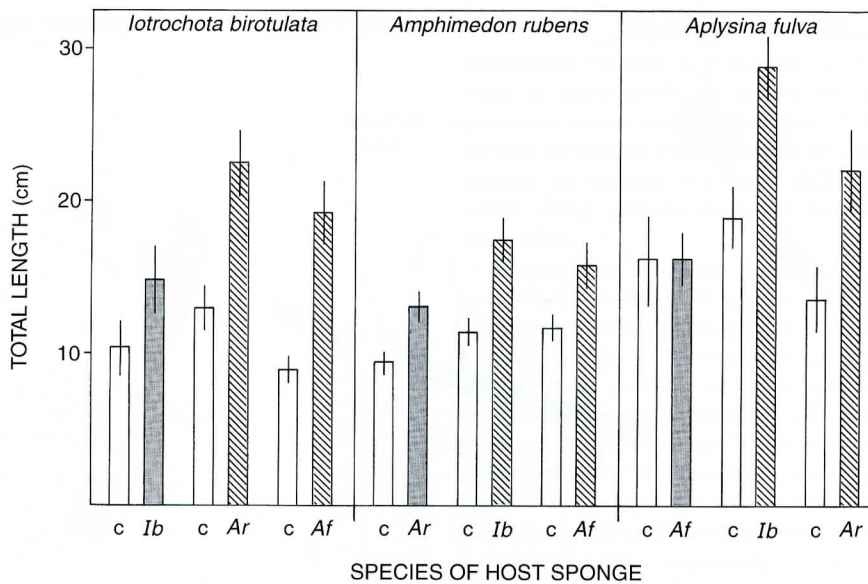
FIG. 6. Total branch length achieved in 12 mo by sponges grown alone on the substratum (C) vs. attached to an intact branch of a sponge of the same or a different species; Experiment 3. All sponges were 8 cm long at the start of the experiment and control and experimental sponges were of the same genotype. *Ib* = *Iotrochota birotulata, Ar* = *Amphimedon rubens, Af* = *Aplysina fulva.* Vertical lines on bars are ±1 standard error.

associated sponges when those sponges were the only substratum offered vs. when a stake was also available for attachment (118 of 122 vs. 74 of 94; *G* test, P < 0.001). Many sponges became attached to each other in more than one place, and this was also more likely when the intimately associated sponges were of different species, with 60.5% of sponges in heterospecific pairs adhering to each other in multiple places, but only 22.2% of sponges in conspecific pairs developing multiple attachment points (significantly different by *G* test, *P* < 0.05). Once sponges had adhered to each other, the attachments almost always remained stable over time. For example, for nearly 2 yr in Experiment 1 there were no significant differences in the proportion of intimately associated sponges that were adherent to each other (94 of 119 after 3 mo vs. 74 of 94 after 25 mo; *G* test, *P* > 0.9).

Natural occurrence and spontaneous development of intimate associations among sponges

Of the 472 large (i.e., 10 cm in at least one dimension) sponge individuals representing 13 species in the 11 m² censused, 61% were adherent to at least one other sponge of a different species, and 56% of these were participating in associations of 3 or more individuals. Multi-species mutually adherent associations of up to 12 individuals were found.

During the course of the experiments, many sponges in the surrounding community adhered to experimental sponges. After 25 mo, 23.3% of the experimental sponges (49 of 210) had been adhered to by neighboring unmanipulated sponges. Spontaneous develop-

ment of these intimate associations occurred in a linear relationship to time since the experimental sponges were put in place (Fig. 4). In the surrounding community, representation of *Iotrochota birotulata, Amphimedon rubens,* and *Aplysina fulva* relative to each other was in the ratio 1.6:1.0:2.7 by total volume (Wulff 1994). When this abundance ratio is used to predict the frequencies with which these species would adhere to experimental sponges, it can be seen that these three species initiated these associations as guests in proportion to their relative abundance (i.e., the numbers of individuals from the community that adhered to experimental sponges was 17, 5, and 30 for the three species, not significantly different from the predicted frequencies, *G* test, *P* > 0.1).

In contrast, participation of the three experimental species as hosts in intimate associations spontaneously initiated by unmanipulated sponges was not in proportion to their relative abundances. Experimental *Amphimedon* individuals were disproportionately more often adhered to by sponges in the community (the numbers of the three species that served as hosts were 13, 28, and 15; *G* test, *P* < 0.01), just as *Amphimedon* disproportionately more often served as host for experimentally associated sponges that had lost all other attachments to solid substrata.

Evaluation of sponge resistance to environmental hazards

Violent water motion: biomechanical experiments.—Breaking stress (strength) and breaking strain (extensibility) are plotted for each of the 25 individuals of each

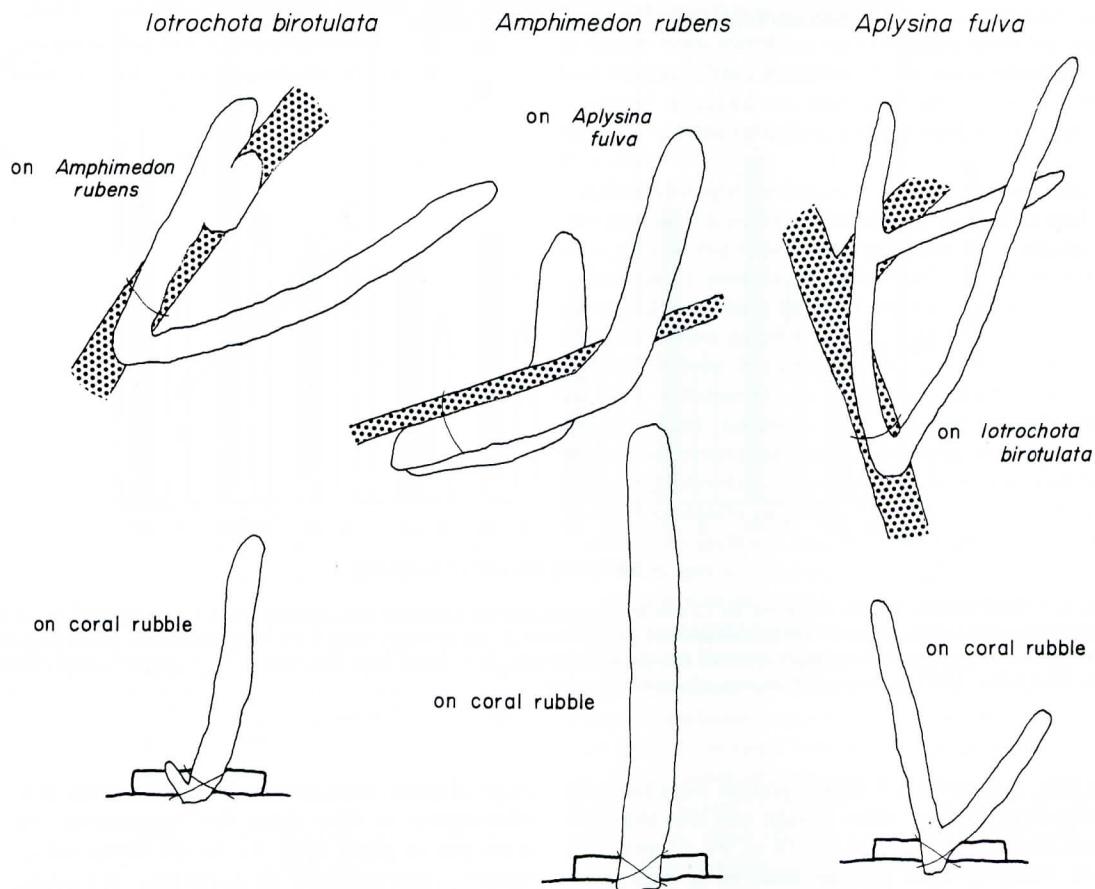*Iotrochota birotulata*   *Amphimedon rubens*   *Aplysina fulva*

FIG. 7. Drawings, to scale, of representative sponges growing on the substratum, attached to coral rubble, vs. growing attached to intact branches of sponges of different species (Experiment 3). Sponges pictured are of the same genotype and were the same size at the start of the experiment, 12 mo earlier.

species that were tested in Fig. 8. Strength did not differ significantly among these species. However, although the means are very similar, the variation is considerable, and a disproportionate number of the individuals with higher breaking stress were of *Aplysina fulva*. Extensibility, however, did differ significantly among these species, with *Aplysina* being more extensible than *Amphimedon*, which, in turn, was more extensible than *Iotrochota*.

Sediment.—*Amphimedon* was significantly less affected by burial under sediment than the other two species. Four weeks after burial, only 16% of the *Amphimedon* biomass had died as a result of burial, compared with 40% of *Iotrochota* biomass and 47% of *Aplysina* biomass. By the results of the experiments using repent fragments, the sponges were ranked the same with respect to susceptibility to sediment. The percentage of sponges with significant (i.e., > 25% of the diameter) necrosis or maceration for *Amphimedon* was only 25% after 6 wk, compared with 44 and 56% for, respectively, *Iotrochota* and *Aplysina* (proportions for *Amphimedon* and *Aplysina* are significantly different by the *G* test, $P < 0.01$).

A total of 218 sediment mounds from holothurian activity were measured during searches of the 20×20 m area on five days. The average area of a mound was 5859.8 cm², and so 6.4% of the area would be affected by a sediment mound at any time. If the mounds are randomly distributed, a given location would therefore be buried under sediment once every 15.6 d.

Pathogens.—Pathogens were not identified, but in all cases were evident by necrotic patches on the sponges, which could be seen to expand from day to day. After a few days, necrotic tissue could no longer be seen, but the skeleton was bared. This stage gave way to colonization by diatoms and filamentous microalgae, and finally the spongin would lose its integrity and the diseased portions would vanish. In none (0 of 140 = 0%) of the cases in which an infected sponge was adherent to another sponge of a different species was the other sponge infected. By contrast, in 83.3% (10 of 12) of the cases in which an infected sponge was adherent to a sponge of the same species, both individuals were infected at the point of adherence.
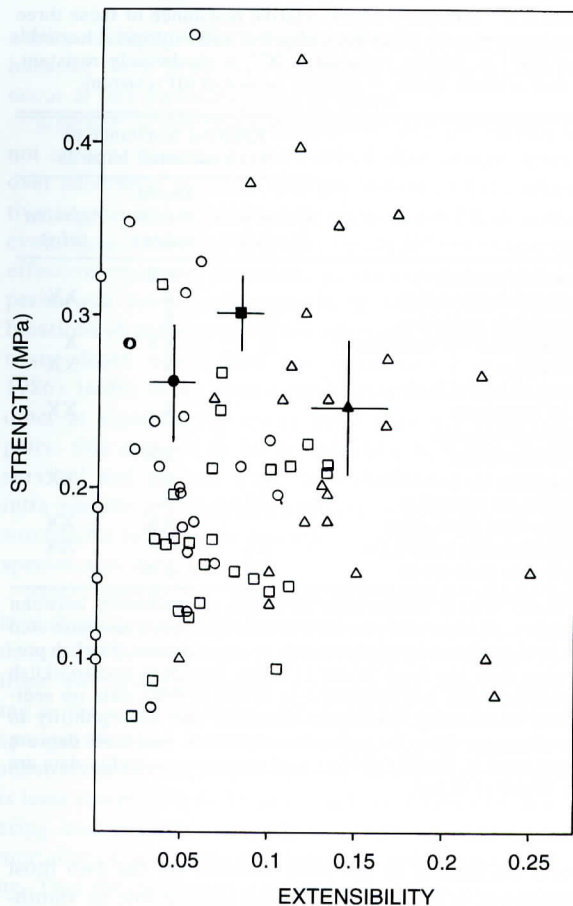
FIG. 8. Breaking stress (strength) and breaking strain (extensibility; a unitless ratio of lengths) of 25 individuals of each of the three sponge species. Solid symbols represent the means, and the vertical and horizontal lines represent 95% confidence intervals around the means.

DISCUSSION

Enhanced growth and survival of sponges in intimate association with sponges of other species

Intimate associations between sponges of different species increase growth rates and decrease loss rates for participating sponges. Growth was significantly greater for sponges growing in heterospecific than in conspecific pairs on stakes, and was also significantly greater for sponges growing attached to an intact branch of a sponge of a different species than alone on a stake. This positive effect on growth of intimate association with a sponge of a different species is mysterious, and no clear explanation can be advanced at this time. It is possible that a sponge growing above the substratum, in the branches of another sponge, would be in a significantly more favorable environment with respect to water flow, and therefore able to feed more. However, growth was not enhanced for sponges attached above the substratum to intact branches of

conspecifics, and growth was also enhanced by intimate association (though significantly so for only one species) in experiments in which all individuals were grown on stakes on the substratum. Whatever the basis for this surprising effect, it must be substantial to compensate for the loss of surface area available for water intake where participating individuals are adherent to each other.

Decreases in loss rates of sponges growing adherent to sponges of different species were even more consistent than increases in growth rates. Losses were significantly lower for sponges in heterospecific vs. conspecific pairs growing on stakes, and also significantly lower for sponges in heterospecific pairs on stakes vs. growing alone. Although losses of sponges adherent to intact branches of different species were not different from losses of sponges alone on stakes, rate of loss of the former sponges includes both loss of the host as well as loss of the experimental sponges. Cases in Experiment 4 in which the only remaining portions of what had been a large sponge were those that had become adherent to branches of a neighboring sponge of a different species directly illustrate the potential for enhancing genotype survival by adhering to a neighbor. Although "loss," as evaluated here, is not entirely equivalent to mortality, two independent measures of fragment survival for these species indicate that only $\approx$ 30% of the fragments survive for a year after they are generated (Wulff 1985a, 1991), and so in a sense "loss" is equivalent to a 70% chance of mortality. In that context, although population dynamics and individual life histories of these sponge species are dominated by their capacity to generate fragments that can disperse, reattach, and continue to grow and repeat the cycle, there is a definite selective advantage to engaging in behaviors that lessen the chance that a genotype will be entirely lost in the course of fragmentation. If the three species of sponges are differentially susceptible to various physical and biological hazards, and these hazards occur independently of each other in space and time, individuals of these three species may enhance their genotype survival by adhering to a neighboring sponge of a species that will not be affected by the same hazards.

Differential susceptibility of the sponge species to environmental hazards

Clear differences in susceptibility of these sponge species to smothering by sediment and to breakage by physical disturbances were demonstrated by the experiments described here: *Amphimedon rubens* is significantly less affected by sediment, which can smother basal portions, and *Aplysina fulva* is more extensible, rendering it less susceptible to breakage by periodic short-term disturbances such as by waves or by foraging activities of eagle rays. The only conclusion about pathogens that can be made from the few data at hand is that they seem to be species-specific; they

can be transmitted between adherent conspecific individuals, but not between adherent heterospecific individuals. Susceptibility to other hazards has been documented in previously published studies, as summarized below.

Susceptibility of these three species to physical damage was evaluated by the effects of a hurricane (Wulff 1995a). Significantly more individuals of *Iotrochota* were lost than of *Amphimedon*, which lost significantly more individuals than *Aplysina* (57.6% vs. 42.9% vs. 31.6%). This ranking of loss rates coincides with the relative extensibility reported on here, and also with the rates of fragmentation and partial mortality of 140 unmanipulated individuals that were monitored over a 9-mo period (62, 43, and 32%; Wulff 1990). Biomass losses due to Hurricane Joan reflected a combination of susceptibility to fragmentation and ability to reattach rapidly to solid substrata, resulting in *Amphimedon* being significantly more resistant (Wulff 1995a). Toppling of sponges, i.e., basal failure causing an entire sponge to assume a repent rather than upright position, was resisted significantly more by *Aplysina* (Wulff 1995a).

The only large predators on these sponges are a few species of highly specialized fishes and the large starfish *Oreaster reticulatus* (Randall and Hartman 1968, Scheibling 1979, Wulff 1994, 1995b). Of the 615 bites observed to be taken on these three species by the angelfishes *Pomacanthus arcuatus* and *P. paru* on Guigalatupo reef during a 12-yr period, 69.3, 11.7, and 19.0% were taken on *Iotrochota, Amphimedon,* and *Aplysina*, respectively. These data contrast with the percentages of the combined volume of these three species represented by *Iotrochota, Amphimedon,* and *Aplysina,* which are 30.9, 18.7, and 50.4%, respectively. The data demonstrate preference for *Iotrochota,* but relative rejection of *Aplysina.* By contrast, the trunkfishes *Acanthostracion quadricornis* and *A. polygonius* fed on *Aplysina* disproportionately heavily, with 85.4% of the 2374 bites observed taken on this species, although *Aplysina* constituted only 29% of the total volume of all 42 species of sponges in the study area (Wulff 1994).

The starfish, *Oreaster reticulatus,* which was often common in the seagrass meadows at Guigalatupo, everts its stomach onto repent and basal portions of a sponge, and digests the tissue, causing the naked skeleton to degenerate and the entire sponge to become disengaged from the substratum. When individually caged starfish were offered pieces of these sponges in the field for a total of 101 trials, *Iotrochota* was eaten in 38 of 39 trials and *Aplysina* was eaten in 34 of 38 trials, but *Amphimedon* was rejected in all 24 trials (Wulff 1995b).

A summary of the differential resistance of the three sponge species to the environmental hazards studied is presented in Table 2. By this summary, *Iotrochota birotulata* appears to be poorly adapted for success on the

TABLE 2.   Summary of the relative resistance of these three sponge species to various physical and biological hazards. "XX" = highly resistant, "X" = moderately resistant, and a blank space = slightly or not at all resistant.

	Relative resistance to environmental hazards		
	Iotrochota birotulata	*Amphimedon rubens*	*Aplysina fulva*
Starfish predation		XX	
Angelfish predation		X	XX
Trunkfish predation	X	X	
Smothering by sediment	X	XX	X
Breakage		X	XX
Loss of individuals in hurricane		X	XX
Loss of biomass in hurricane		XX	
Toppling by hurricane	X	X	XX
Fragment mortality	XX	X	
Iotrochota pathogens		XX	XX
Amphimedon pathogens	XX		XX
Aplysina pathogens	XX	XX	

Note: Where differences in levels of resistance between species are indicated, the differences have been demonstrated to be significant by observations or experiments. Starfish predation data are from Wulff (1995b), angelfish and trunkfish predation data are published in Wulff (1994), data on sediment smothering, pathogen infection, and susceptibility to breakage are from the present contribution, hurricane data are published in Wulff (1995a), and fragment mortality data are in Wulff (1985a).

reef, because it is not only favored by the two most important predators, but is also susceptible to smothering by sediment and is most easily broken. However, *Iotrochota* also differs from the other species in that fragments are able to reattach rapidly to solid carbonate substrata (Wulff 1985a), allowing *Iotrochota* to recoup many of the potential losses due to fragmentation.

Differences among the three species in skeletal materials, tissue density, and secondary chemistry underlie the differential resistance they muster against environmental hazards such as predators, physical disturbance, and sediment. Pathogens are a somewhat different kind of hazard, in that it is not clear that any particular characteristics would make one sponge species less susceptible to infection by pathogens in general. However, it does appear that these pathogens are species-specific, and that the three sponge species may differ most in their susceptibility to these hazards.

Evolution of mutualism among sponges

A selective advantage could be expected for a sponge that is capable of adhering to a neighboring sponge that is not susceptible to the same set of environmental hazards. As long as the different hazards do not occur simultaneously, this behavior could prevent at least some portion of the genotype from being exposed to the additional hazards that cause 70% mortality of errant fragments. The benefit of adhering is mutual, because even though each sponge has a significant prob-

ability of being affected at some time by any of the hazards, there is no way to predict which hazard will occur at any particular time or place.

Whether or not these mutualisms are coevolved is not certain. Patterns in the control that sponges exert over adherence by other sponges appear to have adaptive aspects that would not be predicted without some evolutionary shaping. Sponges are capable of mounting effective rejection reactions, as demonstrated by experimental intra-specific grafts, in which some combinations of genotypes are not adherent, and even cause tissue death where they are in contact (e.g., Wulff 1986). In this study, intra-specific pairs adhered to each other at significantly lower rates than heterospecific pairs; this appears to be an adaptive behavior, since survival and growth were not enhanced by intimate intra-specific associations, and conspecific sponges are susceptible to the same hazards, including infection by species-specific pathogens.

More specifically, *Amphimedon rubens* served as host disproportionately frequently, relative to its abundance, for both spontaneous development of associations with nonexperimental sponges and also for serving as the sole attachment substratum for experimental sponges that had lost their own grip on the carbonate substrata provided. *Amphimedon* is also the species that is least susceptible to hazards, such as sediment smothering and *Oreaster reticulatus* predation, that cause mortality of basal portions, a pattern with adaptive value. That the demonstrated resistance to these hazards actually affects patterns of partial mortality in *Amphimedon rubens* is corroborated by an analysis of partial mortality and morphology demonstrating that, although a greater proportion of total branch length in this species is in repent or basal portions (vs. in erect portions) relative to the other two species (24.2% vs. 16.0 and 13.5%), a relatively smaller proportion of partial mortality occurred in these portions (45.3% vs. 48.4 and 58.3%; Wulff 1990). Preference for *Amphimedon rubens* as a host would therefore decrease the probability that an entire individual would become detached.

A third apparently adaptive nonrandom pattern in how sponges adhere to each other, is that sponges that have lost other attachments to solid substrata have a significantly greater rate of adherence to intimately associated sponge individuals. It is clearly advantageous to adhere to another sponge if other attachment points are no longer holding, but how a sponge would be able to tell if it has lost its attachment to solid substrata is mysterious.

Clonal organisms have been predicted to be more likely than nonclonal organisms to develop mutualistic associations (Wulff 1985*b*). This prediction is based on morphological and life history characters of clonal organisms that might allow intimate associations of any nature to arise by chance, and then to spread through a population and ultimately evolve to be mutualistic in nature. In this scheme, sponges, as clonal organisms

with especially well-developed powers of fragmentation and independence of parts, would be predicted to be particularly prone to evolution of mutualistic associations. Their extreme homogeneity and flexibility of design might allow sponges to participate in intimate associations without mortal disruption of their functioning. It is not, therefore, surprising that sponges participate in a multitude of mutually beneficial intimate associations with representatives of a variety of other phyla and kingdoms. These include: cyanobacteria (e.g., Wilkinson 1983, 1987*a*, *b*), bacteria (Reiswig 1981), zoanthids (West 1976), dinoflagellates (Rosell and Uriz 1992), corals (Goreau and Hartman 1966, Wulff and Buss 1979), scallops (Bloom 1975, Forester 1979), ophiuroids (Hendler 1984), and mangroves (Ellison and Farnsworth 1992). Sponges also participate in associations with telestaceans, hydroids, entoprocts, macroalgae, and scyphozoans (Uriz et al. 1992, Rützler 1990; J. Wulff, personal observation), which may also be mutually beneficial. Intimate associations of sponges with species in other phyla or kingdoms are less likely to be influenced by competition for similar resources that is predicted when intimately associated individuals are similar. The role of presumed competition for food in intimate associations between sponges has not been resolved. Since sponges are extremely efficient filter-feeders (e.g., Reiswig 1971), intimate association among sponge individuals constitutes a situation in which sponges closely adjacent to each other are essentially blowing well-used water at each other, a situation which certainly would appear to be negative. Not only is the water being depleted of food, but surface area of incurrent pores by which water can be taken in is decreased for both sponges in a mutually adherent pair. Positive effects of such associations among sponges would have to be large to outweigh this blockage of filtering area, although it is possible that some compensation could be achieved by reorganization of canal systems of participating sponges (Hartman and Reiswig 1973) or specialization on different components of the suspended organic material. For associations that are neither obligate nor specific to have become significantly coevolved may seem far-fetched, but the possibility that intimate associations among sponges of different species in dense and diverse communities might be mutually beneficial was also seriously considered by Sarà (1970) and by Rützler (1970). The cases of mutually beneficial intimate association reported on here could only be revealed by long-term monitoring on an unusually fine scale, and more than a decade devoted to developing an understanding of all aspects of the interactions of the sponges with each other, and their physical environment, predators, and pathogens. It may be that our imagination of what is possible, with respect to reciprocal evolution of mutual benefit, is limited by lack of information. At any rate, there seems to be much to learn still of the possibilities

for mutual benefit in intimate associations among species.

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