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Is There a Trade-Off Between Wound-Healing and Chemical Defenses Among Caribbean Reef Sponges?[1]

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SYNOPSIS. **On Caribbean coral reefs, some sponge species produce chemical defenses, while others do not and are non-fatally grazed by predatory fishes. It has been hypothesized that the latter may compensate for fish grazing by growing faster or rapidly healing wounds. Rates of wound-healing were measured for chemically defended and undefended tubular and vase-shaped sponges on patch reefs in the Florida Keys and Bahamas in 2002. Healing rates were significantly faster during the first few days of the experiment, with rates leveling off after the third day. Chemically undefended sponges healed at significantly faster rates (*Callyspongia plicifera*, 8% area regenerated per day; *Callyspongia vaginalis*, 6%; *Niphates digitalis*, 6%; *Xestospongia muta*, 6.5%) than chemically defended sponges (*Cribrochalina vasculum*, 2%; *Ircinia campana*, 2%; *Verongula gigantea*, 0%). Orientation of wounds relative to the tidal current had no influence on healing rates. Specimens of *Niphates digitalis* growing in tubular form had faster healing rates than individuals with vasiform shapes. Our results suggest that Caribbean reef sponges followed two different evolutionary trajectories: chemically defended species deter fish predation and have slow healing rates, while chemically undefended species allocate resources to rapid wound-healing in response to grazing.**

INTRODUCTION

Coral reef habitats are noted for intense levels of predation (Huston, 1985). Sponges are conspicuous members of the reef community and, as sessile soft-bodied animals, appear to be vulnerable to predation. Sponges are preyed upon by gastropods (Pawlik *et al.*, 1988), polychaetes (Fauchald and Jumars, 1979; Pawlik, 1983), asteroids (Dayton *et al.*, 1974; McClintock, 1987), echinoids (Ayling, 1981), turtles (Meylan, 1988), and fishes (Bakus, 1966; Randall and Hartman, 1968; Ayling, 1981). Some fishes eat large, exposed sponges on coral reefs (Randall and Hartman, 1968; Reiswig, 1973; Hoppe, 1988). Randall and Hartman (1968) analyzed the gut contents of 212 species of Caribbean reef fishes and found sponge in the stomachs of 21 species, with sponge tissue comprising more than 6% of the gut contents of 11 species. Sponges constituted the majority of stomach contents of angelfishes of the genera *Holacanthus* and *Pomacanthus* (>95% and >70% of volume, respectively) and the filefish *Cantherines macrocerus* (>85%). Parrotfishes, most notably of the genus *Sparisoma*, have subsequently been reported to graze sponges (Dunlap and Pawlik, 1996, 1998). The results of these studies demonstrate that two groups of fishes exist on reefs: a few species that eat sponges, and a great majority that do not. The persistence of sponges on reefs suggest that they have evolved highly effective methods for discouraging predation (Randall and Hartman, 1968).

Some sponges deter predators by producing chemicals that are unpalatable to fishes (Pawlik *et al.*, 1995; Uriz *et al.*, 1996; Chanas and Pawlik, 1997; Kubanek *et al.*, 2002; Pawlik *et al.*, 2002). Sponges have yielded the greatest diversity of secondary metabolites isolated from marine organisms (Faulkner, 2000 and reviews cited therein). Secondary metabolites are structurally complex and are often highly concentrated in sponge tissue (Pawlik *et al.*, 1995). Synthesis of secondary metabolites likely requires considerable metabolic cost, and therefore should provide some benefit to the organism (Paul, 1992; Pawlik, 1993; McClintock and Baker, 2001). Secondary metabolites are thought to function in antifouling, anti-overgrowth, and UV protection, but the most commonly studied role is that of predator deterrence (Pawlik, 1993; Pawlik *et al.*, 1995; Chanas *et al.*, 1996; McClintock, 1997; Wilson *et al.*, 1999; Waddell and Pawlik, 2000*a*, *b*).

Pawlik *et al.* (1995) surveyed 71 species of Caribbean demosponges and determined that 69% yielded deterrent crude extracts in aquarium assays using a generalist fish predator. Crude extracts of sponges preferred as prey items by sponge-eating fishes were palatable to generalists; these undefended species live in mangrove habitats, in refugia under rock ledges or in coral rubble, or exposed on the reef (see analysis in Pawlik, 1997, 1998). Undefended sponges that live exposed on the reef are frequently grazed by sponge-eating fishes. Compiling survey data from several studies, Pawlik (1997) noted that the fourth most common sponge on Caribbean reefs, *Callyspongia vaginalis*, a species lacking chemical defenses, was the most abundant sponge found in the stomachs of reef fishes (Randall and Hartman, 1968; Pawlik, 1997). The absence of chemical defenses in sponges does not appear to be compensated by structural or nutritional defenses (Chanas and Pawlik, 1995, 1996; Uriz *et al.*, 1996). Specifically, glass spicules do not appear to play an important role in defending sponges from fish predators (Pawlik *et al.*, 1995; Chanas and Pawlik, 1996).

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Instead, sponges lacking chemical anti-predatory defenses may direct energy otherwise used to produce secondary metabolites to increase reproduction, growth, regeneration, or wound-healing (Pawlik, 1998).

Partial predation of sponges by fishes results in a breach of the defensive outer layer of the sponge, creating a wound that can become infected with pathogenic microorganisms (Sará and Vacelet, 1973; Smith and Hildemann, 1986). Fish bites may also alter the flow of water through the sponge. The velocity of the excurrent stream through the osculum may be several hundred times that at the level of the choanocytes (Vogel, 1974). Due to the physical structure of the choanocyte chambers and oscular chimneys, water can passively flow through the sponge without the choanocytes actively pumping (Vogel, 1974). This flow is important, not only for feeding, but also for gas and ion exchange (Vogel, 1974, 1977; Bell, 2002). A wound could disrupt the natural flow through the sponge, possibly causing death (Jackson and Palumbi, 1979). It may be important for sponges to heal wounds rapidly to prevent infection and re-establish feeding currents and structural stability.

Sponges repair tissue damage by either an infiltration of archaeocytes and other mesohyl cells to the wound area or by localized increases in mitosis that result in ingrowth (Smith and Hildemann, 1986). Sponges heal wounds much faster than their normal rate of growth and wound-healing could represent a significant expediture of energy (Ayling, 1983; Smith and Hildemann, 1986; Hoppe, 1988; Bell, 2002). Sponges with anti-predatory chemical defenses may not be able to heal wounds at the same rates as sponges lacking these defenses because the former allocate energy for metabolite synthesis and storage.

Considering the foregoing, this study addresses the following questions: Do different species of Caribbean reef sponges of similar morphologies heal similar wounds at different rates? Is there a relationship between healing rates and the elaboration of chemical defenses among these sponge species? Does sponge morphology affect the healing rates of individual sponges within a species?

MATERIALS AND METHODS

Wound-healing experiments were conducted to determine if differences exist in the healing rates of different species of sponges. To account for growth differences that may occur between sponges with different morphologies, only sponge species that grow in tubular or vasiform shapes were used. The first experiment was conducted at 10 m depth at North Dry Rocks Reef (25°07.850N, 80°17.521W) in the northern Florida Keys in May 2002. Sponge species used in the first experiment were *Callyspongia plicifera* (n = 16, chemically undefended; Pawlik, *et al.*, 1995, and see below), *Callyspongia vaginalis* (n = 14, undefended), *Ircinia campana* (n = 7, chemically defended), and *Niphates digitalis* (n = 14, undefended). Individual sponges of similar size (tube or vase length <20 cm) were numbered and tagged with flagging tape. A scalpel was used to cut a circular hole in each sponge approximately 2 cm^2 in area and 3 cm from the oscular lip of the sponge. The wound was intended to simulate an area of tissue that is lost when a predator bites into the sponge; circular wounds similar to these are frequently seen on *C. vaginalis* and *N. digitalis* in our study areas in the Florida Keys and Bahamas (Walters and Pawlik, personal observation). The wound location was chosen because the tissue of tubular and vasiform sponges is most uniform in thickness approximately 3 cm from the lip of the sponge. Immediately after it was cut, the wound was photograped with a digital camera in a water-tight housing. A measurement scale reference was included in all digital photographs. For this experiment, a second photograph was taken after 10 days. The digitizing software ImageTool was used to measure initial and final wound areas in square centimeters (two-dimensional healing). Percentage healing was calculated as the change in wound area (area of regenerated tissue) divided by the initial wound area, multiplied by 100. Daily healing rates for each sponge species were estimated by dividing the total percentage of area healed by the number of days between photographs. A linear regression was calculated to assess the relationship between healing rate and levels of chemical defense using data from Pawlik *et al.* (1995) (and see below).

The first experiment showed a difference in healing rates of sponges with different levels of chemical defenses. A second experiment was conducted to replicate the first in a different location and with additional sponge species. The second experiment was conducted at 5 m depth for *C. vaginalis* and 15 m depth for all other species at Sweetings Cay (26°25.212N, 77°53.347W) in the Bahamas in June 2002. Sponge species used in this experiment were *Callyspongia vaginalis* (n = 16; undefended), *Cribrochalina vasculum* (n = 10, defended), *N. digitalis* (n = 14; undefended), *Verongula gigantea* (n = 5, defended), and *Xestospongia muta* (n = 18, undefended). The same protocol used in the first experiment was used to measure healing rates of sponges. This experiment was conducted for 8 days for *V. gigantea*, 9 days for *Cribrochalina vasculum*, *N. digitalis*, and *X. muta*, and 12 days for *Callyspongia vaginalis*.

A third set of experiments was conducted in the northern Florida Keys in October 2002 at 15 m depth at Pickles Reef (24°59.272N, 80°17.521W) for *X. muta* and at 10 m depth at North Dry Rocks Reef (25°07.850N, 80°17.521W) for all other sponge species. This experiment repeated the methods of the first two experiments, and included serial photographs of wounds over the experimental time period. Experiments were also conducted to determine if healing rates were potentially confounded by the orientation of wounds relative to the tidal current or if changes in sponge shape (tubular to vasiform) affected the healing rates of sponges within a species. Sponge species used in these experiments were *Callyspongia plicifera* (n = 17, undefended), *Callyspongia vaginalis* (n = 16, undefended), *I. campana* (n = 10, defended), *N. digitalis* (n = 20, undefended), and *X. muta* (n = 17, undefended). The sponges were wounded and photographed as previously described. The experiments were conducted for 12 days. To investigate patterns in daily healing rates, successive photographs of individual wounds were taken for four species of sponges. Three individuals of *N. digitalis*, *Callyspongia plicifera*, and *Callyspongia vaginalis* at North Dry Rocks Reef were photographed at days 0, 3, 6, 10, and 12. Three individuals of *X. muta* at Pickles Reef were photographed at days 0, 3, 9, and 12. The percentage of regenerated tissue was calculated for each wound over each time interval. A one-way analysis of variance was calculated to determine if significant differences existed between healing rates at different times during the experiment.

As an additional part of the third set of experiments, we compared the healing rates of wounds that were oriented differently relative to the direction of the oscillatory tidal flow over the reef. Ripples in the sand between hardbottom areas of the reef were used to assess the orientation of the tidal current. Five individuals of each sponge species were cut with a wound facing both the direction of the tidal current and a wound in the direction perpendicular to the tidal current. A paired *t*-test comparing the healing rates of wounds facing perpendicular directions relative to tidal flow was calculated for each species.

Also as part of the third set of experiments, photographs were taken of the side and oscular aspects of each individual of *Niphates digitalis*, the only sponge used in this study exhibiting a gradation of morphologies from tubular to vasiform. Sponge heights and oscular diameters were measured using ImageTool. The oscular diameter was divided by the sponge height to give a shape ratio for each sponge. A linear regression of sponge ratios and healing rates was calculated for this species.

All data on the chemical defenses of the sponge species employed in this study were taken from previous studies. Pawlik *et al.* (1995) include a survey of the palatability of crude organic extracts of tissue samples from 73 species of Caribbean sponges; extracts were incorporated into a food mixture that was fed to the generalist fish predator, *Thalassoma bifasciatum*, in aquarium assays. For each assay, an extract was considered deterrent if the mean number of food pellets eaten in independent tests was less than or equal to 6 of 10. This protocol was also used by Chanas and Pawlik (1997), Pawlik *et al.* (2002), and Neilson and Pawlik (unpublished manuscript) in experiments conducted to determine the palatability of crude organic extracts of *Xestospongia muta*, *Ircinia campana*, and *Niphates digitalis*, respectively. We used data from these experiments as well as Pawlik *et al.* (1995) to investigate the relationship between chemical defense and wound-healing.

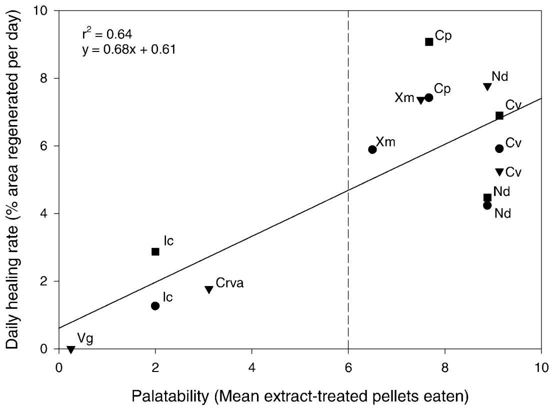

FIG. 1. Relationship between palatability of crude organic tissue extracts and healing rates for 7 species of sponges. Sponge extracts were considered deterrent if the number of pellets eaten was less than or equal to 6, as indicated by the vertical dashed line; a value of 0 is the most deterrent and 10 is the least deterrent (Pawlik *et al.*, 1995, 2002). Circles, experiments at Key Largo, FL in October 2002; triangles, experiments at Sweeting Cay, Bahamas in June 2002; squares, experiments at Key Largo, FL in May 2002. Sponge species tested: *Callyspongia plicifera* (Cp), *Callyspongia vaginalis* (Cv), *Cribrochalina vasculum* (Crva), *Ircinia campana* (Ic), *Niphates digitalis* (Nd), *Verongula gigantea* (Vg), and *Xestospongia muta* (Xm).

RESULTS

The three sponge species without anti-predatory chemical defenses healed wounds faster than chemically defended sponges (ANOVA $p < 0.001$; Fig. 1). In many instances, individuals of undefended species sealed the entire wound with tissue before the experiment was completed in 10–12 days. In *Callyspongia plicifera*, *C. vaginalis*, *Niphates digitalis*, and *Xestospongia muta*, growth was fastest during the first few days after the wound was cut (Fig. 2). The daily heal-

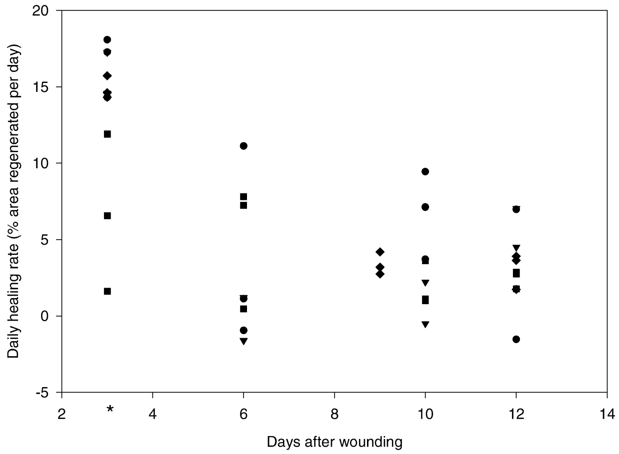

FIG. 2. Rates of healing as a function of time after wounding. The percentage of regenerated tissue was calculated on days 3, 6, 10 and 12 for three individual sponges of *Callyspongia plicifera* (circles), *Callyspongia vaginalis* (triangles), *Niphates digitalis* (squares), and on day 3, 9, and 12 for *Xestospongia muta* (diamonds). The rate of growth was significantly higher only for the first interval, indicated by the asterisk (0–3 days; repeated measure ANOVA $P < 0.001$; Tukey, $P < 0.05$).

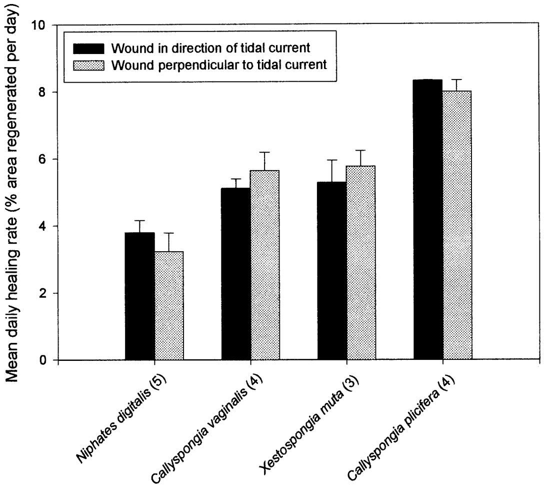

FIG. 3. Effect of wound orientation relative to water flow on healing rate in four sponge species. Error bars indicate standard error. Number of replicate sponges is shown in parentheses.

ing rates of these four species were significantly higher during the interval between the initiation of the experiment and day 3 than later (ANOVA $P < 0.001$; Tukey; $P < 0.05$); healing rates appeared to level off after the third day (Fig. 2). Many individuals of *C. plicifera*, *C. vaginalis* and *N. digitalis* grew a thin transparent membrane across the entire wound area during the first few days of the experiment. This membrane was often found torn on subsequent days, but persisted the duration of the experiment in other specimens. The membrane was not used in measurements for wound-healing calculations; rather, only opaque regenerated sponge tissue was used to calculate the wound area regenerated per day.

Ircinia campana, a chemically defended sponge, exhibited tissue necrosis surrounding wounds at the conclusion of experiments in 3 of 10 cases. Tissue necrosis was never observed on rapidly healing, chemically undefended sponge species.

The orientation of wounds relative to the oscillatory tidal current did not significantly alter the healing rates of sponges. The healing rates of the perpendicularly positioned wounds were not significantly different in any of the sponge species tested (paired *t*-tests; *C. plicifera*, $P = 0.42$; *C. vaginalis*, $P = 0.35$; *N. digitalis*, $P = 0.24$; *X. muta*, $P = 0.36$; Fig. 3). Specimens of *N. digitalis* growing in tubular form (low shape ratio) had faster healing rates than sponges that grew in a vasiform shape (ANOVA $P = 0.024$; Fig. 4).

DISCUSSION

The results of this study indicate that chemically undefended sponges on Caribbean reefs have evolved mechanisms for more rapidly healing wounds than chemically defended species, ostensibly in response to non-fatal grazing by spongivorous reef fishes. Further, the results suggest that the metabolic cost of wound-healing mechanisms represents an evolutionary alternative to secondary metabolite synthesis used by chemically defended species.

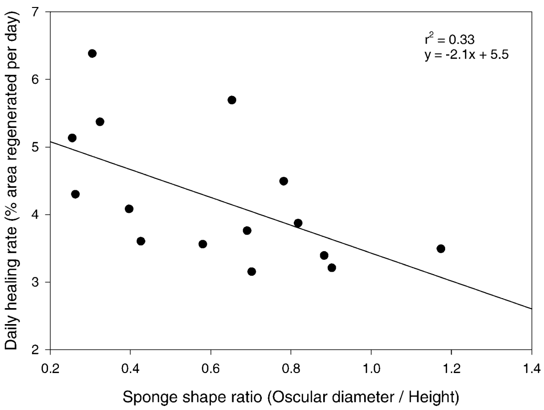

FIG. 4. Relationship between sponge morphology of *Niphates digitalis* and healing rate. Sponges with low sponge shape ratios are more tubular in form and sponges with higher ratios are more vasiform.

The interaction between plants and herbivores and the ecology of chemical defense has been well studied in both terrestrial and marine ecosystems. To persist in a community, plants must escape, deter, or tolerate herbivory. Plants have adapted two major strategies for dealing with herbivory, either to grow fast or to produce defensive chemicals (Coley *et al.*, 1985). Resource allocation within the plant determines the strategy a particular species might use (Bazzaz *et al.*, 1987). Fast-growing species invest a large proportion of their resources in processes and structures that enhance resource acquisition, resulting in high relative growth rates. Slow-growing species invest a large proportion of resources into non-growth processes and structures required to retain and make efficient use of resources under intense herbivory, resulting in low relative growth rates (Herms and Mattson, 1992). One form of resource investment of slow-growing species is chemical defense in the form of secondary metabolites. The production of secondary metabolites is likely to incur a high metabolic cost to the organism, due to the raw materials needed to make the compounds, production and storage of the secondary metabolites, and prevention of autotoxicity within the organism (Van Alstyne *et al.*, 2001). Producing and maintaining the enzymes required for the synthesis and safe management of potentially toxic compounds could be much more costly than the energy invested in the compounds themselves (Hay and Fenical, 1988). Metabolites are often highly concentrated, have low turnover rates in slow growers and may have dosage-dependent effects on herbivores (Coley *et al.*, 1985). For plants, fast growers suffer high rates of damage from herbivores and have both lower amounts and different types of defensive chemicals than slow growers. Defenses of fast growers are attributable to diverse chemicals that are present and effective in lower concentrations and have high turnover rates (Coley *et al.*, 1985). The dilemma for plants is that they must grow fast enough to compete, yet maintain the defenses necessary to survive in the presence of pathogens and herbivores.

The strategies used by plants to compensate for herbivory may be translatable to sponges and their responses to predation. Caribbean sponges appear to comprise a group of fast wound-healing species and a group of slow healing, chemically defended species. Sponges of the genera *Callyspongia* and *Niphates* are among the most common reef species, are major components of the diet of spongivorous fishes (Randall and Hartman, 1968), yield crude organic extracts that are palatable to generalist fish predators (Pawlik *et al.*, 1995), and these extracts have not been the source of unusual secondary metabolites. In contrast, *Ircinia campana* is known to contain high concentrations of furanosesterterpene tetronic acids that deter fish predators (Pawlik *et al.*, 2002) and *Verongula gigantea* contains high concentrations of brominated tyrosine derivatives (as do other members of the Verongiidae, such as *Aplysina* spp., see Puyana *et al.*, 2003) that serve the same function. Specific deterrent metabolites have yet to be identified from *Cribrochalina vasculum* or *Xestospongia muta*, but both are known to have similarly deterrent crude organic extracts (Pawlik *et al.*, 1995; Chanas and Pawlik, 1997).

Predation may act as a key factor in determining the resource allocation strategies of sponges. In McMurdo Sound, Antarctica, sponge-eating invertebrate predators (primarily seastars) appear to be generalists that feed on the more abundant, non- to mildly chemically defended sponge species (McClintock, 1987). Similarly, Uriz *et al.* (1995) found that the chemically defended Mediterranean sponge *Crambe crambe* has much slower growth rates than *Dysidea avara*, an undefended sponge that is grazed by sea urchins, suggesting that slow growth rates are concommitant with larger investments in anti-grazing defenses. Resources are limiting, and reproduction, growth, and defense may interact at the level of the individual so that an additional investment in one function must be at the expense of the others (Uriz *et al.*, 1995).

Antipredatory chemical defenses may come at the expense of wound-healing capacities that extend beyond tissue repair, as in the case of necrosis in *Ircinia* described above. Some chemically defended sponges may lack effective mechanisms for dealing with microbial invasion and pathogenesis when tissue damage does occur, such as during storm events.

Studies of plant-herbivore interactions have suggested that intermediate levels of plant chemical defenses are correlated with maximum growth rates (Coley *et al.*, 1985). The survey of sponge chemical defenses conducted by Pawlik *et al.* (1995) calculated numerical values corresponding to the levels of tissue extract palatability for each sponge species tested. Sponges with values of 6 or less were considered deterrent to a generalist fish predator. Sponges with values closest to 0 were the most chemically deterrent species, and sponges with values closest to 10 were the least deterrent. In the present study, *Xestospongia muta* (values of 6.5 on Conch Reef, Florida Keys and 7.5 off Grand Bahama Island; Chanas and Pawlik, 1997) and *Callyspongia plicifera* (7.7) had intermediate levels of chemical defense (Fig. 1). *Xestospongia muta* (6.5% wound area regenerated per day) and *Callyspongia plicifera* (8%) also had the fastest rates of wound-healing of the sponge species tested in this study. It is unclear why these species should have the highest healing rates, rather than those with the most palatable organic extracts (*Callyspongia vaginalis* and *Niphates digitalis*), but it should be noted that the allocation of resources to reproduction and growth in any of these species is not yet known, and may be very different.

Sponges expend metabolic energy to pump water through their aquiferous system via the beating of their flagellated choanocytes (Reiswig, 1974). In addition, entrained water flow may induce flow through the body of a sponge during fast flow conditions and act to reduce the energy needed for pumping water through the sponge body (Vogel, 1974). This passive flow may allow more metabolic energy to be used for growth and regeneration. Sponge feeding and respiration may be enhanced by morphology and any deviation from a specific shape may decrease growth; hence, it may be essential for sponges to heal wounds to re-establish flow. In the present study, the undefended sponges *Callyspongia plicifera*, *Callyspongia vaginalis*, and *Niphates digitalis* all created thin membranes during initial wound-healing, and may be using this membrane as a temporary measure to restore induced flow. Specimens of *Niphates digitalis* that were tubular in shape healed wounds faster than vasiform individuals, also suggesting a response to maintain induced flow. Rapid structural repair may be important for tubular, erect sponges because damage, if not repaired quickly, may result in insufficient flow to maintain cellular respiration, let alone feeding (Jackson and Palumbi, 1979). Similarly, *Cliona celata*, a slow-growing sponge, regenerated rapidly after wounding to return the sponge to its original size and shape (Bell, 2002).

In accordance with resource allocation hypotheses derived from studies of plant-herbivore interactions (*e.g.*, Coley *et al.*, 1985), the present study suggests that sponges on Caribbean coral reefs have followed alternate evolutionary strategies in dealing with predation by reef fishes. While this study has focused on the trade-off between chemical defenses and growth-related allocation of resources, another direction for resource allocation, reproduction, has yet to be examined and is the subject of on-going research. While the evolutionary pressure imposed by predation seems to have driven these alternative interspecific strategies, evidence for optimization of the use of chemical defenses within sponge species are surprisingly lacking. Unlike terrestrial plants and marine algae (Herms and Mattson, 1992; Hay and Steinberg, 1992), sponges are not known to differentially deploy or induce production of chemical defenses (Chanas and Pawlik, 1997;

Swearingen and Pawlik, 1998), nor does compelling evidence exist that they convert non-toxic precursor metabolites to more toxic defensive products (Puyana *et al.*, 2003). A better understanding of these apparently less-than-optimal uses of chemical defenses by sponges also awaits future research.

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