



SYMPOSIUM

Regeneration of Sponges in Ecological Context: Is Regeneration an Integral Part of Life History and Morphological Strategies?

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Synopsis Sponges, simple and homogeneous relative to other animals, are particularly adept at regeneration. Although regeneration may appear to be obviously beneficial, and many specific advantages to regeneration of lost portions have been demonstrated, comparisons of regeneration among species of sponges have consistently revealed substantial differences in style (i.e., relative rates of reconstituting surface features, infilling depressions, regaining lost primary substratum), and overall time course, raising questions about adaptive significance of variations in patterns of regeneration. Do sponges simply regenerate as quickly as possible, given constraints imposed by skeletal construction, morphology, or other traits that are determined primarily by evolutionary heritage? Does allocation of energy or materials impose trade-offs between regeneration versus competing processes such as growth or reproduction? Is regeneration time-course and style an integral part of coherent life history and morphological strategies? One approach to answering these questions is to compare regeneration among species that represent a spectrum of higher taxa within the demosponges as well as different growth forms and life-history strategies. Because detailed ecological studies of sponges have tended to focus on small sets of species of the same growth form, community-wide comparisons have been hampered. Data on growth rate, colonization, mortality, susceptibility to predation, and competitive ability have recently been accumulated for species of sponges typical of the Caribbean mangrove prop-root community. Experimentally generated wounds in individuals of 13 of these species allow comparison of the timing and style of regeneration among sponge species that span a range of life histories and growth forms. The species chosen represent four orders of the class Demospongiae, and include four sets of congeneric species, allowing distinction of patterns related to life history and morphology from those determined by shared evolutionary heritage.

Introduction

Adept recovery after partial mortality can strongly influence the net effect of damage by physical disturbance, predation, and disease for sponges. Specific boosts to survival conferred by regeneration include enabling a damaged individual to maintain competitive superiority in space-limited systems (Jackson and Palumbi 1979), reattach if fragmented (Wulff 1985; Battershill and Bergquist 1990; Wilkinson and Thompson 1997), discourage fouling of exposed skeletal elements (Leys and Lauzon 1998), prevent settlement of algae on bared substratum separating portions of damaged encrusting sponges (Turon

et al. 1998), and to regain sizes and shapes optimal for feeding (Bell 2002; Walters and Pawlik 2005).

Although the advantages of regenerating damaged portions seem clear, and the relatively simple homogeneous structure of sponges may facilitate regeneration, actual regeneration of wounds varies widely. Monitoring of experimentally generated wounds, and observations of responses to naturally dealt damage and to purposeful transplantation, have determined that regeneration can be influenced both by characteristics of the wound and by inherent characteristics of particular species of sponges (Boury-Esnault and Doumenc 1978; Jackson and Palumbi 1979; Simpson

1984; Hoppe 1988; Wilkinson and Thompson 1997; Turon et al. 1998; Schmahl 1999; Bell 2002; Duckworth 2003; Henry and Hart 2005; Wulff 2006a), as elaborated in the following paragraphs.

Comparisons of differently dealt wounds in many individuals of the same species have revealed that the amount of damage, type of damage, size of the sponge, and location on the individual sponge can influence recovery, and even susceptibility to further damage by other agents (Henry and Hart 2005 for a recent review). For example, Shield and Witman (1993) found that only 16% of the lesions caused by starfish feeding on the finger-shaped sponges *Isodictya* spp. in the Gulf of Maine healed. Size of lesions influenced success of recovery, and lesions at the base of fingers increased breakage during storms. Similarly, individuals of the massive basket-shaped sponge *Xestospongia muta* that were badly damaged by a vessel grounding in the Florida Keys regenerated more slowly than did individuals with only minor damage (Schmahl 1999), and three of the four individuals that were ultimately lost to disease had suffered serious damage, suggesting that damage may increase vulnerability to disease.

Comparisons of similar wounds in sponges of different species have demonstrated that variation in regeneration among species may be tied to differences in growth form, internal construction, growth rate, and vulnerability to damaging agents. Species of sponges that are internally differentiated into stalk and flared portion, or which have a distinct cortex layer over the choanosome, appear to be less adept at regeneration. For example, Reiswig (1973) noted the inability of the large vase-shaped Caribbean reef species *Mycale laxissima* to reattach if its stalk snapped in a storm. Stalked forms and flattened (sunlight-collecting) forms with photosynthetic symbionts also stood out as being unable to reattach among 16 sponge species (3200 individual sponge pieces) for which reattachment success in transplant experiments on the Great Barrier Reef was compiled by Wilkinson and Thompson (1997). All wounded individuals recovered after Duckworth (2003) made large wounds in two subtidal New Zealand species, but individuals of the species with an ectosomal skeleton that is differentiated into multiple layers recovered much more slowly.

Susceptibility to damage by physical disturbance or predators has been inversely related to regeneration rate. Hoppe (1988) compared regeneration among three massive Caribbean species for which he had experimentally determined susceptibility to both physical damage and predation. Although initial scar formation on experimental wounds,

1 cm × 1 cm × 1 cm, was most rapid in the tough and inedible *Ircinia strobilina*, full regeneration was quickest in *Neofibularia nolitangere*, the species most easily broken and most susceptible to predation by angelfishes. Experimentally generated fragments of three erect branching species of Caribbean reef sponges reattached to solid substrata (a key step in full regeneration) at rates that were inversely related to their extensibility (measured as breaking strain in biomechanics experiments), which was in turn positively related to resistance to breakage (measured as percent unbroken) in a hurricane Wulff 1985, 1995, 1997). Regeneration rates of holes, 4 mm in diameter, made in seven species of encrusting sponges on the undersurfaces of coral plates varied from one day to never (Jackson and Palumbi 1979). Contrasting descriptions of rapid regenerators (1–2 days) as “wairy” or “firm” and slow regenerators (21–30 days to never) as “tough” and “coarse and tough (hard to penetrate)”, hints at an inverse relationship between resistance to and recovery from damage.

Recovery of sponges after the larger-scale and uncontrolled damage meted out by natural disturbances, such as hurricanes, simultaneously exhibits variation due to differences in type and size of wounds and also to species’ characteristics. After a major hurricane hit reefs on the north coast of Jamaica, 576 sponges representing 67 species were monitored for 5 weeks for regeneration or continued deterioration (Wulff 2006a). An inverse relationship between resistance to damage by physical disturbance and ability to recover was revealed by dividing the data into categories defined by amount of damage, type of damage, and sponge growth form and skeletal composition. High-profile sponges of erect branching growth forms were particularly badly damaged during the storm, but were also best at recovery. At the opposite extreme, sponges that resist breakage or surface wounds, such as the tough *Ircinia* spp., were disproportionately often crushed instead, a type of injury from which they appeared to be unable to recover. Ultimate losses (i.e. after 5 weeks of recovery or continued deterioration) of nearly the same proportion of individuals in each of the growth form/skeletal composition categories (erect branching, vase or tube, massive breakable, massive tough, encrusting) suggest trade-offs between sets of traits that promote regeneration and traits that prevent the need for regeneration.

Although costs of regeneration in sponges have been explicitly considered in only a few cases (reviewed by Henry and Hart 2005), the possibility that regeneration is not free suggests that sponges

may employ their powers of regeneration with discretion. Other life history and morphological strategy characteristics may provide a context for the rate and style (i.e., relative timing of surface healing, depression infill, and substratum reclamation) of regeneration. Availability of data on colonization, growth, survivorship, and susceptibility to predation, for several of the common mangrove prop-root-inhabiting species of sponges in the Caribbean (Wulff 2004, 2005, 2006c, 2009) prompted initiation of experiments to test the hypothesis that rates and styles of regeneration primarily reflect its integral role in coherent life history and morphological strategies for maintaining a presence in this crowded community. Experimentally generated lesions, modeled on trunkfish-bite wounds, were made in individuals of 13 of the most common sponge species. Four of the 13 extant demosponge orders are represented, and four of the eight genera are represented by more than one species, allowing evaluation of the relative importance of evolutionary heritage versus ecological strategies.

Methods

Wound healing and regeneration were studied for 13 of the most common sponge species (Table 1 provides names of all species and their authors, and photographs of most of the species are in Wulff 2009) living on mangrove prop-roots at two sites, Sponge Haven and Hidden Creek, in Twin Cays, Belize (map in Wulff 2004). These species represent the full range of life history and morphological variation in the Caribbean mangrove prop root community (Wulff 2009), and 4 of the 13 recognized (Hooper and van Soest 2002) extant orders of the Class Demospongiae: the Haplosclerida, Poecilosclerida, Halichondrida, and Dictyoceratida. Four of the genera studied are represented by more than one species, allowing comparison of rates and styles of regeneration among closely related species.

Predation by trunkfish is the most common way whereby small pieces are naturally removed from sponges at these sites, and so trunkfish bites were chosen as the model for wounds. Wounds were made using a stainless steel razor blade, and I aimed for a uniform size of 16 by 9 mm in area, although shapes of a few individual sponges required slight adjustments in shape of the wound, and rough seas on one day impaired precision in wielding of the razor blade. Two types of wounds were made, depending on the thickness of the sponge tissue. Wounds in encrusting species (i.e., ≤ 3 mm in

Table 1 Species of sponges included in experimental wounding at Sponge Haven and Hidden Creek

Sponge taxa	Growth forms
Order Dictyoceratida	
<i>Spongia obscura</i> Hyattt 1877	Massive
Order Halichondrida	
<i>Halichondria magniconulosa</i> Hechtel 1965	Massive, clusters of mounds
Order Haplosclerida	
<i>Haliclona curacaoensis</i> (van Soest 1980)	Clusters of tubes, encrusting
<i>Haliclona implexiformis</i> (Hechtel 1965)	Massive, rounded mounds
<i>Haliclona manglaris</i> Alcolado 1984	Tiny mounds, encrusting
Order Poecilosclerida	
<i>Biemna caribea</i> Pulitzer-Finali 1986	Branches, tubes, encrusting
<i>Clathria campecheae</i> Hooper 1996	Very thin encrusting
<i>Clathria venosa</i> (Alcolado 1984)	Thin encrusting
<i>Lissodendoryx isodictyalis</i> (Carter 1882)	Massive, thick large tubes
<i>Mycale magnirhaphidifera</i> van Soest 1984	Thin encrusting
<i>Mycale microsigmatosa</i> Arndt 1927	Encrusting, sometimes thick
<i>Tedania ignis</i> (Duchassaing and Michelotti 1864)	Massive, rounded mounds
<i>Tedania klausii</i> Wulff 2006	Massive, tall mounds

Photographic portraits of most of these species are in Wulff 2009.

thickness) were always made to the underlying substratum (as is the case for trunkfish bites). For sponges >5 mm thick, wounds were made 3 mm deep, and were therefore surrounded on all sides and bottom by live sponge tissue. In order to compare recovery of wounds exposing bare substratum with recovery of wounds surrounded entirely by live tissue, specimens of massive species were sought in which portions were thin enough that wounds would expose the underlying substratum. Wounds were made in a total of 11–16 individuals (a single wound per individual) of each of the 13 species.

Each wound was measured (all three dimensions) and photographed at $t=0, 2, 6, 10, 14$, and 18 days. The time-consuming nature of the experimental set-up and of monitoring required that the experiments be initiated in staggered sets. Records were made of the progress of reconstitution (color and texture) of the surface, reclamation of exposed primary substratum, and infilling of depressions.

Results

For both types of wounds (i.e., with live tissue completely surrounding the wound versus with primary substratum exposed by the wound), differences

among species in recovery rate and style were striking (Fig. 1 includes photographs of some species at selected times). In contrast, individuals of the same species that were wounded in the same way tended to follow a similar time course and series of steps in

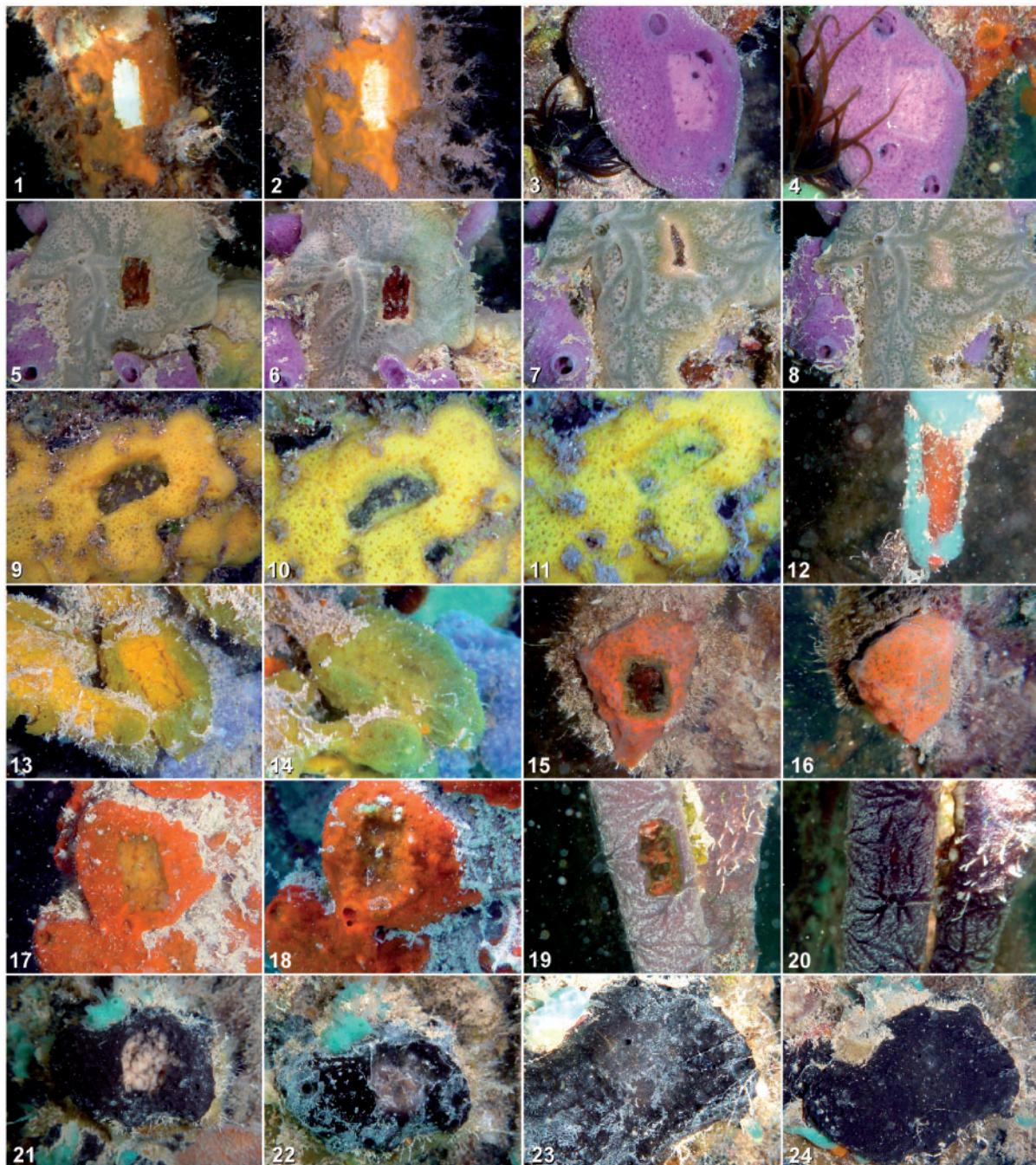


Fig. 1 Time series photographs of wounds to mangrove-inhabiting sponge species, Twin Cays, Belize, November–December 2009. Examples were chosen to illustrate the variety of time courses and styles of regeneration after experimental wounding. All times elapsed since wounding are given in number of days. Labels for each row of photographs are listed from left to right. Species authors are in Table 1. Row 1: #1, 2 *Clathria campecheae* $t=0, t=10$; #3, 4 *Haliclona implexiformis* $t=0, t=14$; Row 2: #5, 6, 7, 8 *Clathria venosa* $t=0, t=2, t=10, t=18$; Row 3: #9, 10, 11 *Biemna caribea* $t=0, t=6, t=10$; #12 *Haliclona manglaris* $t=10$; Row 4: #13, 14 *Halichondria magniconulosa* $t=0, t=14$; #15, 16 *Mycale microsigmatosa* $t=0, t=2$; Row 5: #17, 18 *Tedania ignis* $t=0, t=14$; #19, 20 *Mycale magnirhaphidifera* $t=0, t=2$; Row 6: #21, 22, 23, 24 *Spongia obscura* $t=0, t=2, t=10, t=18$.

their recovery. For all wounds, reconstitution of the surface pinacoderm was the first step.

Wounds in from one to three individuals of each of four species acquired further damage in the days following wounding. Expanded wounds in *Halichondria magniconulosa* and *Tedania klausii* were observed to be caused by feeding by a large juvenile gray angelfish, *Pomacanthus arcuatus* (Linnaeus 1758), that was present at the Sponge Haven site for 2 days (but is not a normal resident). Additional wounds in *Haliclona curacaoensis* had the characteristic shape of bites of spotted trunkfish, *Lactophrys bicaudalis* (Linneaus 1758), that are rare but normal residents of these Twin Cays sites. Enlarged wounded areas in *Haliclona manglaris* showed no signs of predation and the cause remains a mystery.

Regeneration of wounds surrounded by living tissue

All individuals with wounds surrounded entirely by live tissue had fully re-constituted their surface pinacoderm within the first 2 days. In all species, except *Halichondria magniconulosa*, for which surface color is distinct from inner-tissue color, redevelopment of normal surface color lagged behind that of surface texture (Fig. 2A). Rates at which the depressions made by experimental wounding were re-filled varied widely among species (Figs. 2B, C and 4A); species that began to fill wound holes relatively quickly were not necessarily the species that continued to completely regenerate the removed tissue rapidly (Figs. 2C and 4A). Wound filling proceeded in three different patterns (photographs in Fig. 1): (1) wounds initially increased in areal extent, as the edges smoothed and rounded, and the depression widened and then flattened as the center refilled, with 100% of the wounded individuals regenerating completely within 18 days (e.g. *Spongia obscura*, *Halichondria magniconulosa*, and *Tedania klausii*); (2) initially rapid refilling (1/3 filled within 6 days, Fig. 2B) of the wound depression, with subsequent refilling slowing such that only 20–30% of the individuals had completed regeneration by 18 days (e.g. *Haliclona implexiformis* and *Biemna caribea*); or (3) initial refilling at a sedate pace (Fig. 2B), but continuing steadily such that 50–70% of the wounds were fully recovered by 18 days (e.g. *Tedania ignis* and *Lissodendoryx isodictyalis*, Fig. 2C).

Neither generic level nor ordinal level relationships predicted rates and styles of recovery (Figs. 2A–C and 4A). The two *Tedania* species do not cluster with each other with respect to rates of any of the steps of regeneration; and the four species that

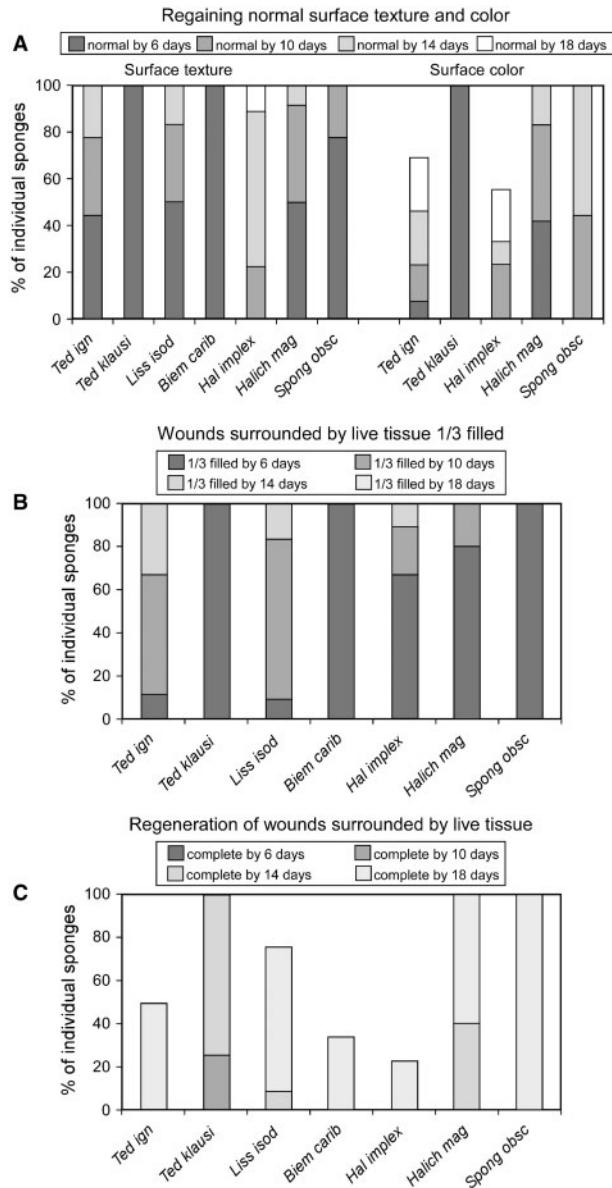


Fig. 2 Percent of wounds that were surrounded by live tissue that (A) regained normal surface texture and color, (B) filled wound depressions by 1/3, and (C) completely filled wound depressions by 6, 10, 14, or 18 days.

represent the Order Poecilosclerida (genera *Tedania*, *Lissodendoryx*, and *Biemna*) were not more similar to each other than they were to the three species which each represent a different demosponge order.

Reclaiming primary substratum

All wounds in individuals of *Clathria venosa*, *C. campecheae*, and *Mycale magnirhaphidifera* exposed primary substratum, because these species grow only in a thinly encrusting form. Four other species grow in thicker shapes as well as thin sheets,

but attempts to follow wound recovery in the thicker shapes failed in three of these species because individuals were either too small in areal extent (*Haliclona manglaris*) or so fragile that they broke within 24 h of wounding (*Mycale microsigmatosa*, *Haliclona curacaoensis*). In three of the more massive species (*Tedania klausii*, *Halichondria magniconulosa*, *Spongia obtusa*), no individuals were found that had thin portions in which wounds exposing primary substratum could be made, but in four species wounds exposing bare substratum were successfully made and monitored (Figs. 3A–C and 4B).

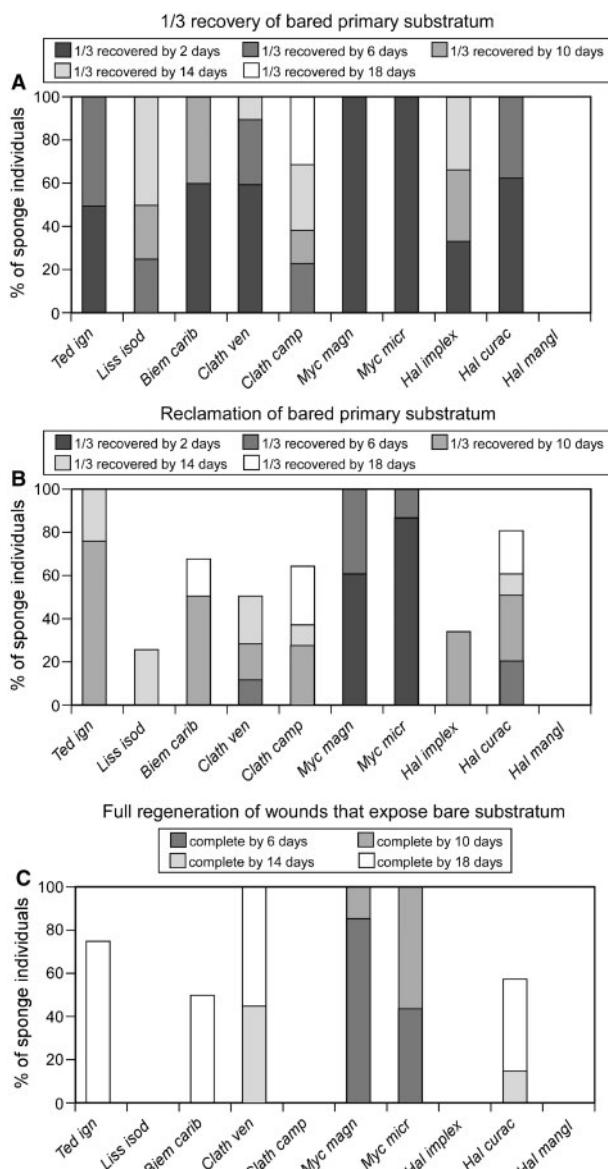


Fig. 3 Percent of wounds that exposed primary substratum and (A) reclaimed 1/3 of the bared substratum, (B) fully reclaimed bared substratum, and (C) tissue regenerated to be flush with undamaged surface by 2, 6, 10, 14, or 18 days.

Regeneration of wounds that exposed bare substrata followed one of four paths (illustrated in Fig. 1): (1) virtually immediate covering of the bare substratum with a thin layer of tissue that rapidly thickened (illustrated by *Mycale microsigmatosa* and *M. magnirhaphidifera*), (2) reclamation of the bared substratum, but little (*Haliclona curacaoensis* and *Biemna caribea*) or no (*Clathria campecheae*) thickening of tissue to fill the depression made by the wound, (3) gradual encroachment over the bared patch from all sides of the wound (*Clathria venosa* and *Tedania ignis*), or (4) simple healing of the walls of the wound with no (*H. manglaris*) or only a few individuals (*Haliclona implexiformis*, *Lissodendoryx isodictyalis*) reclaiming the bared substratum.

Rates and style of repair of wounds exposing primary substratum were similar among individuals of the same species (Figs. 3A–C and 4B), but differed among individuals representing different species in the congeneric pair *Clathria venosa* and *C. campecheae*, and the congeneric trio *Haliclona manglaris*, *H. curacaoensis*, and *H. implexiformis*. Only *Mycale microsigmatosa* and *M. magnirhaphidifera* were similar in time course and style of recovery. For the four species in which both types of wounds could be made, timing of recovery from one type of wound

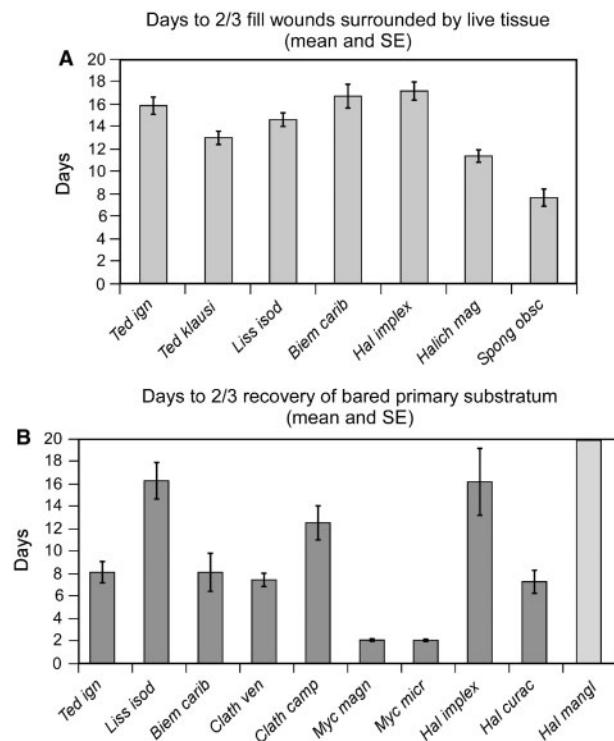


Fig. 4 Mean (and SE) number of days for (A) wounds surrounded by live tissue to be 2/3 refilled, and (B) primary substratum exposed by wounds to be 2/3 reclaimed.

was a poor predictor of recovery in the other type of wound (compare Fig. 2B and C with Fig. 3A–C; and Fig. 4A with 4B). *Tedania ignis* and *Biemna caribea* refilled wounds more quickly when primary substratum was bared; and in contrast *Lissodendoryx isodictyalis* quickly regenerated wounds that were surrounded by live tissue, but beyond simple reconstitution of the surface pinacoderm at the cut edges, most individuals failed to regenerate wounds that exposed primary substratum.

Discussion

Regeneration patterns are not well predicted by shared evolutionary heritage

Patterns of regeneration were strikingly different among sponges of different species. For these 13 species, which represent four demosponge orders, the hypothesis that rate of regeneration is primarily influenced by phylogenetic position is readily rejected, at least at the taxonomic level of Order. For example, the order Poecilosclerida was represented by *Mycale magnirhaphidifera*, which patched up wounds so rapidly that most could not be seen after 6 days and by *Lissodendoryx isodictyalis*, which failed to regenerate any wounds that exposed bare substratum within 18 days.

Even at the level of genus, shared evolutionary heritage was a poor predictor of timing and style of regeneration. *Tedania klausii* completely reconstructed surface texture and color within 2 days and filled depressions within ≤ 10 days, but after 18 days only 50% of *T. ignis* had filled depressions and only 69% had regained normal surface color. Likewise, *Clathria venosa* steadily marched in from all sides of a bared patch, not only recovering the primary substratum (photographs in Fig. 1) but also filling it to be flush with the undamaged portions of the sponges within 6–10 days. Only 63% of congeneric *C. campecheae* individuals slowly recovered bared primary substratum with a layer so thin that it was nearly invisible, and no individuals even began to infill the wounded patch (photographs in Fig. 1). Congeners in the genus *Haliclona* (Order Haplosclerida) also differed: *H. manglaris* reconstituted surface pinacoderm at the cut edges of the wounds, but did not recover the substratum that was bared by wounding; no individuals of *H. implexiformis* regenerated wounds to bare substratum beyond reconstituting pinacoderm at the cut edges, and only 20% completely infilled wounds surrounded by live tissue within the 18 days; *H. curacaoensis* consistently recovered bared substratum with a thin layer of tissue that thickened to the point that

60% had completely refilled the wound by 14–18 days. At odds with the lack of consistency in other genera, the two species most rapid at complete recovery were congeners *Mycale magnirhaphidifera* and *M. microsigmatosa*. Both *Mycale* species grow as thin sheets, but *M. microsigmatosa* is also capable of growing as thicker cushions, especially when it can make use of large sabellid polychaete tubes for support.

Thirteen species are not a sufficient sample of sponge diversity for discerning circumstances under which shared evolutionary heritage may trump ecological characters in influencing regeneration. Further attempts to disentangle these influences may need to focus on more species-rich sponge faunas, such as on coral reefs, so that multiple congeners of diverse growth forms can be included. For this set of some of the most common and ubiquitous species in the Caribbean mangrove root sponge fauna, however, there is little evidence that shared evolutionary history exerts the primary influence on regeneration.

Specific traits that might influence regeneration

Specific traits that are not necessarily influenced by phylogeny have been related to regeneration rates for some sponges (reviewed by Henry and Hart 2005). Curiously, growth rate is one species characteristic that does not reliably predict regeneration rate. Reiswig (1973) remarked on the rapid regeneration of holes in the large vase-shaped sponge *Verongula reiswigi*, which grew so slowly that growth could not be measured reliably over a 28 month period. Ayling (1983) measured both growth and regeneration rates of 11 species of thinly encrusting sponges in a subtidal canyon off New Zealand, and discovered that regeneration could be from 22 to 2900 times as fast as growth. Still, growth rates and regeneration rates may not be entirely independent of each other, as the rank orders of growth rates and regeneration rates for the 11 species were very similar (Ayling 1983); *Neofibularia nolitangere* in Hoppe's (1988) study both grew the fastest and also completely filled in experimentally dealt wounds the fastest of three massive species.

Growth rates do not predict regeneration rates well for the mangrove-inhabiting sponges in this study. Volume increases per unit initial volume over a 7 month period have been reported for five of these species (Wulff 2005). Of these five species, regeneration of wounds surrounded by live tissue was most rapidly completed by fast-growing *H. magniconulosa*, but slow-growing *L. isodictyalis*

ranked next (Figs. 2C and 4A). For infilling wounds to 1/3 of the removed volume, fast-growing *B. caribea* and *H. magniconulosa* ranked 1st and 2nd, but slowly-growing *H. implexiformis* was a close 3rd (Fig. 2B and C). Similarly growth rates of congeners *T. ignis* and *T. klausii* over a period of 6 months scarcely differed (Wulff 2006b), but *T. klausii* regenerated much faster (Fig. 2A–C). Regeneration rate of wounds exposing primary substratum did rank with growth rate, with fast growers *T. ignis* and *B. caribea* reclaiming bared substratum more rapidly than did slow growers *L. isodictyalis* and *H. implexiformis* (Figs. 3 and 4B). Cellular-level comparisons of regeneration in these species may provide insight into the inconsistent relationship of growth and regeneration rates, as recovery of sponges has been demonstrated to encompass a variety of processes, including wound patching by cell migration as well as by growth (Simpson 1984; Duckworth 2003; Henry and Hart 2005).

Morphological variety among species of sponges that are typical of mangrove prop roots is less than that among species in other habitats. Internally differentiated forms, with a stalk or armored cortex, that seem less adept at regeneration (Reiswig 1973; Wilkinson and Thompson 1997; Duckworth 2003) are not common in mangroves. Ayling (1983) noted a lack of influence of thickness of encrusting sponges on the rate at which they reclaimed primary substratum; and this was also the case among the species inhabiting mangroves. *Mycale magnirhaphidifera* and *Clathria campecheae*, the thinnest sheets, illustrate opposite extremes, with the former among the most rapid of complete regenerators, and the latter never progressing further than a nearly invisible thin layer over the bared substratum that was only accomplished by 2/3 of the individuals (Fig. 1).

Susceptibility to predation has been positively correlated with regeneration in a few species from coral reefs, but it has been difficult to separate out this one variable. In Hoppe's (1988) study of three massive reef species, *Neofibularia nolitangere* regenerated most quickly, and was most susceptible to angelfish predation; but also grew fastest and was most vulnerable to damage by physical disturbance. In another study (Walters and Pawlik 2005), refilling of holes (2 cm² in area) cut through the walls of seven vase and tube-shaped reef species was positively correlated with a proxy for vulnerability to predation (consumption of sponge-extract pellets by captive non-spongivore fishes), but variation in tube wall thickness and tissue density with pellet palatability may have confounded the data by causing variation in the volume of tissue removed.

Spongivory does not appear to be as pervasive in mangroves as it is on coral reefs, where a variety of vertebrate spongivores have been demonstrated to consume, to varying degrees, a majority of the species present (reviewed by Wulff 2006b). The only piscine predators that normally have access to mangrove sponges in Twin Cays are trunkfish, which consumed *Mycale magnirhaphidifera* and *Haliclona curacaoensis* more than they consumed other species of sponges (J. Wulff, manuscript in preparation). Occasionally, as during this study, a reef fish fetches up among the mangroves briefly. When species of sponges typical of mangroves were made available to reef-dwelling fishes by transplanting them to the reef, angelfish fed most eagerly on *Tedania ignis* and *Biemna caribea*, but also consumed *T. klausii*, *Halichondria magniconulosa* and a blue color morph of *Lissodendoryx isodictyalis* (Wulff 2005, 2006c). Reef-dwelling parrotfish feed on *Halichondria magniconulosa*, and a small mangrove-dwelling nudibranch consumes this species as well (J. Wulff, manuscript in preparation). The large starfish *Oreaster reticulatus* can occasionally make its way up prop roots that reach the substratum, and is able to consume many of the species of sponges in mangroves (J. Wulff, manuscript in preparation). *Tedania klausii*, one species that is rejected by *Oreaster* (Wulff 2006c), differs from the other mangrove-inhabiting species in that it also inhabits the seagrass meadows that are the normal haunt of this starfish.

When each species of sponge is vulnerable to different predators, they cannot be ranked by general “palatability”; vulnerability to each predator must be considered separately. Relative palatability to predators that do not normally challenge sponges in mangroves (e.g., angelfishes or *Oreaster*) has neither a positive nor a negative association with regeneration among these species; but sponge species most likely to be consumed by mangrove-dwelling trunkfish and nudibranchs are especially rapid regenerators (*H. magniconulosa*, *H. curacaoensis*, and *M. magnirhaphidifera*). If only wounds that expose substratum are considered, regeneration rate ranks with vulnerability to angelfishes, but this pattern may be confounded by *T. ignis* and *B. caribea* also ranking high in growth rate.

Simultaneous variation in multiple traits stymies interpretation of relationships between regeneration and specific other traits (e.g., growth, reproduction, recruitment, competitive prowess, predator defense) as trade-offs imposed by allocation of limiting resources. As well, regeneration may not necessarily drain resources to the point that other life processes

are compromised (Henry and Hart 2005 for a recent review). For example, Duckworth (2003) found that individuals of *Latrunculia wellingtonensis* and *Polymastia croceus* from which either 50, 75, or 90% of their volume was experimentally removed grew at the same rate; and Duckworth and Battershill (2003) further demonstrated that individuals from which significant biomass was harvested for biologically active metabolites grew at the same rate as sponges that were uncut. Intricate combinations of traits such as “resistance to damage,” which amalgamates specific morphological and skeletal traits (e.g., low profile, high spongin:spicule ratio, or collagen fibers), provided better prediction of recovery (which is also a complex combination of the abilities to evict damaged portions, reattach, reorient, and patch wounds) than did individual traits after severe hurricane damage (Wulff 2006a). An alternate approach to attempting to disentangle effects on regeneration of individual traits that vary together is to consider multiple traits together as integrated packages.

Regeneration as an integral component of life history and morphological strategies

Regeneration rates were included by Jackson (1979) in sets of predictions relating morphology of sessile animals to a variety of ecological and evolutionary traits. In this scheme, rates and styles (i.e. relative timing of component stages) of regeneration are integral components of life history and morphological strategies for maintaining a presence on marine hard substrata. Clonal and colonial animals of tree or vase morphologies, in which the fate of a small basal attachment profoundly influences the further survival of the entire organism, were predicted to regenerate with particular alacrity. Although the facility with which many sponges reattach may relax this specific pressure somewhat, still directly relevant to sponges is the general prediction that regeneration will be most important to species for which it is most important to maintain sovereignty over a particular patch of substratum.

Species of sponges typical of mangrove prop roots can be sorted by the importance of a particular patch of substratum to their life history and morphological strategies by reference to an accumulation of data on colonization rate, size frequency, natural community dynamics (with respect to both numbers of individuals and volume), and rates of mortality, partial mortality, and fragmentation, for the most common species (e.g., Wulff 2004, 2005, 2006c, 2009).

Recruitment rate is one life-history characteristic that is directly related (inversely) to how focused a species is on maintaining its presence on a particular patch of substratum. Recruitment of mangrove-inhabiting sponges onto eight initially bare PVC pipes suspended among the prop roots at Hidden Creek was evaluated after 20 months (Wulff 2004). By total number of individuals, the species included in this study of regeneration fall into three groups: (1) 11–14 recruits each for *B. caribea*, *H. curacaoensis*, *C. campecheae*, and *H. manglaris*, (2) 2–7 recruits each for *L. isodictyalis*, *H. magniconulosa*, and (3) no recruits for *T. ignis*, *S. obscura*, *H. implexiformis*. The remaining four species are not found in Hidden Creek.

Data on survivorship, taken from repeated yearly censuses at both Hidden Creek and Sponge Haven, yield clusters of species with annual survival rates of: (1) 50–70% for *T. ignis*, *H. implexiformis*, *S. obscura*, *T. klausii*, and *L. isodictyalis*; (2) 50% at Hidden Creek and 20% at Sponge Haven for *H. magniconulosa*; (3) 20–35 % for *B. caribea*, *H. curacaoensis*, and *M. microsigmatosa*; and (4) 0–10% for *H. manglaris* and *C. campecheae* (Wulff 2009). Data on survival are lacking for two species that were not found on censused roots: *C. venosa* often recruits onto, and covers, bivalve shells on the roots or short root segments embedded in peat banks, and *M. magnirhaphidifera* is disproportionately frequently found on new roots.

Combining recruitment and survival data divides these species into two broad groups: (1) relatively ephemeral or early successional species that sometimes persist into later stages of community development; and (2) reliable space holders that recruit relatively slowly. Subdivision of these groups by details of growth form, microhabitat distributions, and susceptibility to predation, yields the following clusters of species with similar strategies for maintaining their presence in this crowded community.

There are multiple ways to be an effective early-succession species in this system. First, are species that are quite ephemeral, with rapid cycling life histories focused on colonization. One of these, *Clathria campecheae*, grows as an extremely thin crust that loses in all competitive encounters. The other, *Haliclona manglaris*, grows as very small (generally <1 cm in largest dimension) mounds on primary substrata or epizooically on superior competitor species, especially *Spongia obscura*, but when it recruits onto an otherwise uncolonized fresh root tip it tends to cover it in a continuous layer 2 mm thick (Fig. 1).

Second are the relatively early-recruiting species. These are able to cope with later-recruiting better competitors by growing up and over them, although they are ultimately squeezed off the substratum unless they grow epizoically on *Spongia* spp. *Haliclona curacaoensis* exhibits encrusting growth form at first, and subsequently develops low tubes, and *Biemna caribea* starts out encrusting but then develops long branches from which low tubes sprout. Their relatively flimsy skeletons limit the degree to which they can grow unsupported, and each is particularly vulnerable to predation, but by different fish: *H. curacaoensis* by spotted trunkfish, and *B. caribea* by angelfishes.

Third are species that require primary substratum, but are not good at defending their spot against competitors. These species (*Mycale magnirhaphidifera*, *M. microsigmatosa*) focus on preventing colonization by other sponges, quickly spreading thinly over all primary substratum, and seem to specialize on covering the tips of roots that have newly entered the water. *Mycale magnirhaphidifera* is consistently overwhelmed by other species, especially *T. ignis*, if they are able to recruit onto the same root (J. Wulff, personal observation, Bocas del Toro, Panama).

Among the later-recruiting good space holders, two strategies are represented. The majority of reliable space holders recruit relatively slowly and grow as massive mounds or clusters of volcanos (*T. ignis*, *H. magniconulosa*, *T. klausii*, *H. implexiformis*, *S. obscura*, *L. isodictyalis*). Two of these species stand out from the others, each for different reasons. *Spongia obscura* holds space particularly well, and once an individual colonizes it suffers very low mortality rates, grows slowly (Wulff 2009), and tolerates epizoism extremely well (Fig. 1, bottom row). *Halichondria magniconulosa* also stands out, but in the opposite way; it grows most quickly of the massive species, and is the only species susceptible to predation by a small mangrove-dwelling nudibranch (J. Wulff, manuscript in preparation). Three of these space-holding species (*Tedania ignis*, *T. klausii*, *Halichondria magniconulosa*) are more likely to be consumed occasionally by vagrant angelfish than the others.

The other strategy for reliable space holding, illustrated by *Clathria venosa*, is to cover small separate substrata such as bivalve shells or short root segments embedded in the peat. This thinly encrusting species can be overgrown by massive species, but it is not easy for them to grow from prop roots onto discrete substrata, and the inverse relationship between colonization and competitive ability lowers

the probability that they can recruit to small discrete substrata. *Clathria venosa* can remain unchallenged as long as it prevents colonization of superior competitors by maintaining full coverage of small substrata.

Does regeneration increase with commitment of an individual sponge to a particular patch of substratum? In this group of Caribbean species that inhabit mangrove prop roots, small clusters of species that are defined primarily by life history and morphological characteristics tend to regenerate similarly. The time course and series of steps of regeneration do vary with commitment of an individual to a patch, but the relationship is not monotonic.

The two sponge species that stand out as ephemeral (*Haliclona manglaris*, *Clathria campecheae*) are also notable for meager repair, with not a single individual completing regeneration within 18 days. At the opposite extreme are the encrusting species, *Mycale microsigmatosa* and *M. magnirhaphidifera* that recruit to root tips that they can quickly cover completely and hold until superior competitors recruit. These species rapidly reclaim bared primary substratum, erasing any trace of a wound. Intermediate in regeneration are species that are early successional but still able to persist (*B. caribea*, *H. curacaoensis*) by growing outward from the roots, either as narrow tubes or long lobate branches, or by becoming epizoic on other species. Also intermediate in regeneration is the one species (*C. venosa*) that tends to recruit to bivalve shells and other small discrete substrata, which constrain its areal extent but also protect it from competitors.

Later-recruiting good space holders differ in the rates at which they reclaim primary substratum versus fill in wounds surrounded by live tissue. Massive species that regenerate wounds surrounded by tissue at intermediate rates are those most vulnerable to predation (*Halichondria magniconulosa*, *Tedania ignis*, *T. klausii*). Of these species, wounds exposing substratum could only be made in *T. ignis*, and these filled in rapidly. The species that holds space the best, but recruits slowly and tolerates epizoism well, *Spongia obscura*, regenerates relatively quickly and reliably. The slower regenerators among the massive species that hold space well and are less vulnerable to mangrove-dwelling predators (*L. isodictyalis*, *H. implexiformis*) make virtually no progress in regenerating wounds that expose bare substratum.

In conclusion, shared evolutionary history does not appear to exert the primary influence on rate and style of regeneration for mangrove-dwelling

species of sponges. As well, no single trait such as recruitment rate, vulnerability to predators, or competitive ability alone predicts regeneration success; and even combining traits into “early successional” versus “late successional” fails to predict regeneration rate and style. However, more intricate combinations of traits that place a species on a continuum defined by how important for completion of the life cycle it is to maintain sovereignty over a particular patch of substratum predict patterns of regeneration well. Least focused on regaining control over a substratum patch lost to wounding are both the most ephemeral species and the species most able to out-compete a neighbor. Most focused on reclaiming lost substratum are the species that are incapable of standing up to a competitor and therefore depend on preventing a possible competitor from recruiting to a wound site. A species that plays this game, but on small discrete substrata can afford to take more time, but still needs to regenerate fully, as does the slowest growing species that recruits very slowly but tolerates being overgrown. Along with the great variety of ways in which these species of sponges balance colonization with ability to compete for space or evade being outcompeted, rates and styles of regeneration are integral elements of coherent strategies for successfully gaining and maintaining a presence in these crowded communities.

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