Resistance *vs* recovery: morphological strategies of coral reef sponges

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Summary

1. An inverse association between ability to regenerate and structural complexity (i.e. internal differentiation and integration), illustrated by comparisons among animal phyla, suggests a dichotomy between suites of morphological traits that promote recovery from damage *vs* traits that promote resistance to damage.

2. The phylum Porifera is particularly suited for exploration of relationships among regeneration, resistance to damage and complexity. Sponges are noted for their structural simplicity and great facility at regeneration, relative to members of all other animal phyla; but sponge species vary widely in ability to recover from damage, and in overall morphology and skeletal properties.

3. Morphological strategies related to resistance to damage and recovery from damage were explored using data on the amount and type of damage incurred by 576 sponge individuals representing 67 species in a major hurricane. Five weeks of monitoring each individual for continued deterioration or recovery demonstrated an inverse relationship between the extent of injuries dealt by the storm and recovery success.

4. A trade-off between morphological strategies that promote resistance to damage *vs* those that promote efficient recovery could result in the disproportionate and permanent loss of resistant species, as these poor recoverers are increasingly overwhelmed by multiple simultaneous challenges.

Key-words: Coral reefs, hurricane damage, Porifera, regeneration

Introduction

A pattern of decreased regenerative ability with increased structural complexity is evident in comparisons among animal phyla (e.g. Huxley 1912), suggesting the possibility of a trade-off between regeneration and complexity. If 'complexity' can be defined for living organisms as greater internal differentiation and integration among parts (e.g. Bonner 1988; Slobodkin 1992), complex organisms stand to lose more by injury or partial mortality than do simple organisms. Thus apparent incompatibility between complexity and regeneration may be related to both the difficulty of regenerating multiple parts and also to selection for traits that prevent injury, and thereby preserve structural integrity. Complexity, regeneration and resistance to damage may be related to each other in interesting ways that shape morphological strategies for coping with physical disturbance.

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Comparisons among phyla direct attention to the possibility of trade-offs among complexity, regeneration and resistance; but exploration of mechanism is best made within particular groups. The phylum Porifera is especially intriguing for studies of strategies for coping with, or preventing, injury. Sponges are known for their legendary ability to survive severe damage, regenerate and reorganize to function fully again, as well as for extreme simplicity and homogeneity of structure. But although all sponges, which 'endure mutilation better than any known animal' (de Laubenfels 1949, p. 221), cluster together at one end of a continuum between simply constructed efficient regenerators *vs* complexly constructed poor regenerators, sponge species do vary in their ability to recover from damage, as well as in their ability to resist damage, and in the degree to which they are internally differentiated.

Morphological traits likely to help sponges resist damage include low profile (i.e. high base : volume ratio), tough or extensible skeletal materials (high spongin : spicule ratios), a sturdy cortex, collaboration with organisms that have resistant characteristics

(e.g. algae, corals), and ability to inhabit cryptic spaces in the reef frame. Traits favouring efficient recovery include rapid growth rate, quick reconstruction of surfaces, ability to reattach with any part of their surface and ability to reorganize for efficient pumping (necessary for food capture and gas exchange) in a new orientation. Why traits conferring resistance might be incompatible with traits promoting recovery is not immediately clear, but it may be related to the other requirements that shape suites of morphological traits (e.g. Jackson & Hughes 1985). For example, overall growth form and skeletal materials influence resistance to injury, but these traits may also be shaped by the need to overgrow neighbours, or to obtain light for photosynthetic symbionts. Likewise, rapid growth rate may speed recovery, but growth rate may be curtailed by expenditures of energy and materials on sexual reproduction, skeletal construction, and chemical and physical defences. The high morphological diversity of sponges in many habitats, including coral reefs (e.g. Rützler 1978; Wulff 2001), may reflect the variety of ways in which the ability to resist damage (by storms, predators, disease) can be balanced against ability to recover.

To explore these ideas, hurricane damage to 576 fore-reef sponges (representing 67 species), and their first several weeks of recovery, is here analysed with respect to suites of morphological characters. A preliminary analysis of a subset of the data was included in a general report on the immediate effects of Hurricane Allen on the reefs near Discovery Bay, Jamaica (Woodley *et al*. 1981). At that time it seemed that the reef, and its sponges, would surely recover; but the reef has not recovered, and failure of coral reefs to recover has now become a worldwide phenomenon (Bellwood & Hughes 2001; Lang 2003; Gardner *et al*. 2003; Wilkinson 2004; Pandolfi *et al*. 2005). It is time to apply all relevant data to understanding why some organisms recover and others continue to deteriorate after injury. Monitoring individual sponges allowed the amount and type of damage sustained by each sponge to be directly related to its subsequent deterioration or recovery, to answer the question: do sets of traits conferring (a) resistance to damage *vs* (b) efficient recovery from damage represent opposing morphological strategies?

Methods

SPONGES

Sponges are the simplest multicellular animals, but their species diversity exceeds that of any other group of sessile clonal invertebrates on coral reefs (640 described species in the Caribbean reported by van Soest 1994), and they play many key functional roles in reef ecosystems (e.g. Diaz & Rützler 2001; Wulff 2001; Rützler 2004). Sponges exhibit a wide variety of species-specific morphologies, from thin crusts to intricately branching bushes, to vases, and massive globular shapes.

Individual sponges can be from less than a centimetre to over 2 m in largest dimension, and in some reef zones they constitute the most abundant animals. A sponge individual is essentially a mass of impermanently specialized, and somewhat independent, cells, pervaded by a supportive skeletal framework and by a canal system through which water is continuously pumped. As a consequence of their relatively homogeneous and informal organization, sponges are masters of regeneration and remodelling after partial mortality.

STUDY SITES AND TECHNIQUES

Beginning on the day after an exceptionally strong hurricane passed near the north coast of Jamaica, the damage to, and recovery of, the diverse and abundant sponge fauna of the fore-reef was quantified. At Discovery Bay, on 6 August 1980, Hurricane Allen winds reached 110 km h^{-1} and waves of over 12 m were observed breaking in water 15 m deep, causing extensive damage to corals and reef framework as deep as 50 m (Woodley *et al*. 1981). On the fore-reef, between 12 m and 15 m, two census plots were established in areas of contrasting topography and coral growth forms. One (95 m^2) was on the edge of a buttress composed primarily of a dense thicket of the Staghorn Coral *Acropora cervicornis* on Upper Buoy Reef, and the other (71 m^2) was on a flat plane dominated by medium-sized massive corals, gorgonians and sponges on the East Fore Reef (sites D and E in Fig. 1 of Woodley *et al*. 1981; sites explicitly compared with respect to coral communities and underlying geomorphology, and how these might influence, and be influenced by, hurricanes, by Liddell & Ohlhorst 1981).

Data recorded for each of the 576 sponge individuals (in 67 species) that were in the two plots included volume (by approximation to geometric solids), substratum type (massive *vs* branching corals), and the amount and type of damage. Fragments of tissue that could readily be identified to species remained on the substratum, even from sponges that were torn off at the base or otherwise seriously damaged. Estimates of original size of sponges before hurricane damage were made on the basis of species-characteristic growth forms, informed by familiarity with the sites and their sponges as a result of daily diving focused on sponges during the 6 weeks prior to the storm. Although imprecise, these estimates did allow each individual to be confidently placed in one of the following four broad categories: 'unharmed'; 'minor damage' (i.e. <1/3 lost, killed or damaged), 'serious damage' (i.e. >1/3 lost, killed or damaged) and 'completely dead' (i.e. the entire sponge was necrotic or only the skeleton remained). Distinction between the second and third categories was generally unambiguous, as injuries to most sponges influenced either less than 1/4 or more than 3/4 of their original tissue volume. It should be stressed that inference of prestorm sponge presence was only possible because (1) it was done in the first

days after the storm, before any damaged sponges deteriorated completely and vanished, and (2) the specific sites and their sponges (including species identities) were well known prior to the hurricane.

The sponge faunas of the two sites were similar, sharing 72% of the total number of sponge species, but they appeared quite different because of a few large and conspicuous species present in the EFR plot but not in the UB plot (*Xestospongia muta*, *Mycale laxissima* and *Callyspongia plicifera*). Species diversity was slightly higher on the EFR (61 species *vs* 59 species at UB), and there were twice the number of sponge individuals in the EFR plot as in the UB plot.

Detailed maps of the sites, on which every sponge was plotted, allowed monitoring of recovery, or continued deterioration, of every individual. Recovery of a sponge was deemed complete when the surface cell layer (pinacoderm) was fully reconstituted and the sponge was pumping (determined by ejection of injected fluorescein dye). Detached fragments were labelled with numbered pieces of forestry tape so their reattachment could be monitored for up to 5 weeks after the hurricane.

Patterns in the amount and type of damage, and subsequent recovery, were evaluated by dividing the 67 sponge species into six morphological categories based on a combination of profile presented to moving water, skeletal materials and construction (i.e. resistance to breaking or tearing), and exposure (i.e. entire sponge out in the open *vs* inhabiting cryptic spaces in the reef frame). Categories based on profile, skeletal properties and exposure (illustrated in Fig. 1) were: (1) 'erect branching', small bases and relatively constant branch diameters throughout ('trees' or 'vines' in Jackson 1979; 'ropes' in Woodley *et al*. 1981); (2) 'fans, vases, tube clusters', small bases with flared tops; (3) 'massive, breakable', large bases and soft or brittle consistency (in most cases a high proportion of siliceous spicules relative to spongin fibres); (4) 'massive tough', large base and tough consistency; (5) 'encrusting', very low profile; and (6) 'cryptic', generally amorphous lumps assuming the shape of their crevices, or encrusting forms and small tubes on undersurfaces of corals.

The 67 species represented 12 of the 13 recognized (Hooper & van Soest 2002) extant orders of the class Demospongiae, and one order of the class Calcarea. Although some sponge orders exhibit only a few growth forms, and skeletal materials (i.e. only spongin *vs* silica spicules and spongin) are determined by taxon, in general taxonomic relatedness of these Jamaican reef sponges did not reliably predict growth form categories, or vice versa: each of the form categories included representatives of three to six orders (mean number of orders represented in a form category was five), and individual sponge orders were represented in from one to five form categories (mean number of form categories in which each order was represented was 2·3).
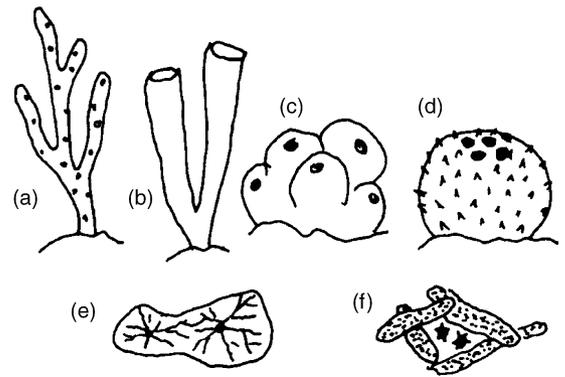

Fig. 1. Examples of the six morphological categories: erect branching, fan or vase, massive breakable, massive tough, encrusting and cryptic. The following were the most common species in each category. Erect branching*: Iotrochota birotulata* Higgin, *Aplysina cauliformis* Carter, *Amphimedon compressa* Duchassaing & Michelotti, *Callyspongia armigera* (Duchassaing & Michelotti), *Agelas sceptrum* (Lamarck); Fan, tube, vase: *Aplysina fistularis* (Pallas), *Verongula gigantea* (Hyatt), *Niphates digitalis* (Lamarck), *Callyspongia plicifera* (Lamarck), *Mycale laxissima* (Duchassaing & Michelotti). Massive soft or brittle: *Neofibularia nolitangere* (Duchassaing & Michelotti), *Ectyoplasia ferox* (Duchassaing & Michelotti), *Erylus formosus* Sollas, *Xestospongia muta* (Schmidt). Massive tough: *Ircinia strobilina* (Lamarck), *Verongula rigida* (de Laubenfels), *Aoiochroia crassa* (Hyatt), *Geodia neptuni* (Sollas), *Agelas dispar* (Duchassaing & Michelotti), *Smenospongia aurea* Hyatt. Encrusting: *Chondrilla nucula* Schmidt, *Scopalina ruetzleri* (Wiedenmayer), *Spirastrella hartmani* (Boury-Esnault *et al*.), *Dysidea etheria* de Laubenfels, *Placospongia intermedia* Sollas, *Cliona varians* (Duchassaing & Michelotti);.Cryptic: *Mycale laevis* (Carter), *Halichondria* sp., *Haliclona* sp., *Callyspongia* sp.

Results

AMOUNT AND TYPE OF DAMAGE

Amount of damage, in terms of the proportion of the original sponge individual that was lost to immediate damage during the hurricane (i.e. none, $<1/3$ = 'minor', $1/3$ = 'serious', or all tissue gone or dead), differed significantly among the six morphological categories ($G = 27\cdot8$, $P < 0\cdot005$, Fig. 2). Sponges with smaller base : volume ratios suffered more serious damage (significant differences between small base : volume, i.e. erect branching and vases, *vs* all others except cryptic, G = 20·9, $P < 0·001$); and those of the lowest profile, encrusting sponges, suffered the least damage (significant differences between encrusting and all others except cryptic, G = 57·3, $P < 0·001$). Cryptic sponges were excluded from these statistical analyses of differences among growth forms, because the number of undamaged cryptic sponges was certainly underestimated, as many surviving individuals were tucked too deep in the reef frame to be counted. Data for the two sites and two substratum types were combined, as the amount of damage did not differ between sites ($G = 0·25$, $P > 0·5$), and damage to

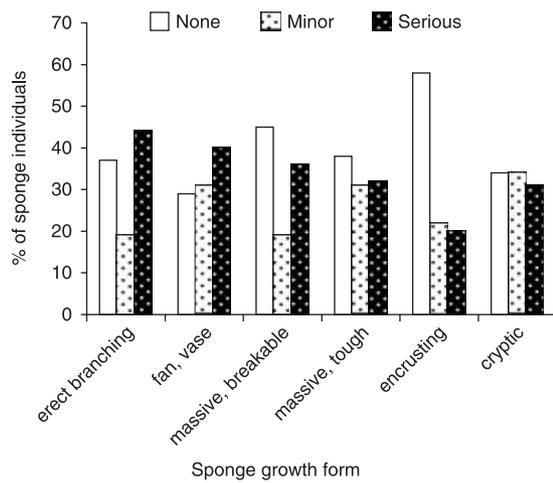**Fig. 2.** The percentage of sponge individuals in six morphological categories that were not damaged, lost <1/3 of their prestorm volume (i.e. minor damage), or lost >1/3 of their prestorm volume (i.e. serious damage) in Hurricane Allen, Discovery Bay, Jamaica. Of the 576 sponge individuals monitored after the hurricane, the 83 unattached fragments are not included in this analysis, so *n* = 493. Total numbers of individuals in each morphological category (the complete list can be obtained from the author): 84 erect branching, 77 fan or vase, 66 massive breakable, 114 massive tough, 91 encrusting, 61 cryptic.

Fig. 3. Percentage of sponge individuals battered, macerated (due to being buried, crushed or exposed) or broken off during Hurricane Allen, Discovery Bay, Jamaica. Total numbers of damaged individuals in each morphological category: 53 erect branching, 55 fan or vase, 36 massive breakable, 71 massive tough, 38 encrusting, 38 cryptic. Of the 576 sponges followed, only the 291 individuals that were damaged are included in this figure. Common species in each morphological category are listed in the caption of Fig. 1.

sponges on massive *vs* branching substrata did not differ (*G* = 0·09, *P* > 0·9).

Type of damage fell readily into three categories: 'battered', with pieces removed by impact of flying debris; 'macerated', with living cells rotting away from or lost from part or all of the skeletal framework (massive sponges became macerated by being buried or crushed, whereas cryptic sponges became macerated by exposure due to movement of corals); and 'broken or torn off'. Frequency of different types of damage did not differ between the two plots (*G* = 5·57, *P* > 0·1), but growth forms were damaged differently (*G* = 4·54, *P* < 0·001). Erect branching sponges, and other forms with very small base : volume ratios or massive forms with soft or brittle skeletons, were vulnerable to being torn off; while encrusting species tended to be battered; and cryptic and large base, tough consistency, species were macerated (Fig. 3).

RECOVERY *vs* CONTINUED DETERIORATION

Of the 291 damaged sponges, 41% had completely regenerated their surfaces and were pumping within 4 weeks after the hurricane, but the other 59% of damaged individuals continued to deteriorate or had completely died. The proportion of damaged sponges that recovered after minor damage did not differ significantly among growth forms (*G* = 4·16, *P* > 0·5), but recovery after serious damage did (*G* = 25·63, *P* < 0·001; Fig. 4).

Recovery success differed among types of wounds. Abrasion wounds due to battering healed within a week, as did basal portions of sponges left behind when
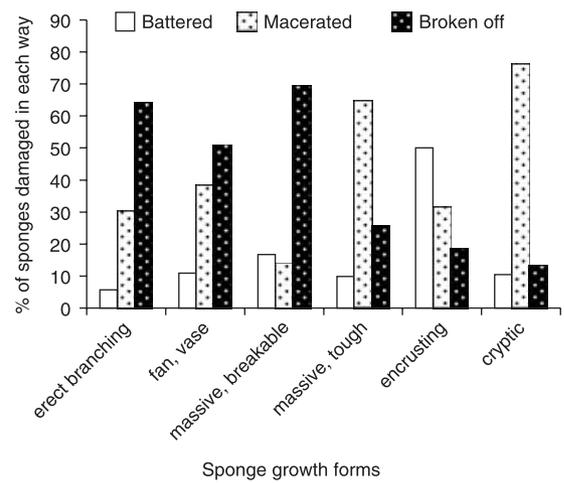
erect portions were broken off. By contrast, necrotic patches often continued to spread, killing sponges by progressive rotting. A few species (e.g. *Amphimedon compressa* and *Agelas* spp.) were able to reconstruct their surface pinacoderm underneath macerated portions, which then fell off as spongin fibres deteriorated. Recovery of some of the cryptic sponges that were exposed as corals broke and overturned was precluded by fishes entirely consuming them.

RECOVERY *vs* RESISTANCE TO DAMAGE

Recovery from serious damage is inversely related to resistance to damage (Fig. 4). The negative correlation between the percentage of individuals of each morphological category that recovered after serious damage and the percentage of individuals with no or only minor damage (i.e. relatively high resistance) in the hurricane was significant (*r* = −1·73; *P* < 0·01).

RECOVERY OF LOOSE FRAGMENTS

During the first 1–3 weeks after the hurricane, 70% of the unattached sponge fragments found on the reef became reattached to solid substrata, and survival of reattached fragments was confirmed by continued monitoring for up to 5 weeks. Reattachment rate was higher for erect branching species (74% of 66 hurricane-generated fragments) than for tubes and vases (33% of 9 hurricane-generated fragments, *G* = 45, *P* < 0·001); and no live fragments of other morphological types reattached (0% of 8 fragments, *G* = 98·6 for comparison of erect branching with all other growth forms, *P* < 0·001). Smaller numbers of live fragments of
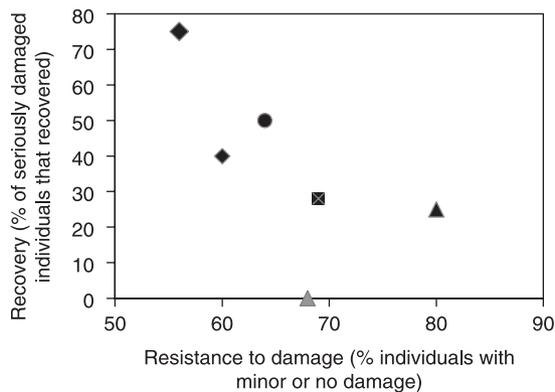
Fig. 4. Inverse association of recovery rate with resistance to damage for 576 individual sponges in six morphological categories (the correlation is significant, with $r = -1.73$, $P < 0.01$). Total numbers of sponge individuals in each morphological category that suffered serious damage: 36 erect branching (large diamond); 30 fan or vase (small diamond); 24 massive breakable (circle); 35 massive tough (square); 16 encrusting (black triangle); 17 cryptic (grey triangle). The resistance of cryptic sponges was greatly underestimated because many undamaged cryptic sponges remained tucked within the reef frame, and could not be counted. The total numbers of individuals in each morphological category are given in the caption of Fig. 2.

massive sponges reflect morphology-dependent transport of fragments off the reef during the storm. Broken-off portions of erect branching and erect flared forms were retained on the reef at a much higher rate (75 live fragments/62 bases = 1·21 fragments/base) than fragments of the large base : volume morphological categories (8 live fragments/55 bases = 0·14 fragments/base).

Discussion

RESISTANCE *vs* RECOVERY

Resistance to and recovery from damage due to physical disturbance appear to represent opposing strategies for coral reef sponges (Fig. 5). Although responses of a diverse assortment of sponges to naturally dealt injuries have not been reported before, sponge recovery has been the focus of many intriguing studies in the field and lab. The potential for ultimate losses to be much greater than indicated by immediate partial mortality has been pointed out by authors who have monitored individual sponges after damage by natural disturbances (Reiswig 1973; Shield & Witman 1993; Schmahl 1999). Relatively poor recovery of more resistant species was also suggested by comparisons of transplantation success among Australian coral reef sponges (Wilkinson & Thompson 1997). Regeneration after experimental wounding has demonstrated the importance of rapid regeneration to prevent fouling of exposed skeletal elements (Leys & Lauzon 1998), prevent settlement of algae on bared substratum separating portions of damaged encrusting sponges (Turon *et al.* 1998), maintain competitive superiority

in space-limited systems (Jackson & Palumbi 1979), reattach if fragmented (Wilkinson & Thompson 1997), and to regain optimal size and shape for feeding (Bell 2002).

Data from the present study, on recovery *vs* continued deterioration of individuals of many sponge species after a hurricane, provides a framework for evaluation of other data on sponge responses to damage by physical disturbance, organized by morphological categories (Fig. 5), as follows.

Completely hidden sponges: cryptic species

Cryptic sponges rely on their hidden habitat to protect them from physical disturbance or large mobile predators. When sponge species that live concealed to different degrees were exposed to parrotfishes, grazing rate increased with the normal degree of concealment (Fig. 4 in Wulff 1997b). Fish have also been observed to completely consume some cryptic sponges that live under coral slabs in the west Pacific (Bakus 1964), under coral rubble in the Caribbean (Dunlap & Pawlik 1996), and under cobbles and in crevices in the reef frame in the tropical eastern Pacific (Wulff 1997c). The poor recovery of cryptic sponges observed in this study is not surprising in this context: ability to regenerate is a moot point for a sponge that has been entirely consumed.

Very low profile sponges: encrusting species

Encrusting sponges escaped damage by Hurricane Allen altogether (58%) better than those of any other growth form (although escape by cryptic species was underestimated). Half the damaged individuals were battered, which is especially problematic for encrusting species because tissue is removed to the substratum, allowing opportunistic algae to colonize bared spaces between separated bits of an individual (also remarked on by Turon *et al.* 1998). Encrusting sponges that lost >1/3 of their original bodies recovered at a low rate (25%).

Small holes made by Jackson & Palumbi (1979) in seven species of encrusting sponges regenerated at rates ranging from 1 to 2 days to 21–30 days to never. Descriptions (by the authors) of slowly regenerating species as 'tough' and 'coarse and tough (hard to penetrate)', contrast with their descriptions of rapidly regenerating species as 'wispy' or 'firm', suggesting that, even within the 'encrusting' morphological category, sponge regeneration rate is inversely related to resistance to damage.

Breakable vs *tough massive sponges*

Contrasting abilities to resist damage *vs* recover are well illustrated by breakable *vs* tough massive sponges. Fragments of soft, crumbly, or brittle massive sponges ended up in sand channel graveyards of dead and dying sponges, but bases regenerated readily. By
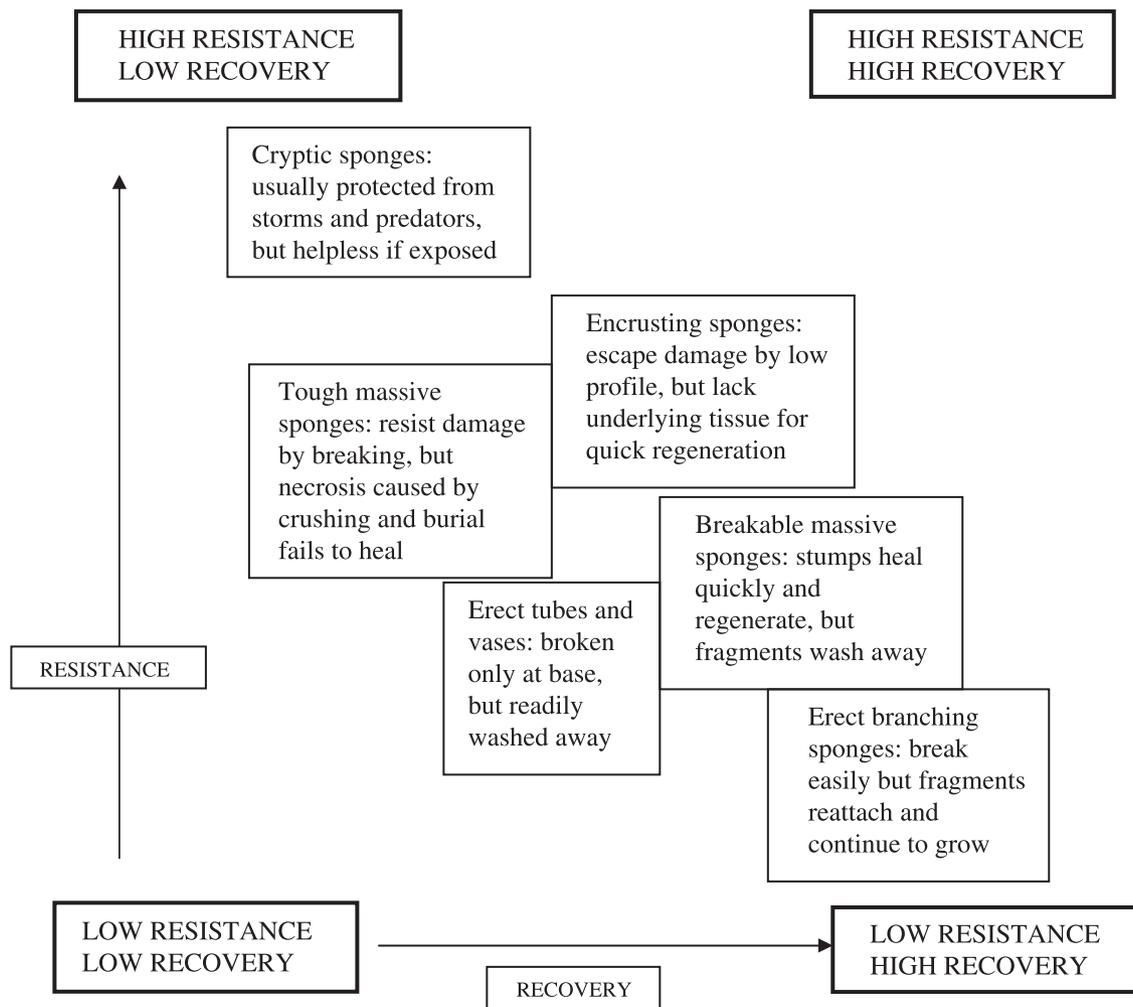
| HIGH RESISTANCE LOW RECOVERY | | HIGH RESISTANCE HIGH RECOVERY |

Cryptic sponges: usually protected from storms and predators, but helpless if exposed

Encrusting sponges: escape damage by low profile, but lack underlying tissue for quick regeneration

Tough massive sponges: resist damage by breaking, but necrosis caused by crushing and burial fails to heal

Breakable massive sponges: stumps heal quickly and regenerate, but fragments wash away

RESISTANCE

Erect tubes and vases: broken only at base, but readily washed away

Erect branching sponges: break easily but fragments reattach and continue to grow

| LOW RESISTANCE LOW RECOVERY | RECOVERY | LOW RESISTANCE HIGH RECOVERY |

Fig. 5. Contrasting morphological strategies of coral reef sponges. Morphological categories are based on a combination of overall growth form, skeletal materials, and cryptic *vs* exposed life habit. Evaluations of relative resistance and recovery ability are made on the basis of reactions of sponges in each morphological category to the severe physical damage meted out by Hurricane Allen in Discovery Bay, Jamaica.

contrast, many massive sponges with tough skeletons were unscathed; but those that were crushed or buried developed necrotic patches, which spread until the sponges died. Thus the hurricane ultimately killed a larger percentage of tough massive sponges than those in any other morphological category (total losses after 5 weeks were 36% for massive tough, *vs* 21·4% for erect branching, 27·3% for massive breakable, and 27·5% for encrusting sponges). Resistance of massive tough sponges to rough water movement *per se* helps them to survive moderate disturbance (e.g. Wulff 1995); but a storm extreme enough to hurl chunks of solid carbonate resulted in low survival. Corroborating these data, regeneration of small holes made in the surfaces of three massive sponge species, two highly resistant and one very easily broken, was most rapid in the easily broken species (Hoppe 1988).

Branched vs *flared morphologies of erect sponges*

Small base : volume sponges were damaged mostly by breakage. Bases of fans and vase left on the substratum recovered well, but the flared portions were not adept at reattaching; a pattern also reported by Reiswig (1973) and Wilkinson & Thompson (1997). By contrast, any living portion of an erect branching sponge is able to reattach to solid carbonate, facilitating fragment recovery. Propagation by fragmentation is an integral part of the life histories of branching sponges (e.g. Wulff 1985, 1986, 1991), so selection for attributes contributing to fragment survival is continuous in these species.

Influence of skeletal materials on resistance and recovery of erect species

Influence of skeletal materials on resistance to breakage is illustrated by effects of a hurricane on six common erect sponge species (four erect branching species, one erect tube cluster and one open vase) in Panama (Wulff 1995). Bases of sponges with skeletons solely of spongin snapped less than half as frequently as bases of sponges with skeletons combining spicules and spongin.
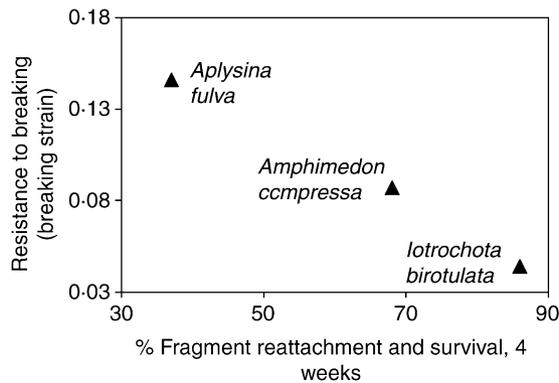
Fig. 6. Inverse relationship between mean breaking strain (i.e. resistance to breaking, $n = 25$ for each species; data from Wulff 1997a) and percentage reattachment and survival of fragments for the first 4 weeks after experimental fragment generation ($n = 100$ for each species; data from Wulff 1985) of the erect branching sponge species *Iotrochota birotulata*, *Amphimedon compressa* and *Aplysina fulva*.

Skeletal materials further subdivide the erect branching sponges with respect to a resistance–recovery continuum. Significant differences in extensibility among three species (Wulff 1997a) coincided with differences in survival of attached sponges during a hurricane: *Iotrochota birotulata*, with lowest breaking strain, survived the worst ($42 \cdot 4\%$, $n = 430$), *Amphimedon compressa* was intermediate ($57 \cdot 1\%$ survived, $n = 202$), and *Aplysina fulva*, capable of stretching the most with each wave before snapping, survived the best ($68 \cdot 8\%$, $n = 386$).

After the storm waves calm down, recovery of loose fragments depends on their reattachment to solid substrata. Traits that ensure success at reattachment differ from traits that aid survival of individuals that remain attached, as experimentally generated fragments of these same three species differed in survival for the critical first 4 weeks (Wulff 1985), in an inverse relationship to resistance to breaking (Fig. 6).

INTEGRATION WITHIN AN INDIVIDUAL, AND THE COMPLEXITY–REGENERATION TRADE-OFF

Julian Huxley explored the trade-off between increased complexity and decreased ability to regenerate in his 1912 book *The Individual in the Animal Kingdom*. Sponges intrigued him as a clear endpoint in a continuum between simplicity/regeneration and complexity/integration; but debate on how to define an individual in sponges continued until Hartman & Reiswig (1973) compiled sufficient evidence to confirm that a sponge is morphologically, developmentally and physiologically an integrated individual, capable of reorganizing itself to optimize the functioning of the entire individual during size and orientation changes associated with growth and recovery from injury.

For all organisms, internal integration is most important for species with functional and morphological differentiation among parts. Sponges exhibit the least differentiation among parts of all multicellular animals, but some sponges have differentiated, for example, into supportive stalks with flared upright portions, cortex portions surrounding inner medulas, or bulbous bases with upright papillae or fistules. Years of transplantation experiments on the Great Barrier Reef illustrate relatively poor recovery of internally differentiated sponges (Wilkinson & Thompson 1997). Among 16 sponge species representing various growth forms and higher taxa, the three stalked species stood out by never reattaching. The authors suggested that the stalks, differentiated to provide support, had lost the ability to reattach. Reiswig (1973) also reported the inability of a stalked vase-shaped Caribbean species, *Mycale laxissima*, to reattach; and vase-shaped sponges broken by Hurricane Allen reattached significantly less than the morphologically homogeneous erect branching forms.

Some sponges are functionally differentiated into surface *vs* inner tissue. Concentration of predator-deterrent compounds in surfaces (Uriz *et al*. 1996; Wulff 1997b; Becerro, Paul & Starmer 1998; Schupp *et al*. 1999; Furrow *et al*. 2003) may optimize deployment of expensive secondary metabolites, as long as the surface is not breached. *Mycale laevis*, one of the most common semicryptic species on the Jamaican fore-reef, is protected from consumption by parrotfishes when the surface is intact, but consumed when the surface is removed (Wulff 1997b); and was never observed to recover after damage by Hurricane Allen.

A tough outer cortex surrounding an inner medulla may also protect against predators (with the exception of Hawksbill Turtles, with their large and powerful beaks) and most physical disturbances, but sponges with cortex regions (e.g. *Geodia neptuni* and *Cinachyrella keukenthali*) were never seen to heal after damage by Hurricane Allen, and in a comparison of 2 temperate sponge species (Duckworth 2003), experimental wounds regenerated move slowly in the species with structured surface layers. The amount and type of damage appear to influence regeneration success in species with tough cortex regions (e.g. Connes 1966, as cited by Simpson 1984; van Dam & Diez 1997; Hoffmann *et al*. 2003).

Curiously, as was also pointed out by Jackson (1979) in his discussion of 'Morphological strategies of sessile animals', regeneration might be expected to be most important for forms with internal division of function, because the individual depends on integration among all its parts. Yet, among the sponges, these are the forms that appear least able to regenerate, suggesting an incompatibility between resistance and recovery strategies that is not negotiable.

These accumulated data raise the following questions about underlying mechanism: are there physiological or morphological conflicts in what is required to be adept at resistance *vs* recovery that make these inherently opposing strategies? If so, might phylogenetic constraints influence these conflicts? Or do the patterns result from an allocation issue, with limited resources

divided differently between resistance and recovery by each species?

RESISTANCE *vs* RECOVERY IN THE CONTEXT OF CORAL REEF CONSERVATION

Sponges play many key functional roles on coral reefs, many of which are influenced by sponge growth form. Of particular importance with respect to health of coral reef ecosystems are efficient water-filtering by sponges and the ability of sponges to mediate regeneration of damaged reefs, and to increase survival of living corals for which basal attachment has been compromised (e.g. reviews in Diaz & Rützler 2001; Wulff 2001, 2006; Rützler 2004).

Collection of postdisturbance data solely in the form of population or community level data on percentage cover, or number of individuals (i.e. the typical approach) would have provided an overly optimistic view of hurricane survival (59% of the individual sponges that had partially survived the storm had died or continued to deteriorate 1 month after the storm), and also obscured the trade-off between resistance to damage and the capacity to recover (Figs 4 and 5) that may explain how the more resistant species suffered the greatest losses.

Sponges are not the only sessile clonal animals for which resistance and recovery may be opposing strategies. An inverse relationship between resistance to breaking and rate of recovery was reported for two branching coral species (*Acropora palifera*, *A. millepora*) in Australia (Liddle & Kay 1987); and studies of recovery from hurricane damage by readily fragmented Caribbean species such as *Acropora cervicornis* (Staghorn Coral) and *A. palmata* (Elkhorn Coral) conclude that their rapid growth and ability to reattach help to transform damage into propagation (e.g. Highsmith, Riggs & d'Antonio 1980; Tunnicliffe 1981; Highsmith 1982). This transformation can be derailed, however, as it was for *A. cervicornis* damaged by Hurricane Allen. The unanticipated death, within 5 months, of 98% of the live fragments that were labelled and monitored after the storm (Knowlton *et al*. 1981) focused attention on recovery threshold effects that depend on disturbance size and responses of coral predators (Knowlton, Lang, & Keller 1990).

For species that have been served well, until now, by suites of traits that promote resistance instead of recovery; the ability to resist might be overwhelmed by the increasing rate and intensity of physical disturbances affecting coral reefs. If there is a trade-off between resistance and recovery, we might expect to see disproportionate, and difficult to remedy, loss of resistant species. Although most clonal animals are also capable of recovery at the population level by recruitment of sexually produced larvae, this mode is steadily becoming less effective as growth of filamentous and fleshy algae renders reef surfaces inhospitable to settlement of larvae (e.g. Pandolfi *et al*. 2005).

Exclusive focus on population or community level responses to physical disturbance fails to distinguish susceptibility to injury from lack of recovery. This is a critical distinction. Conservation concerns tend to be focused on species most drastically and directly diminished by disturbance. But the counterintuitive results reported here make a strong case for more attention to the resistant species that may be less immediately affected, but ultimately lost because they are unable to recover. At the same time, learning how to facilitate recovery of organisms that are adept at individual recovery after damage may be useful. These good regenerators may increasingly come to characterize life on coral reefs; as population level recovery by recruitment is stymied by reef surfaces coated with opportunistic algae, and resistance to damage is increasingly overwhelmed by disturbances that are too novel, frequent or large. The degree to which resistance and recovery are incompatible strategies for other groups of organisms may influence how biotas change in response to increasing disturbance in other ecosystems.

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References

Bakus, G. (1964) The effects of fish-grazing on invertebrate evolution in shallow tropical waters. *Allan Hancock Foundation Occasional Paper* **27**, 1–29.

Becerro, M.A., Paul, V.J. & Starmer, J. (1998) Intracolonial variation in chemical defenses of the sponge *Cacospongia* sp. and its consequences on generalist fish predators and the specialist nudibranch predator *Glossodoris pallida*. *Marine Ecology Progress Series* **168**, 187–196.

Bell, J.J. (2002) Regeneration rates of a sublittoral demosponge. *Journal of the Marine Biology Association UK* **82**, 169–170.

Bellwood, D. & Hughes, T.P. (2001) Regional-scale assembly rules and biodiversity of coral reefs. *Science* **292**, 1532–1534.

Bonner, J.T. (1988) *The Evolution of Complexity by Means of Natural Selection*. Princeton University Press, Princeton, MA.

van Dam, R.& Diez, C.E. (1997) Predation by hawksbill turtles at Mona Island, Puerto Rico. *Proceedings of the 8th International Coral Reef Symposium, Panama*. **2**, 1421–1426.

Diaz, C. & Rützler, K. (2001) Sponges: an essential component of Caribbean coral reefs. *Bulletin of Marine Science* **69**, 535–546.

Duckworth, A.R. (2003) Effect of wound size on the growth and regeneration of two temperate subtidal sponges.

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Functional Ecology,
20, 699–708

Journal of Experimental Marine Biology and Ecology **287**, 139–153.

Dunlap, M. & Pawlick, J. (1996) Video-monitored predation by Caribbean reef fishes on an array of mangrove and reef sponges. *Marine Biology* **126**, 117–123.

Furrow, F.B., Amsler, C.D., McC., Lintock, J.B. & Baker, B.J. (2003) Surface sequestration of chemical feeding deterrents in the Antarctic sponge *Latrunculia apicalis* as an optimal defense agaist sea star spongivory. *Marine Biology* **143**, 443–449.

Gardner, T.A., Côté, I.M., Gill, J.A., Grant, A. & Watkinson, A.R. (2003) Long-term region-wide declines in Caribbean corals. *Science* **301**, 958–960.

Hartman, W.D. & Reiswig, H.M. (1973) The individuality of sponges. *Animal Colonies, Development and Function Through Time* (eds R.S. Boardman, A.H. Cheetham & W.A. Oliver, Jr), pp. 567–584, Dowdon, Hutchinson and Ross, Stroudsberg.

Highsmith, R.C. (1982) Reproduction by fragmentation in corals. *Marine Ecology Progress Series* **7**, 207–226.

Highsmith, R.C., Riggs, R.C. & D'Antonio, C.M. (1980) Survival of hurricane-generated coral fragments and a disturbance model of reef calcification/growth rates. *Oecologia* **46**, 322–329.

Hoffmann, F., Rapp, H.T., Zöller, T. & Reitner, J. (2003) Growth and regeneration in cultivated fragments of the boreal deep water sponge *Geodia barretti* Bowerbank, 1858 (Geodiidae, Tetractinellida, Demospongiae). *Journal of Biotechnology* **100**, 109–118.

Hooper, J.N.A. & van Soest, R.W.M., eds (2002) *Systema Porifera: A Guide to the Classification of Sponges*. Kluwer Academic/Plenum Publishers, London.

Hoppe, W.F. (1988) Growth, regeneration and predation in three species of large coral reef sponges. *Marine Ecology Progress Series* **50**, 117–125.

Huxley, J.S. (1912) *The Individual in the Animal Kingdom*. Cambridge University Press, Cambridge.

Jackson, J.B.C. (1979) Morphological strategies of sessile animals. *Biology and Systematics of Colonial Organisms* (eds G. Larwood & B.R. Rosen), pp. 499–555. Academic Press, London,.

Jackson, J.B.C. & Hughes, T.P. (1985) Adaptive strategies of coral-reef invertebrates. *American Scientist* **73**, 265–273.

Jackson, J.B.C. & Palumbi, S.R. (1979) Regeneration and partial predation in cryptic coral reef environments: preliminary experiments on sponges and ectoprocts. *Colloques Internationaux du CNRS* **291**, 303–308.

Knowlton, N., Lang, J.C., Rooney, M.C. & Clifford, P. (1981) Evidence for delayed mortality in hurricane-damaged Jamaican staghorn corals. *Nature* **294**, 251–252.

Knowlton, N., Lang, J.C. & Keller, B.D. (1990) Case study of natural population collapse: post-hurricane predation on Jamaica staghorn corals. *Smithsonian Contributions to the Marine Sciences* **31**, 1–25.

Lang, J.C. (2003) Status of the Coral Reefs in the Western Atlantic: Results of Initial Surveys, Atlantic and Gulf Rapid Reef Assesment (AGRRA) Program. *Atoll Research Bulletin* **496**, i–630.

de Laubenfels, M.W. (1949) *Life Science*, 4th edn. Prentice Hall, Inc. New York.

Leys, S.P. & Lauzon, N.R.J. (1998) Hexactinellid sponge ecology: growth rates and seasonality in deep water sponges. *Journal of Experimental Marine Biology and Ecology* **230**, 111–129.

Liddell, W.D. & Ohlhorst, S.L. (1981) Geomorphology and community composition of two adjacent reef areas, Discovery Bay, Jamaica. *Journal of Marine Research* **39**, 791–804.

Liddle, M.J. & Kay, A.M. (1987) Resistance, survival and recovery of trampled corals on the Great Barrier Reef. *Biological Conservation* **42**, 1–18.

Pandolfi, J.M., Jackson, J.B.C., Baron, N., Bradbury, R.H., Guzman, H.M., Hughes, T.P., Kappel, C.V., Micheli, F., Ogden, J.C., Possingham, H.P. & Sala, E. (2005) Are U.S. coral reefs on the slippery slope to slime? *Science* **307**, 17225–11726.

Reiswig, H.M. (1973) Population dynamics of three Jamaican Demospongiae. *Bulletin of Marine Science* **23**, 191–226.

Rützler, K. (1978) Sponges in coral reefs. *Coral Reefs: Research Methods* (eds D.R. Stoddart & R.E. Johannes) Monographs on Oceanographic Methodology Vol. 5, UNESCO, Paris.

Rützler, K. (2004) Sponges on coral reefs: a community shaped by competitive cooperation. *Bollettino Dei Musei Istituti Biologici* **68**, 85–148.

Schmahl, G.P. (1999) Recovery and growth of the giant barrel sponge (*Xestospongia muta*) following physical injury from a vessel grounding in the Florida Keys. *Memoirs of the Queensland Museum* **44**, 532.

Schupp, P., Eder, C., Paul, V. & Proksch, P. (1999) Distribution of secondary metabolites in the sponge *Oceanapia* sp. and its ecological implications. *Marine. Biology* **135**, 573–580.

Shield, C.J. & Witman, J.D. (1993) The impact of *Henricia sanguinolenta* (O.F. Müller) (Echinodermata: Asteroidea) predation on the finger sponges, *Isodictya* spp. *Journal of Experimental Marine Biology and Ecology* **166**, 107–133.

Simpson, T.L. (1984) *The Cell Biology of Sponges*. Springer Verlag, New York.

Slobodkin, L.B. (1992) *Simplicity and Complexity in Games of the Intellect*. Harvard University Press, Cambridge, MA.

van Soest, R.W.M. (1994) Demosponge distribution patterns. *Sponges in Time and Space: Biology, Chemistry, Paleontology* (eds R.W.M. van Soest, T.M.G. van Kempen & J.-C. Braekman,), pp. 213–224. A.A. Balkema, Rotterdam.

Tunnicliffe, V. (1981) Breakage and propagation of the stony coral *Acopora cervicornis*. *Proceedings of the National Academy of Science USA* **78**, 2427–2431.

Turon, X., Tarjuelo, I. & Uriz, M.J. (1998) Growth dynamics and mortality of the encrusting sponge *Crambe crambe* (Poecilosclerida) in contrasting habitats: correlation with population structure and investment in defence. *Functional Ecology* **12**, 631–639.

Uriz, M.J., Becerro, M.A., Tur, J.M. & Turon, X. (1996) Location of toxicity within the Mediterranean sponge *Crambe crambe* (Demospongiae: Poecilosclerida). *Marine Biology* **124**, 583–590.

Wilkinson, C.R. (2004) *Status of Coral Reefs of the World: 2004*. Australian Institute of Marine Science, Townsville, Australia.

Wilkinson, C.R. & Thompson, J.E. (1997) Experimental sponge transplantation provides information on reproduction by fragmentation. *Proceedings of the 8th International Coral Reef Symposium, Panama* **2**, 1417–1420.

Woodley, J.D., Chornesky, E.A., Clifford, P.A., Jackson, J.B.C., Kaufman, L.S., Lang, J.C., Pearson, M.P., Porter, J.W., Rooney, M.C., Rylaarsdam, K.W., Tunnicliffe, V.J., Wahle, C.W., Wulff, J.L., Curtis, A.S.G., Dallmeyer, M.D., Jupp, B.P., Koehl, M.A.R., Neigel, J. & Sides, E.M. (1981) Hurricane Allen's impact on Jamaican coral reefs. *Science* **214**, 749–755.

Wulff, J.L. (1985) Dispersal and survival of fragments of coral reef sponges. *Proceedings of the Fifth International Coral Reef Congress, Tahiti* **5**, 119–124.

Wulff, J.L. (1986) Variation in clone structure of fragmenting coral reef sponges. *Biological Journal of the Linnean Society* **27**, 311–330.

Wulff, J.L. (1991) Asexual fragmentation, genotype success, and population dynamics of erect branching sponges. *Journal of Experimental Marine Biology and Ecology* **149**, 227–247.

Wulff, J.L. (1995) Effects of a hurricane on survival and orientation of large, erect coral reef sponges. *Coral Reefs* **14**, 55–61.

Wulff, J.L. (1997a) Mutually beneficial associations among species of coral reef sponge. *Ecology* **78**, 146–159.

Wulff, J.L. (1997b) Parrotfish predation on cryptic sponges of Caribbean coral reefs. *Marine Biology* **129**, 41–52.

Wulff, J.L. (1997c) Causes and consequences of differences in sponge diversity and abundance between the Caribbean and eastern Pacific at Panama. *Proceedings of the 8th International Coral Reef Symposium, Panama* **2**, 1377–1382.

Wulff, J.L. (2001) Assessing and monitoring coral reef sponges: why and how? *Bulletin of Marine Science* **69**, 831–846.

Wulff, J.L. (2006) Rapid diversity and abundance decline in a Caribbean coral reef sponge community. *Biological Conservation* **127**, 167–176.