

JANIE L. WULFF\*  
Bingham Laboratories  
Department of Biology  
Yale University  
New Haven, Connecticut 06511

## Patterns and Processes of Size Change in Caribbean Demosponges of Branching Morphology

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### Abstract

The processes by which branching demosponges can change size and shape were studied in three species of different orders for almost two years. During this time, individuals of *Amphimedon rubens* (Haplosclerida), *Aplysina fulva* (Dictyoceratida), and *Iotrochota birotulata* (Poecilosclerida) were monitored undisturbed to determine the relative importance of gradual size change compared to growth and abrupt changes caused by fragmentation into smaller portions or fusion with other individuals. At the start of the study, detailed drawings and size measurements were made of 50 individuals of each species. The same data were collected after 9 months, and again after 22 months.

Analysis of the drawings and measurements indicates that these sponges grow by adding tissue exclusively to the tips of erect branches. A variety of circumstances favor initiation of new erect branches, but repent branches are formed only when erect branches become prone. Repent and basal portions of the sponges are disproportionately heavily affected by various agents of partial mortality, and a majority of fragments are generated by damage to basal and repent portions.

Patterns of addition and loss of tissues are very similar in these three species, reflecting their common branching morphology. Variation among these species in the relative importance of the different processes of site change may result from differences in skeletal materials and construction.

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Demosponges can increase and decrease in size gradually, by growth and regression, and also abruptly, by fusion among conspecific individuals and by fragmentation into smaller portions. Unusually homogeneous construction, extreme morphological flexibility, and high regeneration capabilities allow some demosponges to add to or lose

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\*Present address: Bunting Institute, 34 Concorde Avenue, Cambridge, Massachusetts 02138.

from any portion of themselves without mortal loss of functional integrity. The processes and consequences of complex size change in sponges may therefore provide a challenging comparison to the biology of size in organisms that are only able to change size according to an inherent growth program.

The part of a sponge where material is lost or added may reflect an adaptive balance between avoiding the effects of various agents of mortality and reaping the benefits of particular positions on the substratum or in the water column. On the other hand, patterns of addition and loss of material may simply be the result of chance and the phylogenetic relationships and gross morphology that place bounds on the adaptive changes possible for a species.

## Methods

Patterns of size change were examined in three species of branching Caribbean demosponges, each representing a different order: *Iotrochota birotulata* (Higgin), *Amphimedon rubens* (Pallas) (= *Amphimedon compressa* Duchassaing and Michelotti, sensu Wiedenmayer, 1977), and *Aplysina* (= *Verongia*) *fulva* (Pallas). For systematic discussion see de Laubenfels (1936) and van Soest (1978). The orders represented are Poecilosclerida, Haplosclerida, and Verongiida, respectively. Overall, the branching growth forms of these three species are very similar, but branch diameter and branching patterns vary both within and among species.

The three species are common on shallow-water Caribbean reefs and live attached to living or dead corals and to carbonate rubble. The populations studied live interspersed on a flat plane (2.1 m to 2.3 m below MLW) and on a slope of about 16 degrees (2.3 m to 5 m below MLW) off Guigala tupo, a small mangrove and coconut palm island near the San Blas Field Station of the Smithsonian Tropical Research Institute in Panama.

From the populations of each species I chose 50 healthy individuals of various sizes and tagged them with tiny plastic cable ties. I then made detailed drawings of these individuals on underwater slates and recorded the size of all branches and branch segments of each sponge (1) at the start of the study, (2) after 9 months, and (3) after 22 months (Figure 1). The sponges remained undisturbed in the field throughout the study.

Branch widths are sufficiently constant within individuals of these species so that total length of all branch segments is proportional to total volume. Total length is therefore a convenient measure of size. Comparisons of size among individuals must be made carefully, of course, and then only in terms of percentage increase or decrease. The cable ties and branching points provide reference points on the drawings so that comparisons of the draw-

ings in time series for each individual indicate the locations in the sponges where material was added or lost.

## Results

Net size changes in all individuals measured at 0, 9, and 22 months are plotted in Figure 2. These plots reflect three characteristics of net growth: (1) fragmentation into independent portions and fusion with other conspecifics in a large proportion of the sponges; (2) highly variable growth rates among individuals, but (3) relatively constant growth rates within individuals, even in some individuals that became fragmented or fused with other individuals.

The processes of growth, fusion, fragmentation, and partial mortality by which the sizes of sponges are changed differ in importance among species, both in terms of the numbers of individuals affected and the amount of biomass involved.

## GROWTH

Growth was the only apparent process by which size changed for nearly half of the sponge individuals in the first 9 months (36.2%, 56.5%, 51.1% of the individuals of *Iotrochota birotulata*, *Amphimedon rubens*, and *Aplysina fulva*, respectively; see Figure 3). Wherever size measurements from both 0 and 9 months could be compared, new material was added only to the tips of erect branches (sample sizes were 27, 47, and 63 for *I. birotulata*, *A. rubens*, and *A. fulva*, respectively). No extension of the centers of branches of basal portions, or of branches lying on the substratum (repen branches) was observed.

The locations at which new branches were initiated could be determined from the drawings in time series (see Figure 1). New erect branches were initiated by bifurcation of tips or by sprouting from the sides of pre-existing erect branches, from the points at which other sponges had adhered to branches, from basal attachments or where repen branches had adhered to the substratum, and from the upward reorientation of the tips of repen branches. New erect branches were initiated in all of these ways in individuals of each species, but the relative proportions of each differed among the species (Figure 4). For example, nearly half (46.9%) of the new branches of *Iotrochota birotulata* sprouted from the sides of existing erect branches, whereas more than half (56.3%) of new branches in *Amphimedon rubens* resulted from the upward turning of the tips of repen branches (for typical examples, see Figure 1).

Repen branches, however, are initiated very differently. Repen branches do not appear to branch in the plane of the substratum. Thus, they do not arise through the branching of pre-existing repen branches but only from erect branches that bend over and become prone or



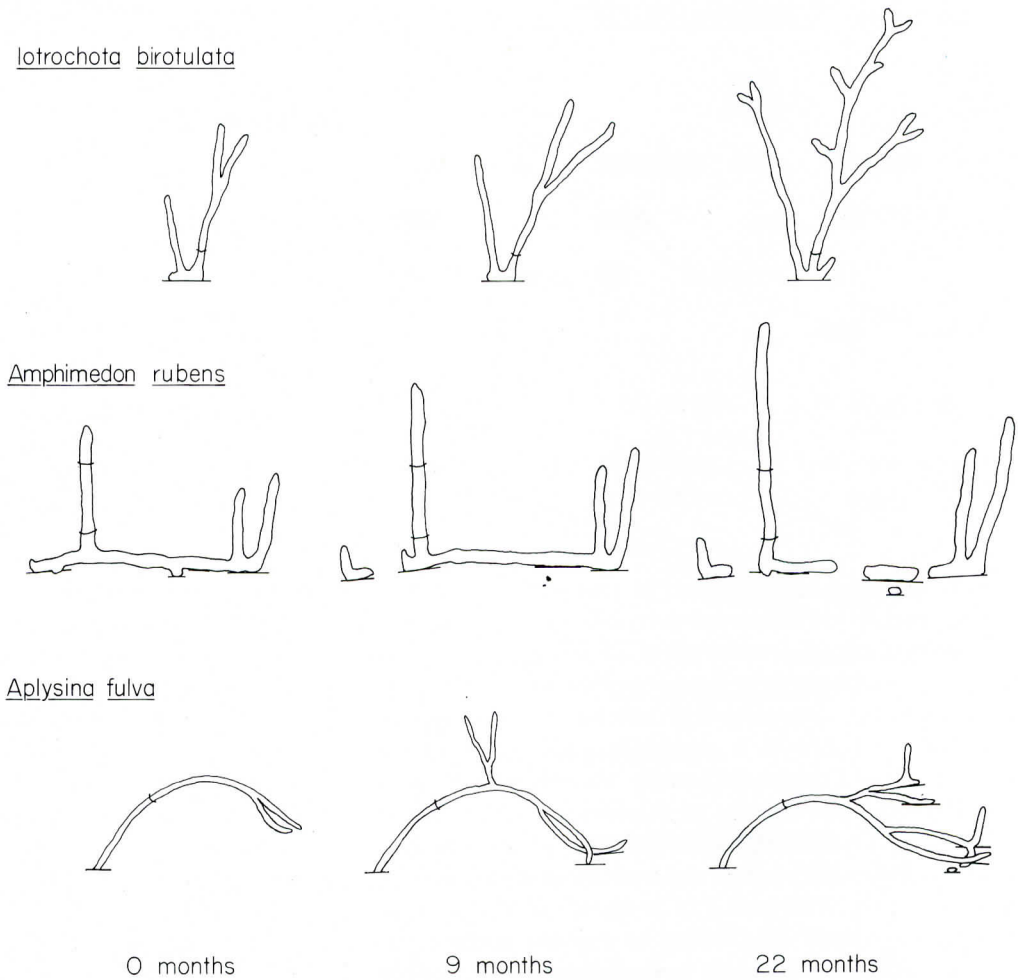


Figure 1. Schematic drawings, in time series, of one representative individual of each species studied. Straight horizontal lines indicate where sponges adhered to substratum (carbonate rubble, primarily from coral skeletons); lines crossing branches are growth reference markers (cable ties).

from fragments of erect branches that come to rest in a prone position (Figure 5).

**FUSION**

Some monitored sponges that came into contact with neighboring conspecific individuals fused with them during the first 9 months (6.4% and 19.1% of the individuals of *Iotrochota birotulata* and *Aplysina fulva*, respectively; Figure 3) and between 9 and 22 months (7.7% and 13.3% in the same species). Fusion merges previously physiologically independent individuals into one confluent sponge. In the Guigala tupo populations of these species, fusion appears, in most cases, to indicate that the independent sponges are clone-mates—that is, that the sponges were derived from each other by an earlier fragmentation (Wulff, 1986a). With regard to change in the size of a physiologically confluent individual, the effects of fusion with another sponge can be striking. The total size of physiologically confluent sponges was increased by fusion by a mean of 177.5% for *I. birotulata* and of 486.6% for *A. fulva* (Figure 3). Obviously, fusion does not actually in-

crease the total amount of biomass. However, if the size of a physiologically continuous individual influences life history parameters, such as mortality and reproduction, fusion with a conspecific neighbor may change the subsequent life of the individual under consideration. The propensity for tissue-compatible branches to fuse is also illustrated by the many individuals in which branches became fused or that produced fragments that subsequently fused back onto the “parent” sponge during the first 9 months (19.2% 4.4%, 14.9% of the individuals of *I. birotulata*, *A. rubens*, and *A. fulva*, respectively) and between 9 and 22 months (38.5%, 23.8%, 60.0% for the same species).

**FRAGMENTATION AND PARTIAL MORTALITY**

Fragmentation and partial mortality are closely related in that some live tissue may be lost in the course of generating fragments, and some of the fragments produced may die. In addition, some sponges that appeared to have suffered partial mortality without producing fragments may have actually produced fragments that I was unable to

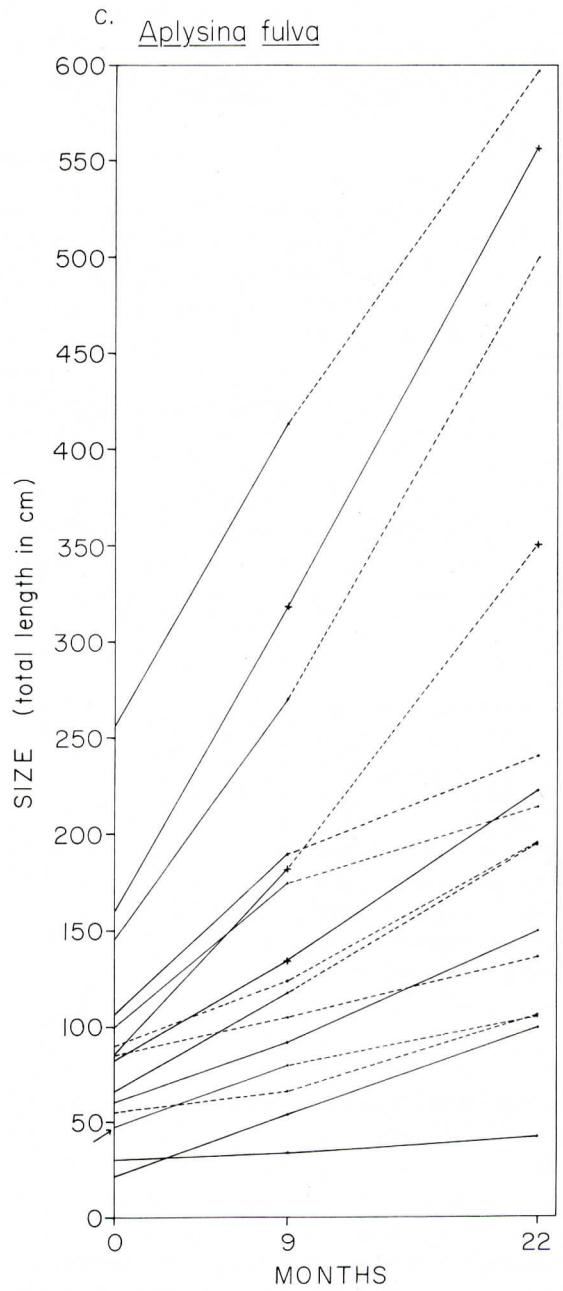
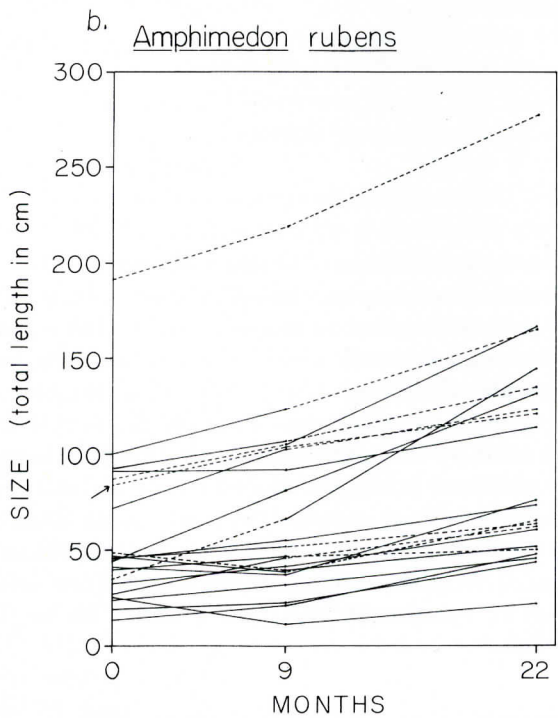
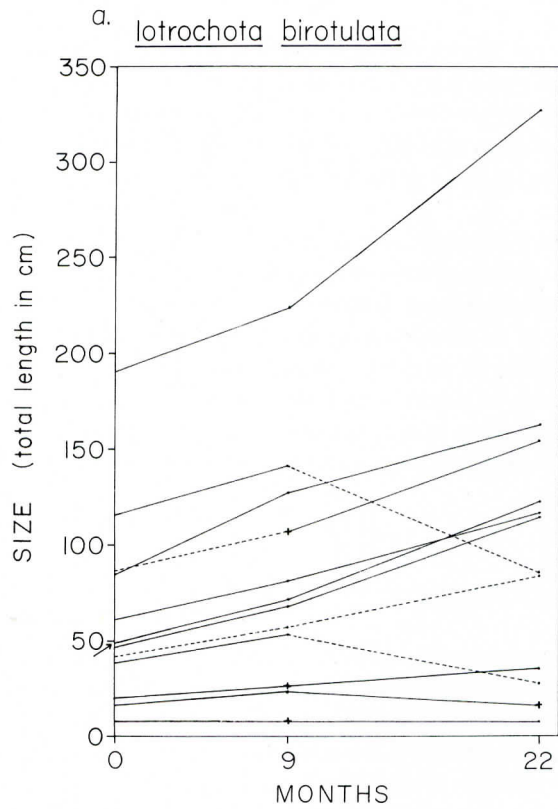


Figure 2. Change in size over time for all individuals for which measurements were made after 9 and 22 months: a, *Iotrochota birotulata*; b, *Amphimedon rubens*; c, *Aplysina fulva*. Fewer than 50 sponges of each species are represented because marker tags were lost from many individuals between observations at 9 and 22 months. Dotted lines indicate that sponge fragmented; all fragments found were combined for total size indicated. Each point at which a sponge was found to have fused with a previously independent conspecific individual marked with a plus (+); additional individual not included in total size. Arrows indicate individuals illustrated in Figure 1.



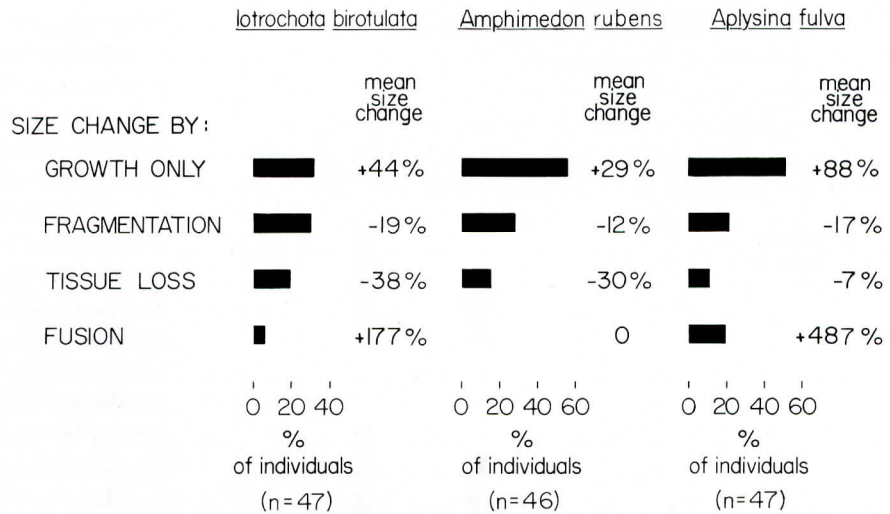


Figure 3. Relative importance of different processes by which size can be changed. Bars represent proportions of individuals that changed size; percentages do not always add up to 100 because a few sponges both fragmented and fused with other conspecific individuals. Numbers indicate mean percent by which size was changed.

find because they had been dispersed. The importance of fragment production relative to partial mortality may therefore be underestimated by this tabulation. Together, fragmentation and partial mortality influenced net size change in 1/3 to 2/3 of the individuals in these populations (62%, 43%, 32% in *Iotrochota birotulata*, *Amphimedon rubens*, and *Aplysina fulva*, respectively) during the first 9-month period of observation (Figure 3) and also between 9 and 22 months (31%, 48%, 60% for these species). One way of assessing the importance of fragmenta-

tion in the dynamics of these sponge populations is to examine the rate of increase in numbers of physiologically independent individuals by asexual fragmentation. For example, of the 47 individuals of *I. birotulata* monitored during the first 9 months, 15 fragmented. These produced a total of 28 new individuals, 3 of which subsequently fused back onto their "parent" sponges. The net increase in numbers of individuals by asexual fragmentation was therefore 53.2% (= 25/47) of the original population size. The populations of *A. rubens* and *A. fulva* were similarly increased by additions of 41% and 23%, respectively, of the original number of individuals. Between 9 and 22 months, the populations of these three species were increased by additions of, respectively, 31%, 43%, and 60% of the number of individuals, solely by asexually produced fragments from monitored sponges.

Fragments can be produced by breakage of branches during storms, the bites of sponge-feeding fishes, localized infections by pathogens, mounds of sediment raised by burrowing shrimp or holothurians, grazing by starfish and foraging by eagle rays, and encroachment by other sessile organisms. Some of these agents of fragmentation or partial mortality tend to damage specific portions of the sponges. For example, violent currents may break erect branches, whereas mounds of sediment may sever repent branches by smothering portions of them. The majority of fragments that came from the monitored sponges resulted from damage to portions of sponges that were lying prone on the substratum, either discrete basal attachments or repent branches. This, presumably, reflects the relative importance of the various agents of fragment generation. Fewer than 1/3 of the fragments produced (33%, 17%, 13% of fragments from *I. birotulata*, *A. rubens*, and *A. fulva*, respectively) resulted from damage to erect branches (Figure 6).

Patterns of the loss of material from these sponges, both in the course of fragment production and when fragments

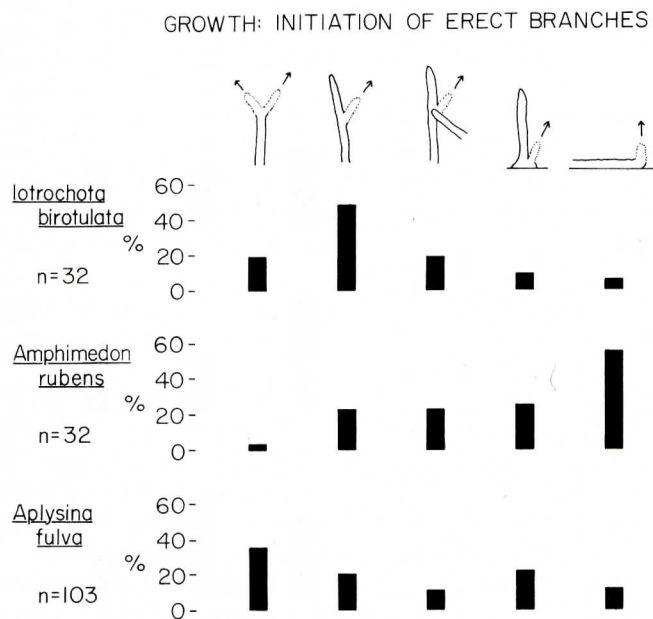


Figure 4. Positions from which new erect branches were initiated: bifurcation of erect branch, sprouting from side of erect branch, area where another sponge adhered to branch, basal attachment to substratum, upward reorientation of tip of repent branch. Bars represent percentage of erect branches initiated between 0 and 9 months.

GROWTH: INITIATION OF REPENT BRANCHES

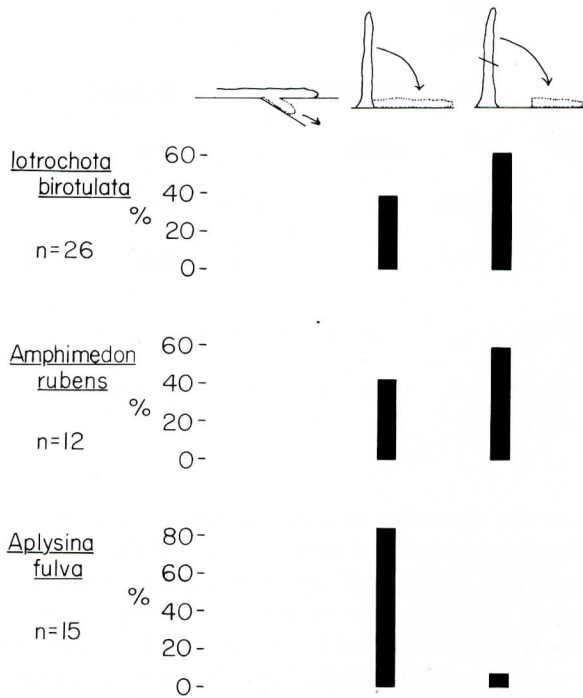


Figure 5. Initiation of new repent branches: branching of repent branch in plane of substratum, by bending down of erect branch to prone position, or by production of fragment from erect branch. Bars represent percentage of repent branches formed between 0 and 9 months.

were not found, also demonstrate disproportionately heavy partial mortality on basal and repent portions. Proportions of the total lengths of sponges that were in repent or basal portions at the initial measurement were less than one quarter (16.0%, 24.2%, 13.5% of the total length for *Iotrochota birotulata*, *Amphimedon rubens*, and *Aplysina fulva*, respectively). If partial mortality is random with respect to the part of the sponge affected, then less than one quarter of the material lost from these individuals would be expected to have come from basal and repent portions. However, about 1/2 of the material lost (48.4%, 45.3%, 58.3% for *I. birotulata*, *A. rubens*, and *A. fulva*, respectively) was from these portions that had been lying on the substratum (Figure 7).

SIGNIFICANCE OF INITIAL SIZE FOR CHANGE IN SIZE

Specific growth rates are compared directly in Figure 8, plotted as the percentage increase against initial size, for all individuals monitored during the first 9 months. Perhaps because of the substantial contributions of fragmentation, fusion, and partial mortality to net size change in

these sponges, initial size appears to be largely unrelated to subsequent size change. Although the few individuals that grew at the most rapid rates were all very small initially (Figure 8), growth appears, on the whole, not to be strongly influenced by initial size. In order to test for dependence of specific growth rate on size, for each species, all individuals that changed in size by growth only were divided evenly into three groups: the third with the largest, the third with the smallest, and the third with intermediate initial sizes (from the data plotted in Figure 8). These three groups did not differ significantly in specific growth rates for *Amphimedon rubens* and *Aplysina fulva* (no significant differences in pairwise comparisons within species by the Wilcoxon rank sum test;  $p > 0.23$ ), but for *Iotrochota birotulata*, small sponges had significantly higher specific growth rates than sponges of intermediate or large initial sizes ( $p = 0.03$  and  $p = 0.05$  for small versus intermediate, and small versus large, respectively).

Smaller sponges were more likely to have changed size by addition of live tissue, that is, by growth or fusion, whereas larger sponges were more likely to have lost tissue (differences significant by the Wilcoxon rank sum test;  $p = 0.015$ ,  $p = 0.005$ ,  $p = 0.025$  for, respectively, *Iotrochota birotulata*, *Amphimedon rubens*, and *Aplysina fulva*).

FRAGMENT GENERATION

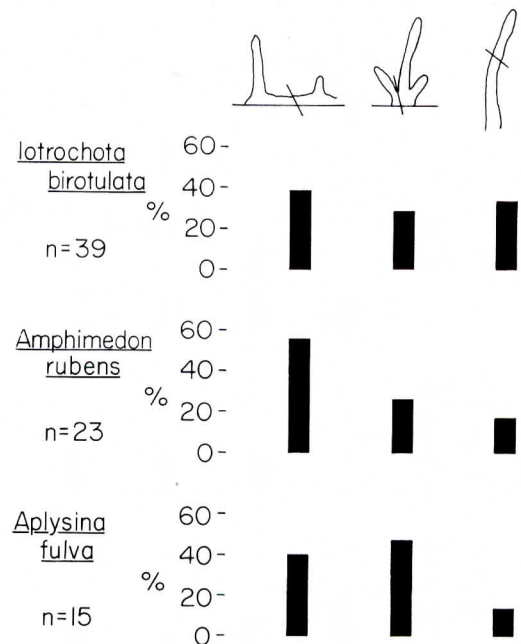


Figure 6. Production of fragments caused by damage to repent branches, to discrete basal attachments, or to erect branches. Bars represent percentage of fragments produced between 0 and 9 months.



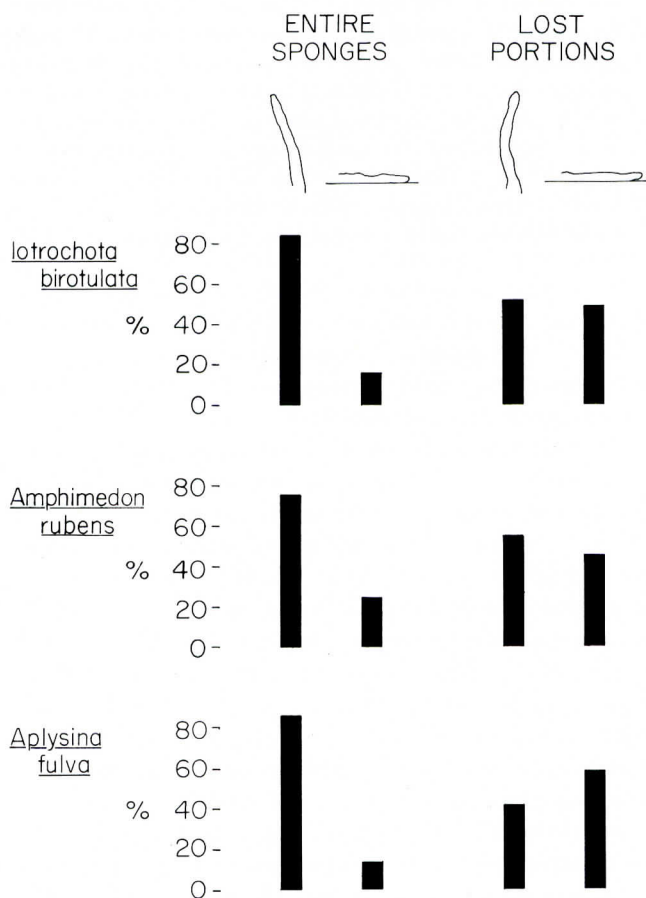


Figure 7. Effects of position relative to substrate on partial mortality. Pairs of bars on left of each set represent percentage of total branch lengths found in erect or repent portions of sponges at start of study. Pairs of bars on right represent percentage losses after 22 months. If partial mortality is random with respect to position of tissue in sponges, percentages lost from erect or repent portions should be the same as percentages of tissue found in erect or repent portions.

**Discussion**

**PATTERNS OF SIZE CHANGE**

Fewer than one half of the individuals in these sponge populations changed size by growth only, nearly one third became fragmented, and the others decreased in size by partial mortality or increased in size by fusion with other conspecific individuals during the first nine months.

Specific growth rates did not differ significantly between sponges of large, medium, or small initial size, except for *Iotrochota birotulata*. Susceptibility to partial mortality did, however, appear to be affected by size in these sponges. For each species, individuals that lost portions or became fragmented were significantly larger, initially, than those that only changed size by growth or fusion.

Increase in the size of individuals by growth occurs only at the tips of erect branches. The field observations on

which this conclusion is based did not provide information on where new cells originate or exactly where, on a microscopic scale, new material is added to the growing tip (see Simpson, 1984 for a review of cellular growth in sponges). New erect branches are formed in a variety of ways from previously existing erect branches and from basal attachments and repent branches. In contrast, repent branches are only formed by changes in the orientation of previously erect branches, or by fragmentation. The majority of fragments are produced by damage to repent or basal portions, and partial mortality is disproportionately heavy on basal attachments and repent branches.

Although casual observations suggest that these sponges appear to be growing as vines, extending along the substratum as they grow, this appearance is misleading. Here I continue to use the term "repent" to refer to the position of the branches that lie adherent to the substratum. However, if "repent" is used to imply active growth along the substratum, as is the case in many plants (e.g., the clover *Trifolium repens*), then this is a misnomer for these sponges. Branches seen in a repent position appear to result invariably from the repositioning of branches that achieved their length in an erect position.

Size change in these sponges can therefore be viewed as a dynamic cycle of addition of new material by growth at the tips, fragmentation and fusion, removal of material from the base by various agents of partial mortality, and the reorientation of toppled or severed branches to again grow upward.

**INFLUENCE OF SIZE ON GROWTH AND SURVIVAL**

Size has been demonstrated to influence growth, mortality, most physiological processes, and sexual reproduction in many organisms (e.g., Calder, 1984; Jackson, 1979). Effects of size may be of special interest when the organisms studied can both increase and decrease in size throughout their lives. For such organisms, primarily clonal invertebrates and plants, the importance of the decoupling of size from age has been recognized (e.g., Connell, 1973; Harper, 1977; Hughes and Jackson, 1980; Hughes, 1984, and references therein). In clonal organisms, such as bryozoans and corals, increased size may increase survival, increase sexual reproduction, and decrease growth rates (e.g., Connell, 1973; Loya, 1976; Jackson, 1979 and references therein).

For the three species of branching sponges considered in this study, the growth patterns of unmanipulated sponges that vary in size and occur in natural populations suggest that effects of size on growth may be nearly swamped by other influences. Although fusion with previously independent conspecific individuals can have a dramatic effect on the total size of a physiologically con-

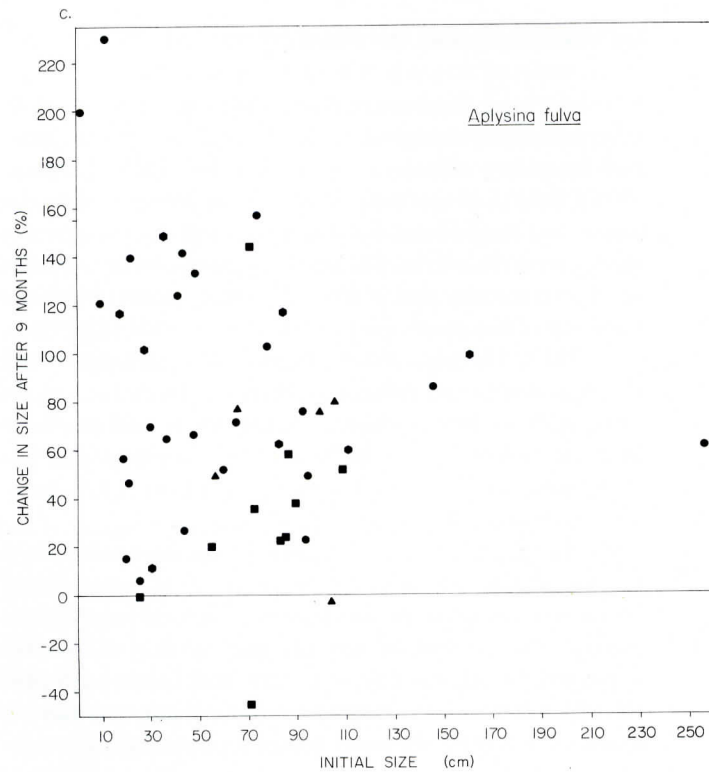
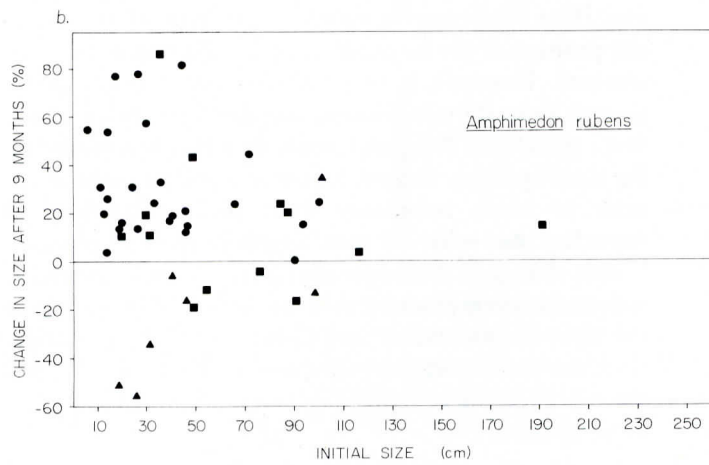
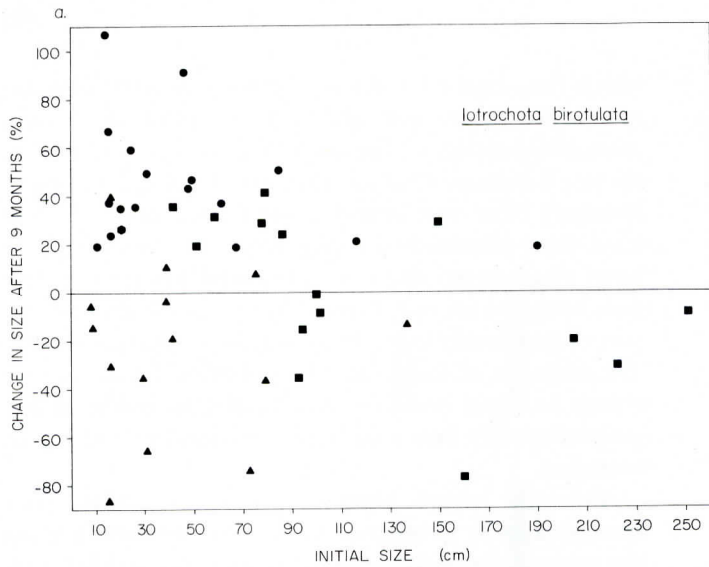


Figure 8. Specific growth rates expressed as percentage size change plotted against initial size for all individuals measured at 0 and at 9 months: a, *Iotrochota birotulata*; b, *Amphimedon rubens*; c, *Aplysina fulva*. Circles represent sponges that changed size only by growth; octagons represent sponges that fused with another conspecific individual and from which no material was lost; squares represent sponges that became fragmented (all fragments combined for total size); triangles represent sponges from which material was lost but no recognizable fragments were found.



fluent individual, growth rates of the originally monitored portions generally did not change when fusion brought about a sudden increase in size (see Figure 2). Similarly, the growth rates of many individuals that became fragmented did not change, even though two or more smaller individuals had taken the place of one larger sponge (Figure 2). On the other hand, continued linearity of these growth curves, plotted on arithmetic axes, demonstrates that the specific growth rate (growth standardized by initial size) of each individual does slow down as the organism increases in size. Enormous variation in growth rates among individuals, even among those that changed size only by growth, may make it impossible to determine the relationship between size and growth in these organisms without experiments in which genotype is controlled.

Slower growth rates have been demonstrated for larger individuals of some sponge species of massive or tubular morphology (e.g., Storr, 1964; Reiswig, 1973; Dayton, 1979). Differences in overall morphology may help to explain why the effects of size on growth rate appear to be more subtle in the three branching species in this study. The growth of massive or tube-shaped sponges is marked not only by changes in size, but also by changes in shape. In particular, ratios of surface area to volume tend to decrease with growth. This may have especially profound effects for filter-feeding organisms and therefore may be an important confounding factor of the interdependence of size and growth. By contrast, the surface-to-volume ratios of the branching species in this study do not change significantly with growth. If decrease in surface area relative to volume is a primary reason for the decreased rate of accumulation of biomass by larger massive sponges, then the apparently milder effect of overall size on growth rates of these branching species may be the expected result.

Partial mortality in these sponges disproportionately affected the larger individuals. Partial mortality has also been observed to disproportionately (with respect to numbers of physiologically independent individuals) affect larger corals in foliaceous species (Hughes and Jackson, 1980). Mortality of entire individuals has been demonstrated to decrease with increased size for scleractinian coral species (e.g., Connell, 1973; Highsmith et al., 1980; Hughes and Jackson, 1980; Hughes, 1984). It is not clear how partial mortality is related to the death of entire individuals in these sponges or perhaps in any clonal species. Fragmentation, which often involves partial mortality, may even increase the survival of the genotype in some cases. Asexual propagation might be predicted to increase with increased size simply because larger individuals have more material into which they can be fragmented. Sexual reproduction was not studied for the monitored individuals of these branching species, and it is possible that increased size increases the production of sexual propagules. However, virtually all successful recruitment into

these populations is by asexual fragments (Wulff, 1986b) and so the overall importance of increased sexual reproduction to these sponges is not clear.

#### ADAPTIVE SIGNIFICANCE OF PATTERNS OF SIZE CHANGE

These three species exhibit strikingly similar patterns of size change. Although they share a common overall growth form (i.e., branching), their skeletal constructions are different to the extent that they are placed in different orders. These common patterns of size change may therefore be related to common branching morphology rather than taxonomic factors and thus may give clues to the advantages and disadvantages of this growth form for demospoges.

Disproportionately heavy mortality of basal and repent portions may give a selective advantage to sponges that actively add of material only to erect branches. Growth at the tips of erect branches also helps to raise more of the sponge into the current above the bottom, where there is, presumably, increased food and decreased resuspended sediment. If decreased partial mortality and access to better water quality accrue to the sponge that only builds upward, perhaps the high rates of fragmentation and production of repent branches seen in these sponges are incidental aspects of their life histories.

One often suggested advantage of repent branches is that they enable the "parent" organism to place genetically identical "offspring" in favorable habitat nearby (e.g., Leakey, 1981 and references therein; Lasker, 1983). This possibility has been explored in some detail for various plants. Extreme examples are plants that are known to "track" favorable microhabitats by the growth of runners or stolons (e.g., Kershaw, 1962; Turkington and Harper, 1979).

If repent branches of these sponges do not grow along the substratum, then it does not seem possible that they are tracking favorable microhabitats by growth. Depending on the relative importance of various sources of mortality, particular microsites may not be predictably good or bad, in any case, and distantly dispersed asexual fragments might provide better insurance against demise of the genotype (Wulff, 1986a). Unattached fragments of these species are able to disperse far, and many survive and become established as independent individuals (Wulff, 1985). Unattached fragments of *Aplysina fulva*, however, have significantly lower rates of survival than those of the other species, both after distant dispersal by a storm and under calm weather conditions (Wulff, 1985). This is also the species for which fewer fragments were formed from erect branches (Figure 6), a greater percentage of lost portions were from repent branches (Figure 7),



a greater majority of repent branches were formed by bending over of erect branches rather than by fragmentation (Figure 5), a higher proportion of resettlement of cleared areas was by repent branches from neighboring individuals (Wulff, 1986b), and a higher proportion of monitored sponges fused with neighboring individuals (Figure 3). The relationship between low survival of unattached fragments and the traits that appear to emphasize fragmentation of repent branches is also evident from the clone structure of this population of *Aplysina fulva*. Those clones (recognized by both tissue compatibility and morphology) with especially large numbers of independent individuals are characterized by overall morphologies dominated by repent branches (Wulff, 1986a), as expected if repent branches play an important role in asexual propagation.

Comparisons among the syntopic populations of these three species might suggest, then, that *Iotrochota birotulata* and *Amphimedon rubens* are designed to propagate by dispersing fragments, whereas *Aplysina fulva* is designed to carefully place its clone members nearby because unattached fragments survive poorly. However, the discovery that repent branches do not grow in that orientation suggests a more cautious interpretation. The characteristics of *A. fulva* that may cause fragments to survive poorly (very narrow branches, elastic skeletal construction) may also be the very characteristics that cause branches to bend over and become prone. Dense tissue of sponges of this genus may also help to make repent branches especially susceptible to being severed by smothering under sediment mounds. Apparent adaptations for careful placement of asexual propagules may therefore be simple consequences of the construction of this species (that is, "exaptations", see Gould and Vrba, 1982). Comparisons of populations in habitats with different disturbance regimes and substratum availability are needed, along with more information on processes of growth on the cellular level, in order to fully understand the advantages and disadvantages, and the adaptive significance, if any, of these patterns of size change for demosponges of branching morphology.

## Conclusions

Size and shape change in these three sponge species results from a combination of growth, fusion, fragmentation, and partial mortality. Fewer than half of the individuals changed size by growth only during the first nine months of the study. Growth adds tissue only to the tips of erect branches. Although repent branches may appear to be growing in the plane of the substratum, they must have achieved their length in an erect position. Specific growth rates of large sponges are either the same as or lower than

those of smaller sponges. New erect branches are initiated in ways that vary in relative importance among the three species. New repent branches result from toppling of erect branches and not from branching in the plane of the substratum. More than half of the sponges changed size abruptly, by fusion, fragmentation, or partial mortality. Large sponges were more likely to fragment or suffer partial mortality than were small sponges. Partial mortality was disproportionately heavy on basal and repent portions and, likewise, the majority of fragments resulted from damage to basal and repent portions. Size and shape change in these branching species is a dynamic cycle of addition of new material by growth at the erect tips, rearrangement by fragmentation and fusion, removal of material from the base by various agents of partial mortality, and the reorientation of toppled or severed branches to again grow upward.

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