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Asexual fragmentation, genotype success, and population dynamics of erect branching sponges

Janie L. Wulff

Maritime Studies, Williams College, Mystic Seaport, Mystic, Connecticut, USA

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Abstract: Three common species of erect branching sponges on Caribbean coral reefs propagate almost exclusively by asexual fragmentation. Fragments are generated frequently, are able to disperse before establishing themselves as independent individuals, survive well, and are responsible for virtually all successful recruitment into their populations. With respect to numbers of individuals, populations are dominated by smaller size classes, reflecting continuous generation of small individuals by fragmentation of large individuals. Because specific growth rates of these sponges decrease with increasing size, fragmentation is predicted to be the preferred strategy for increasing representation of a genotype in the population as long as mortality associated with fragmentation is not high. Fragment dispersal obviates several of the usual constraints on frequency of a genotype in a population by ensuring local genotypic heterogeneity in spite of low overall genotypic diversity in the populations.

Key words: Asexual fragmentation; Coral reef sponge; Population dynamics

Introduction

Asexual fragmentation divides an individual into two or more physiologically independent and smaller individuals of the same genotype. Whether or not the subsequent fate of that genotype will be improved by fragmentation depends on the many biological processes that are influenced, positively or negatively, by organism size and physiological integration. For example, division into many small independent individuals might prevent spread of pathogens throughout the tissue of the genotype, decrease the probability that the entire genotype is killed at once by very local disturbances, and increase specific growth rate (growth rate standardized by size). Dispersal of severed fragments could further decrease the probability that a genotype is eliminated by a single disturbance. On the other hand, a single large individual might be predicted to fare better in competitive interactions, resist pathogens better, increase sexual reproduction, be better buffered against physiological stress, and be more likely to survive predator attacks.

These predicted effects of individual size and physiological integration among ramets on survival, growth, and reproduction are beginning to be tested in field populations of

Correspondence address: J.L. Wulff, Maritime Studies, Williams College, Mystic Seaport, Mystic, CT 06355, USA.

clonal organisms. Large size, resulting from maintenance of connections among ramets, has been demonstrated to aid survival and establishment in clones of the goldenrod *Solidago canadensis* (Hartnett & Bazzaz, 1983) and other clonal plants (e.g., Pitelka & Ashmun, 1986). Large scleractinian corals of foliaceous growth form survive better than small individuals, although large individuals are more likely to suffer partial mortality (Hughes & Jackson, 1980). Sexual reproduction is terminated in a gorgonian if tissue is fragmented into small, physiologically independent portions (Wahle, 1983). On the other hand, growth rates of smaller individuals are faster for at least some scleractinian corals (e.g., Connell, 1973; Loya, 1976) and demosponges (e.g., Storr, 1964; Reiswig, 1973) and particle-capture rates of a soft coral are increased by colony fission into smaller individuals (McFadden, 1986). In summary, maintenance of integrity of the individual (i.e., large size) has been demonstrated to be advantageous in some cases, and fragmentation (i.e., small size) has been demonstrated to be advantageous in others (more examples in Sebens, 1987).

How fragmentation influences the ultimate fate of a genotype must be directly related to growth form, capacity to heal wounds, and characteristics, such as nervous system coordination and internal transport systems, that influence the degree to which the various parts of an individual can be integrated with each other. Thus taxa which differ from each other in these characteristics might be expected to differ from each other in the effects of fragmentation on the fate of a genotype. Theory of asexual propagation has been developing based chiefly on results from plants and cnidarians, groups characterized by internal transport systems through which all physiologically confluent units are integrated. Sponges, which completely lack obvious mechanisms of physiological integration, such as nerve cells or vessels for rapid directional transport of metabolites, provide a useful contrast.

This study describes recruitment, growth, fragmentation, mortality, and population structure for three common species of Caribbean demosponges of branching morphology, placing particular emphasis on the degree to which these population dynamics processes are influenced by the extreme propensity of these sponges to fragment asexually.

METHODS

SPECIES AND STUDY SITE

Branching growth forms are characteristic of coral reef populations of the three species of demosponges chosen for this study: *Iotrochota birotulata* Higgin, *Amphimedon rubens* (Pallas) [= *Amphimedon compressa* D & M, sensu Wiedenmayer (1977)], and *Aplysina* (= *Verongia*) *fulva* (Pallas) [see systematic discussions by de Laubenfels (1936) and van Soest (1978)]. Although overall branching growth forms are very similar for these species, resembling trees, bushes, and vines, their skeletons are constructed differently to the extent that each represents a different order of the class Demospongiae; respectively, Poecilosclerida, Haplosclerida, and Verongiida. Within populations of

each species, individuals differ from each other in branching patterns, branch diameters, and extents to which branches lie adherent to the substratum or grow up into the water column. Branches range in diameter from 0.5 to 3 cm, and physiologically confluent individuals range from < 1 cm up to 2 m in largest dimension of the three dimensional space occupied by the branches. Asexual fragments, generated when branches are severed, can be dispersed by gravity or currents before becoming established as independent individuals (Wulff, 1985). Consequently, clones composed of many genetically identical individuals, derived from each other by fragmentation, can be spread over large areas and can be interspersed with members of other clones (Wulff, 1986)

Demosponges are not generally divisible into unambiguously defined repeating units such as the zooids and polyps of colonial invertebrates or rosettes and tillers of clonal plants. Therefore, by "individual" I will mean all tissue enclosed within a single continuous surface pinacoderm, i.e., physiologically confluent, as suggested by Hartman & Reiswig (1973). For organisms that fragment asexually, "individual" could also refer collectively to all physiologically independent fragments representing a single genotype. When referring to this type of individual, which in these populations can be far flung, I will use "clone".

The populations studied live on a shallow plane and on the slopes of a channel to the leeward of Guigala Tupo, an island near the San Blas Field Station of the Smithsonian Tropical Research Institute in Panama. The substratum is a homogeneous mixture of rubble from ramose coral species, especially *Acropora cervicornis* (Lamarck) and *Porites furcata* Lamarck, dotted with small to medium-sized (up to 1 m in diameter) massive corals of several species. Experiments were established in an area of $\approx 25 \times 25$ m, extending over a flat plane at -2.1 to -2.3 m below MLW and on an adjacent slope of $\approx 16°$ down to -5 m below MLW. The sponges live attached to dead and live coral heads and especially to the ubiquitous rubble.

The sponge fauna is characteristic of lagoon channels, shallow back-reef areas, steep slopes within bays, and some deep fore-reef habitats, throughout the San Blas Islands and elsewhere in the Caribbean (de Laubenfels, 1936; Bonem & Stanley, 1977; Wiedenmayer, 1977; pers. obs. in Jamaica, Belize, and Panama). The demosponges of the Guigala Tupo community are densely distributed (87.2 ± 15.6 individual sponges $\cdot$ m^{-2}, from a complete census of 16 m^2) and diverse (42 species in 16 m^2). In this habitat, sponge biomass exceeds that of any other group of sessile invertebrates, and the morphological types represented include vases, clusters of tubes, vines, encrusters, excavaters, massive balls, and branching forms. The three erect branching species on which I focus are among the most abundant sponges, in terms of both biomass and numbers of individuals.

RECRUITMENT

Recruitment experiments were initiated by measuring and removing all individuals of six common species of large erect sponges, including the three on which this study is

focused [*I. birotulata, A. rubens, A. fulva, Niphates erecta* D & M, *Callyspongia* (= *Spinosella) vaginalis* (Lamarck), and *Desmapsamma anchorata* (Carter)], from 10 quadrats of 1 m^2. For comparison, in another 10 quadrats of 1 m^2 all sponges were mapped, measured, and left undisturbed. These 20 quadrats were randomly positioned (excluding coral heads >40 cm in diameter) in a 10 × 20 m area between −2.3 and −3.2 m below MLW. All sponges in the quadrats were measured and their locations mapped three times over the subsequent year. These data estimate rates of recruitment by both larvae and asexual fragments as well as population flux due to growth, mortality, fusion, and fragmentation.

Sponges that colonized as asexual fragments rather than as larvae could be distinguished unambiguously because they were oriented with their long axes horizontal instead of vertical, and because they were too large to be accounted for by growth from a larva since the previous census. Sizes achievable by growth from larvae were estimated by extrapolating growth curves towards their origins. Recruited sponges that were too small to be unambiguously determined to be from asexual fragments were counted as deriving from sexually produced larvae, giving a conservative estimate of the proportion of recruitment due to asexual fragments.

GROWTH AND SURVIVAL

Influences of size and shape on growth and survival were determined experimentally. Each experimental sponge was grown on a stake made of 16 gauge stainless steel (No. 304) wire, coated with nontoxic plastic (Tygon) tubing, and with one end bent to grip a piece of dead, clean rubble from the ramose scleractinian coral *Porites furcata*. In the field, sponges were attached to these stakes with tiny plastic cable ties such that sponge tissue did not contact the wire and was able to attach rapidly to the coral rubble. Experimental sponges on stakes were then placed in a grid arrangement, with each sponge 1/3–1/2 m from the nearest neighboring experimental sponge. When the stakes were in place on the reef, the pieces of rubble rested on the substratum, and experimental sponges could grow in normal orientations and on stable natural substrata. All manipulations were performed in the field and sponges were never removed from the sea.

In these easily broken organisms, net growth reflects a combination of growth, fragmentation, fusion, and partial mortality (Wulff, in press). Simple measurements of size are not, therefore, adequate for recording the complexities of addition and loss of material. Photographs are also inadequate representations because branching patterns of these sponges result in complex three-dimensional forms. Detailed drawings of each sponge were therefore made to supplement measurements of length and width of all branch segments at each monitoring period. From these drawings and measurements in time series, patterns of addition and loss of tissue could be determined precisely for each sponge. The distinctive branching patterns and sizes recorded in this way allow recognition of individual sponges even if they become fragmented or detached from the substrata. All drawings and measurements were made in the field, leaving the sponges in place and undisturbed.

Sizes of sponges were estimated by measuring diameters and lengths of all branches and then calculating volume by approximation to solid cylinders. Direct volume measurements by displacement disturb experimental sponges too much for accurate determinations of subsequent growth and mortality rates. Because branch diameters do not change in a regular manner within an individual, combined lengths of all branches accurately reflect relative size. Therefore, total branch length was used for size comparisons of the same individual in time series, or between sponges of the same genotype.

The first group of experiments was designed to allow description of normal long-term growth patterns. From branches of healthy sponges, pieces of 10 cm in length were cut. Each of these experimental sponges (35 of each species) was attached to a stake, and detailed drawings and size measurements of them were made at seven irregular time intervals for 43 months (3.6 y).

The second set of experiments was designed to examine effects of size and shape on specific growth rate (growth rate standardized by biomass). Three lengths of 8 cm and one length of 16 cm were cut from the tips of branches of each of 16 sponges of each species. These pieces were attached to stakes as (1) an 8-cm length alone, (2) a 16-cm length alone, and (3) two 8-cm lengths placed next to each other on the same stake so that they fused longitudinally. This third sponge was therefore 8 cm in length, but of biomass equal to that of the 16-cm length. The resultant individuals allow comparisons of growth and survival among sponges of two sizes and two shapes of the same genotype. Growth of these sponges was measured after 8 months and again after 20 months.

POPULATION DESCRIPTIONS

Populations descriptive statistics must be demonstrated to be consistent with the population structure predicted from population dynamics data. Descriptive data collected for these populations include measurements of all individuals found within 24 m^2 located along two transects, 1 m wide, and intersecting at right angles in the center of the study area. Normal abundance of asexually generated fragments in this habitat was estimated by measuring all unattached fragments of the three species found within 100 m^2 after several months without storms.

RESULTS

RECRUITMENT AND POPULATION FLUX

Recolonization of the 10 cleared 1-m^2 quadrats began immediately and continued at a rapid rate. After 1 yr, reconstituted percentages of the original numbers of sponges that had been cleared from these quadrats were, for *I. birotulata*, *A. rubens*, and *A. fulva*, respectively, 54, 57 and 37%, and the percentages of the cleared biomass reconstituted were 56, 92, and 56% (Fig. 1). Unfortunately, quadrat markers were discovered and

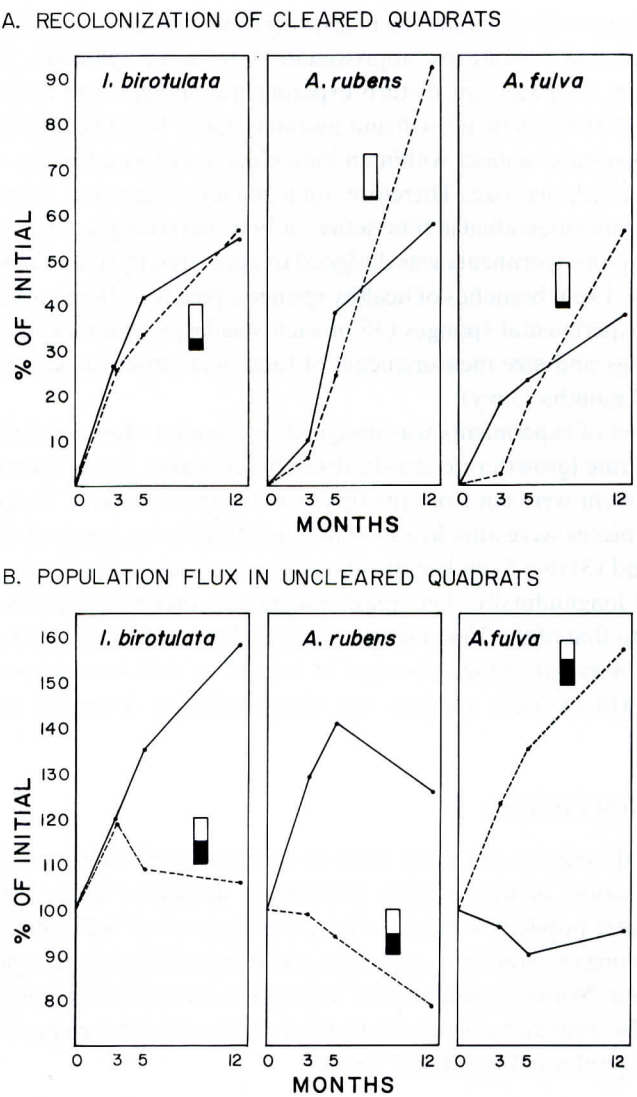


Fig. 1. Recruitment and population flux: Lines represent the percent change from the initial numbers of individuals (solid lines) and initial biomass (broken lines) for cleared quadrats (A) and uncleared control quadrats (B). Experiments were initiated in January–February 1982. Total biomass and the numbers of individuals do not necessarily fluctuate in tandem. Data are combined for 10 quadrats of 1 m^2 each in each treatment. Bar graphs represent the proportions of biomass flux in the final 7 months (between 5 and 12 months after the start of the experiment) due to growth and mortality of resident sponges (filled in) and due to fragment dynamics (open).

removed by unauthorized agents, terminating data collection after 1 yr. However, 2 yr after clearing, no gaps in the sponge cover could be seen by which to locate the cleared quadrats, suggesting, somewhat informally, that recolonization continued apace. Numbers of individuals and biomass fluctuated in the 10 uncleared control quadrats (Fig. 1).

Virtually all recruitment was by asexually produced fragments (distinguished as explained in Methods). Of the 407 recruits that were found in the 20 quadrats, all but nine were unambiguously from asexual fragments. Of six recruits of *A. fulva* with sizes and orientations indicating possible recruitment as larvae, that had colonized by the 3-month census, three vanished during the next 2 months and the other three vanished before the final census. The one possible larval recruit of *I. birotulata* arrived by the 5-month census and vanished before the final census. One more *A. fulva* that may have recruited as a larva was discovered at the final census. Poor survival of these larval colonists contrasts with that of colonists that arrived as asexual fragments. Of the fragments first discovered at the 3-month census, 75% (18/24) survived the next 2 months, and 29% (7/24) survived at least until the final census, at the end of a year. Of the recruited fragments first discovered at 5 months, 51% (17/33) survived the subsequent 7 months (fragment survorship plotted by species in Fig. 2). Initial losses of *A. fulva* fragments were disproportionately high for the first 2 months, but subsequent losses were proportional for all three species. These data may underestimate actual rates of flux, due to undetected turnover of individuals, completed between censuses. Whatever the details of gains and losses of individuals, recolonization clearly proceeded rapidly, both in terms of number of individuals and biomass, and was almost exclusively by asexually generated fragments.

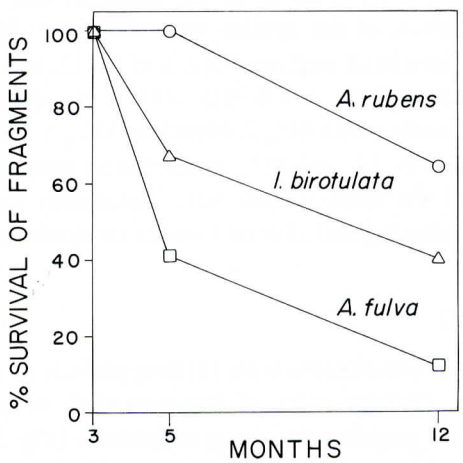


Fig. 2. Loss of colonizing fragments: Lines represent rates of loss of fragments that were first discovered in monitored quadrats at the census 3 months after recruitment experiments were initiated. No distinction is made in this graph between losses due to emigration and those due to mortality.

Asexual propagules colonized primarily as unattached fragments that washed into the marked quadrats and reattached to solid carbonate substrata, such as coral skeletons, and also to other sponges. Colonists were also observed to arrive as repent branches from sponges adjacent to the monitored quadrats. This mode of recolonization was especially important for *A. fulva*. During the final 7 months, 29% of the new asexually generated *A. fulva* individuals in the 20 quadrats entered as repent branches from neighboring sponges rather than as errant fragments, compared to only 8 and 5% of the asexually generated colonists of, respectively, *I. birotulata* and *A. rubens*. This mode of colonization was not common until the final census, because branches of neighboring sponges that extended into cleared quadrats were removed when the experiment was initiated. The time lag of several months reflects the time required for regrowth of branches of neighboring sponges and their subsequent toppling into these quadrats.

Population flux, in terms of turnover in biomass, can be divided into that due to gain and loss of fragments and that due to growth and partial or complete mortality of sponges that are established residents of the monitored quadrats. Estimation of flux due to fragment movement is inherently conservative because some biomass changes tabulated as mortality may have actually represented fragments that dispersed out of the monitored quadrats. Only unambiguous cases of fragment generation and movement were counted as such. Even by this conservative estimate, $\approx 1/2$ of the total biomass changes (52, 56, 42% for, respectively, *I. birotulata*, *A. rubens*, and *A. fulva*) in unmanipulated control quadrats for the final 7 months of monitoring were due to gains and losses of fragments. In the cleared quadrats, during these same 7 months (between 5 and 12 months after clearing), $> 3/4$ of the biomass flux (76, 93, 89% for the three species) can be attributed to fragment dynamics (proportion bars in Fig. 1).

Initial densities, in terms of numbers of individuals, of these three species were 1.7 times as great in uncleared quadrats as in the quadrats that were cleared, but the proportional representations of the species were the same (35% *I. birotulata*, 14% *A. rubens*, and 51% *A. fulva* in cleared quadrats, and 35, 13, and 52% for these species in the uncleared quadrats; G test, $p > 0.981$). After 1 yr, relative proportions of the species were again very similar, with 41% *I. birotulata*, 17% *A. rubens*, and 41% *A. fulva* in cleared quadrats, and 46, 14, and 41% in uncleared quadrats; G test, $p > 0.690$). Relative proportions of the three species were statistically indistinguishable in the cleared quadrats before clearing and after one year of recolonization (G test, $p > 0.386$).

GROWTH AND SURVIVAL

Common to all growth experiments were (1) long periods of constant size increase by individual sponges, (2) high rates of fragmentation or partial mortality, and (3) enormous variation in growth rate among individuals (Fig. 3).

The first striking aspect of growth of these sponges is that size increase appears to have a linear relationship to time (Fig. 3). In most cases, long periods of linear size increase are terminated only by fragmentation or partial mortality. Linear regressions

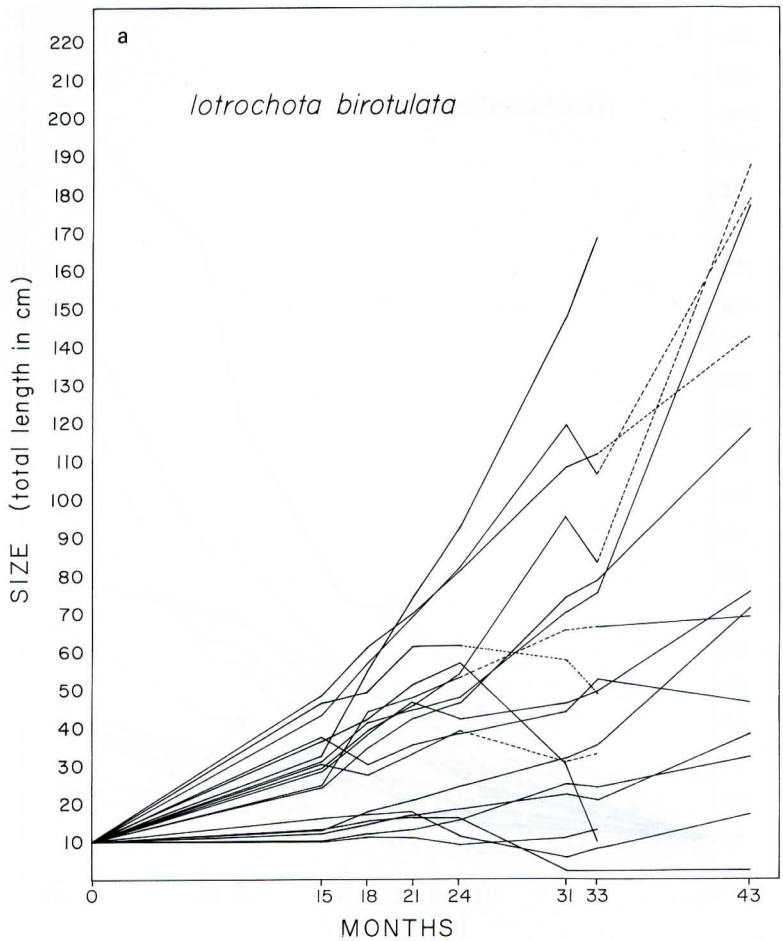
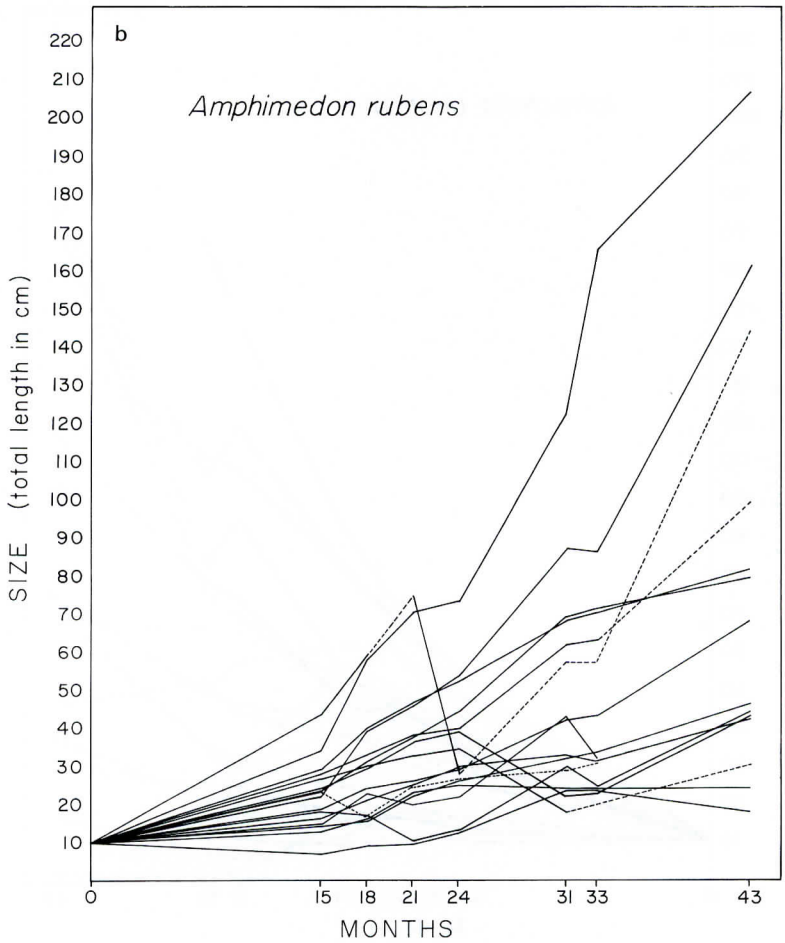


Fig. 3a,b,c. Growth of sponges that were 10 cm in length at the start of the experiment (June 1980). Each line represents size change for one individual. Dotted portions of growth lines indicate that one or more asexual fragments derived from that individual are included in the size measurement. Every sponge was measured at every time interval given on the horizontal axis. To decrease complexity on the graph, only those individuals that remained on their original substrata for at least 33 months are represented.

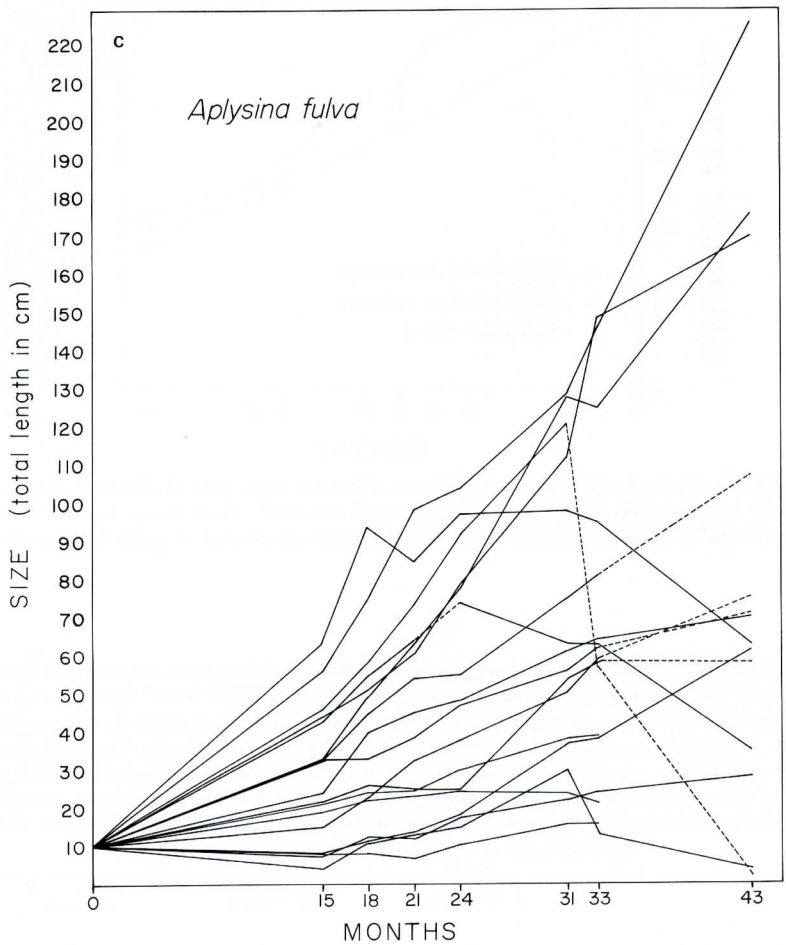
of total branch length on time were performed for all individuals that remained on their original substrata until 33 or 43 months of measurement and did not decrease in size during any interval. Examination of the residuals showed no trends, giving no reason to reject the hypothesis that growth is linear in these sponges, i.e., the increment added in a given time interval is the same regardless of the size of the sponge.

Fragmentation and partial mortality are important aspects of size change for these sponges. Half (55/105) of the experimental individuals decreased in size at least once. A quarter (26/105) of the sponges produced fragments which could be unambiguously



recognized (by comparison with detailed drawings and measurements) to have become established nearby, and many of these individuals produced fragments on more occasions. Size decreases in sponges for which daughter fragments could not be recognized may represent either partial mortality or generation of fragments that became dispersed.

Detachment of sponges at their bases is a special case of fragment generation. Experimental sponges became detached from their original substrata at a steady rate throughout the experiments (Fig. 4), with fewer than half (44/105) remaining attached to the rubble on the stakes after 43 months. Many of the detached sponges could be recognized (by comparison to drawings) to be reattached and growing near their original substrata (22.7, 40.0, 26.3% for, respectively, *I. birotulata*, *A. rubens*, *A. fulva*). This is a conservative estimate of survival since other surviving detached sponges may have dispersed or become unrecognizable.



Specific growth rates (growth standardized by size) decrease with increased size for these sponges. After 20 months, short individuals had higher specific growth than either tall or double individuals in *A. rubens* and *A. fulva* for more genotypes than expected if size does not influence specific growth (pairwise comparisons by the G test, $p < 0.025$). The proportion of genotypes in which growth of tall individuals exceeded that of double individuals (sponges of different shape but equal initial biomass) was statistically indistinguishable from 50% for these species (Table I). As for the other species, specific growth of short *I. birotulata* individuals was higher than that of double individuals for more genotypes than expected if size has no effect (G test, $p < 0.05$). However, sample size of this species was decreased by high losses of experimental sponges (see Table I) to the extent that a few especially vigorous tall individuals affect the results disproportionately. Thus, for *I. birotulata* there were no significant differences in growth between short and tall individuals, and tall individuals had greater specific

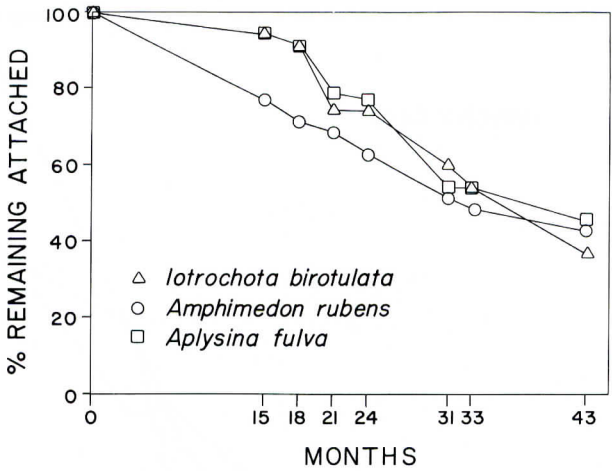


Fig. 4. Detachment of sponges from original substrata. Each line represents the number of the original sponges (35 for each species) remaining on experimental substrata. These losses are not necessarily equivalent to mortality because detached sponges may become established as independent individuals.

TABLE I

Comparison of specific growth rates for two lengths (short, tall) two widths (short, double), and two shapes (tall, double) after 20 months of observation, beginning in May–June 1982. "Short" sponges were 8 cm in length, "tall" sponges were 16 cm in length, and "double" sponges were two sponges 8 cm in length, fused longitudinally. All comparisons were made among sponges of the same genotype. The total number of genotypes for each species was initially 16. Numbers refer to the number of genotypes for which specific growth rates of individuals of different sizes and shapes compared in the indicated fashions. Comparisons that are statistically significantly different by the G test at $p < 0.025$ are marked with two stars, and those significant at $p < 0.05$ are marked with one star.

	I. birotulata	*A. rubens*	*A. fulva*
Short > tall	3	12	12
		**	**
Tall > short	4	3	2
Short > double	6	12	12
	*	**	**
Double > short	1	3	3
Tall > double	7	9	4
	*		
Double > tall	1	7	11

growth than double ones for more intervals than expected if shape has no effect on growth (Table 1).

Loss of these individuals from their original substrata (i.e., fragment generation by basal detachment) was not influenced by size and shape. Of the 48 genotypes (combining the three species), 11 short, seven tall, and seven double individuals became detached from their original substrata in 20 months (no significant difference by the

G test, with $p > 0.47$). Furthermore, decreases in size, due to fragment generation or to partial mortality, did not disproportionately affect individuals of one size or shape. Of the short, tall, and double individuals, respectively 14, 17, and 14 decreased in size during 20 months (no significant difference by the G test, with $p > 0.75$).

POPULATION DESCRIPTIONS

Density of these three species was high in this habitat, with a combined total of 41.5 individuals in an average m^2. Mean numbers of individuals in 1 m^2 for, respectively, *I. birotulata*, *A. rubens* and *A. fulva*, were 17.5, 7.8, 16.2 and mean volumes of live sponges in 1 m^2 were, respectively, 386, 258, and 627 cm^3 for these species.

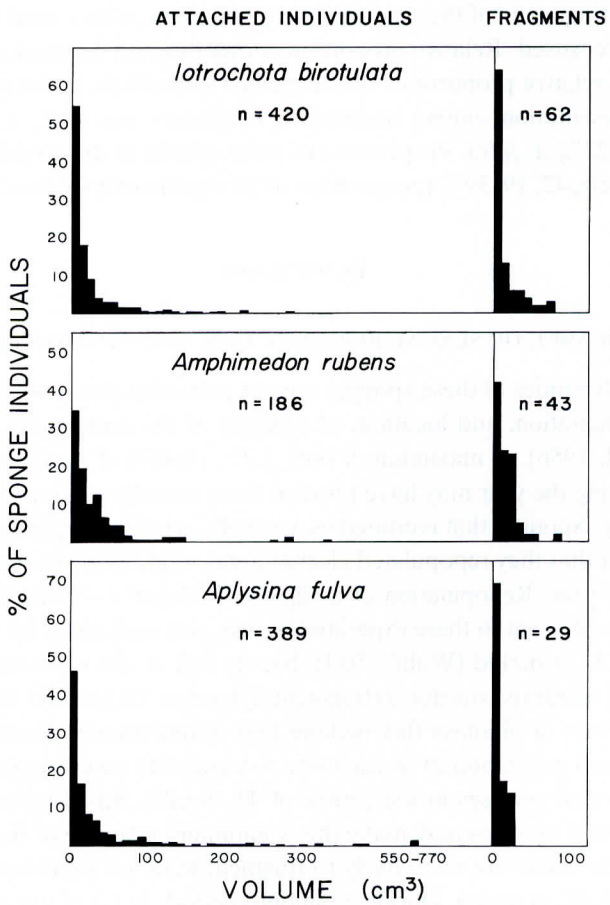


Fig. 5. (a) Size-frequency distributions of populations. All individuals in 24 m^2 were measured. (b) Size-frequency distribution of unattached fragments. All unattached fragments within 100 m^2 were measured after several months without a major storm. Bars represent the proportion of the unattached fragments in size classes defined by 5-cm^3 intervals

Small individuals dominate these populations in terms of numbers of individuals, with $> 1/2$ of the individuals in each species (72, 54, and 63% for, respectively, *I. birotulata*, *A. rubens*, and *A. fulva*) being < 20 cm^3 (first two bars in each histogram in Fig. 5). Despite enormous representation in these very small size classes, individuals of volumes up to 770 cm^3 were found in the censused transects (Fig. 5) and larger individuals can also be found in these populations. In spite of their disproportionately high representation, small individuals make up only a small percentage of the total biomass (15.5, 13.3, 10.2% for, respectively, *I. birotulata*, *A. rubens*, *A. fulva*).

Small size classes are even more swollen for unattached fragments of these species (Fig. 5). All unattached fragments measured were of volumes < 100 cm^3, and $> 2/3$ of the unattached fragments found after several months without major storms were < 20 cm^3 (77, 66, 86% for, respectively, *I. birotulata*, *A. rubens*, *A. fulva*).

Unattached fragments of these species were abundant, with a total of 134 fragments in the 100 m^2 censused. Relative proportions of unattached fragments of these species differ from the relative proportions of established individuals in the populations. Proportional representation among unattached fragments was 46% *I. birotulata*, 32% *A. rubens*, and 22% *A. fulva*. Proportions of these species in the established population were, respectively, 42, 19, 39% (proportions differ significantly by the G test, $p < 0.001$).

Discussion

The insignificance of sexual reproduction for fragmenting sponges

Population dynamics of these sponges consist primarily of reshuffling, by changes in size, shape, orientation, and location, of portions of the same small set of genotypes (also see Wulff, 1986). A maximum of only 2.2% (9/407) of newly recruited sponges discovered during the year may have resulted from sexually produced larvae, and they survived poorly. Sponges that recruited as asexually generated fragments were successful to the extent that they repopulated cleared areas to levels about half of those before clearing in one year. Repopulation of a slightly shallower (-2 m) cleared quadrat of 7.5 m^2, directly adjacent to these experiments, was also exclusively by fragments during the previous 2.5–yr period (Wulff, 1984). Nearly half of the biomass turnover within unmanipulated quadrats was due to fragment dynamics. Other data that are consistent with this high rate of biomass flux include high abundance of unattached fragments (134/100 m^2) and generation of at least one recognizable surviving fragment by $> 1/4$ of the experimental sponges in the course of 43 months. Small initial size (10 cm) of these experimental sponges may make this a minimum estimate of fragmentation rate, since larger individuals are more likely to fragment than are small individuals in these populations (Wulff, in press). During a 9-month period, $> 1/4$ of a group of unmanipulated sponges, representing a wide range of sizes, produced recognized fragments (Wulff, in press). Healthy detached fragments of experimental sponges, recognizable by distinctive branching patterns and sizes recorded in the time series drawings, were found

nearby in 48.1% of the cases in which sponges decreased in size between measurements. Of the experimental sponges that became detached from their substrata, 29.5% successfully reestablished themselves within a few meters of their original substrata. Experiments modeling fragment dispersal for these three sponge species (Wulff, 1985) used fragments of 8 cm in length, which is close to the average sizes of naturally generated fragments in this habitat for *I. birotulata* and *A. rubens* (respectively, 8.9 and 7.3 cm). After 1 yr, 30% of these experimental fragments still survived and had become established as independent individuals (Wulff, 1985). Of natural fragments that colonized cleared areas monitored for recruitment in this study, 29% survived for a year. A fragment survival rate of nearly one third, in each of these cases, may underestimate actual survival, since fragment losses reflect emigration as well as mortality. From these recruitment, fragment generation, and fragment survival data, it seems clear that high representation in small size classes reflects continuous addition of small individuals to their populations by fragmentation of large individuals.

Asexual fragmentation is a fundamental part of the life histories of many plants and sessile marine invertebrates (e.g., see Highsmith, 1982, for a review of coral fragmentation; Cook, 1986, and Pitelka & Ashmun, 1986, for discussions of plant fragmentation). Extreme cases, such as illustrated by these branching sponges, have led to speculation about the adaptive significance of sexual reproduction versus asexual propagation. I did not study sexual reproduction explicitly for these three sponges, in large part because of the apparently minor contribution to the populations of new individuals derived from larvae. Although I found embryos in many individuals of *I. birotulata* and *A. rubens*, the embryos are either not being released, or their survival after release is very poor. Perhaps larvae recruit successfully only after major storms, when hard substrata are scoured of previous sessile residents.

Sexual reproduction also appears to be of minor importance for some other fragmenting sessile reef invertebrates on the time scale of years or even decades (e.g., Bak & Engel, 1979; Lasker, 1983, 1984; Rylaarsdam, 1983). Although sexual reproduction may be essential for recolonization after epidemic disease, temperature stress, or a violent storm have caused large-scale mortality, intervals between such disasters may be more than adequate for genotypes well suited for asexual propagation to come to dominate their populations with respect to numbers of individuals. Clone membership, determined by a variety of means including tissue compatibility, color, population structure, and morphology (Wulff, 1986), for these three species in an area adjacent to the experiments reported on here, indicates that the combined number of individuals in the three clones with the most members (i.e., the three genotypes that had propagated asexually the most) included between 1/3 and 2/3 of the individuals in the populations (36.7, 65.0, 53.3% for, respectively, *I. birotulata*, *A. rubens*, *A. fulva*; Wulff, 1986).

Advantages of asexual propagation may outweigh advantages of sex more for these sponges than for other taxa. Three major arguments that have been made for immediate selective advantage of sexual reproduction may be obviated by the ability of fragments of these sponges to disperse over long distances (Wulff, 1985). First, sexually generated

larvae or seeds are generally necessary for dispersal. For these sponges, swimming or floating propagules may be required for traversal of inhospitable habitat, but their high rates of success at fragment generation, dispersal, and establishment enable them to spread throughout large areas of continuous habitat quickly, without larvae. Second, sexual reproduction can act as a filter against transmission of pathogens or parasites. However, dispersal of fragments of a genotype far from each other could also prevent demise of a genotype by infection, by decreasing the probability that a pathogen will infect every independent portion. Third, genetically diverse (sexually produced) progeny may decrease the efficiency of pathogens, parasites, and predators (Levin, 1975). The possibility of frequency-dependent survival of attacks by biotic agents has been tested in a series of field experiments using the grass *Anthoxanthum odoratum* (Antonovics & Ellstrand, 1984; Ellstrand & Antonovics, 1985; Schmitt & Antonovics, 1986). These experiments demonstrated (1) a fitness advantage for a genotype when it is surrounded by individuals of other genotypes rather than by other individuals of its same genotype, and also (2) increased survival of aphid infestations for plants surrounded by unrelated plants rather than by siblings. These positive effects of genotypic diversity operate on a local scale for this grass. Depending on the host-tracking abilities of the pathogens and parasites whose attacks mediate such an effect, dispersal of asexual fragments may offer benefits comparable to sex. Clonal propagation in these sponges does not produce a cluster of genetically identical individuals as it does for many plants and for invertebrates with heavy skeletons, such as massive corals. Dispersal of fragments ensures that local patches of individuals are genotypically heterogeneous in spite of low genotypic diversity in the population as a whole (Wulff, 1985, 1986).

INDIVIDUAL SIZE AND THE ADVANTAGES OF FRAGMENTATION

Consideration of asexual fragmentation as an alternative to sexual reproduction can be taken one step further by asking if the accumulating biomass of a single genotype is better maintained in one unit or split into few or many smaller units. Depending on environmental circumstances, many small or a few intermediate-sized independent individuals may grow, survive, or reproduce better than a single large individual.

Specific growth rate (growth standardized by size) decreases with increasing size in these sponges, as demonstrated by linear portions of the graphs in Fig. 3. This is corroborated by experimental results demonstrating greater specific growth rates in smaller individuals of *A. rubens* and *A. fulva* (Table I) and also by greater specific growth rates in smaller unmanipulated individuals of *I. birotulata* (Wulff, in press). Lack of a significant effect for all three species in each study reflects fragmentation, partial mortality, and the extreme variability in growth rates among individuals that seems to be characteristic of sponges (review in Simpson, 1984).

Decreases in growth rate with larger size have been reported for sponge species of massive or tube-shaped morphology (Storr, 1964; Reiswig, 1973; Dayton, 1979), as might be predicted because their surface (i.e., water-processing capacity) to volume

ratios decrease with larger size. For the branching species in this study, however, surface and volume maintain virtually the same relationship as individuals grow. Decreased specific growth rate with increased size seems, therefore, a puzzling result. In fact, the opposite result of increased specific growth with increased size might be predicted, since increased stature can raise upper portions of sponges into what may be improved current conditions above the substratum. Perhaps increased allocation to attempts at sexual reproduction diverts material from growth in larger individuals. Simply with respect to accumulation of biomass by a genotype, division into smaller portions appears to be the better strategy. How much better depends on mortality associated with fragment generation and with small size.

Mortality and size may be related differently depending upon the mortality source. Recovery from attacks by predators or pathogens may be more rapid if the damaged portion is physiologically integrated with a large undamaged portion. This has been experimentally demonstrated to be the case for some species of clonal plants (review in Pitelka & Ashmun, 1986). Physiological integration in sponges is not well understood. Lack of transport vessels, such as are found in vascular plants and colonial cnidarians, may limit rates and control of directional translocation of metabolites within a sponge. If different portions of a sponge are essentially nutritionally independent of each other, large size, per se, may not confer improved healing capability. However, Boury-Esnault (1976) discovered that cells bearing large glycogen reserves flocked from adjacent areas to wounds she had inflicted. This result suggests that rapid healing of injuries depends on confluent healthy tissue and also demonstrates very localized internal coordination to minimize effects of partial mortality. From his observations of Antarctic hexactinellid sponges, Dayton (1979) suggested that asteroid predators may damage sponges beyond recovery if they remove >20–30%. Likewise, other experiments, in which tissue has been removed from very small sponges or else repeatedly from the same sponge, suggest limits on regeneration ability that may be related to size (review in Simpson, 1984). A relationship between mortality and size is probably not linear. Very small sponges, such as recent recruits from larvae, may survive poorly, being easily smothered by sediment or encroaching neighbors, or annihilated by grazing gastropods and echinoderms. The resources upon which they can draw for repair may be exhausted rapidly. Thus, survival of damage may increase with size up to some intermediate size, above which mortality per unit volume may be independent of the number of unit volumes that are physiologically confluent. Consistent with this suggestion are patterns of regeneration of experimentally induced injuries in the Caribbean gorgonian *Plexaura homomala*. Wahle (1983) found no statistically significant differences in the time required for regeneration of small (1 cm) injuries between gorgonian colonies of 10–20 cm vs. 40–60 cm in height and width.

Conditions under which fragmentation is selectively advantageous can be evaluated using the following simple model. For the model, let the total size of a sponge be x units, which can be fragmented into a fragments, each of size x/a. Each piece of this sponge, irrespective of its size, adds a growth increment of e units in a given time interval (as

in the linear model that describes growth in these sponges). For a mortality rate associated with fragmentation (mortality of fragments or partial mortality incurred in the act of fragmentation) of m fragments, fragmentation will be favored whenever $(a - m)\ (x/a + e) > (x + e)$ or (after algebraic manipulation) when $m < (a - 1)/(x/ae + 1)$. An example, using data from the experiments and observations reported on here, can be made of a sponge that is initially 32 U long. If it fragments into four fragments (each of 8 U), and the extension rate per fragment is 20, then fragmentation will be favored when $m < 2.14$. That is, as long as < 2.14 fragments die (i.e., partial mortality associated with fragmentation amounting to 53.5% of the initial biomass), the biomass will increase more rapidly if this sponge fragments than if it remains as one integrated large sponge.

This simple model does not take into account size-dependent aspects of sexual reproduction, which may favor maintenance of biomass in one portion. However, if conditions favoring successful recruitment by larvae are rare, it may be difficult to make a selective argument for remaining unfragmented in order to produce more larvae. This is especially true if fragmentation can be demonstrated to be important in keeping the genotype alive. This calculation also does not take into account factors, discussed in the previous section, that favor fragmentation, but are related less to size of fragments, per se, than to division into independent portions that can be dispersed.

Fragmentation does not appear to be induced by the sponges according to an internal program, as in the gorgonian *Plexaura* A, which fragments at constrictions of its axial skeleton (Lasker, 1984). Morphology is not irrelevant to fragment generation, however, and genetically influenced morphological variation within each of these three sponge species may affect susceptibility to a host of fragmenting agents, including feeding fishes and starfish, rough water movements, and pathogens (Wulff, 1986). Narrower branches and branches that lie adherent to the substratum rather than stand erect are fragmented more (Wulff, in press). Consequently, genotypes characterized by these morphological types achieve greater representation in their population, with respect to numbers of independent individuals (Wulff, 1986). More detailed experiments are required to determine if frequency of fragmentation or size of the fragments are the traits upon which selection acts or if these are consequences of selection on some other aspect of morphology.

DEVELOPMENT OF A PREDICTIVE THEORY OF ASEXUAL PROPAGATION: COMPARISONS AMONG TAXA

That the influence of asexual fragmentation on the fate of a genotype has been shown to be positive for some organisms and negative for others suggests that comparisons among taxa may lead to a more comprehensive theory of asexual propagation. This would depend on identifying traits characteristic of different taxa that might influence the balance between advantages and disadvantages of fragmentation.

Sponge fragments may be better suited to distant dispersal before reestablishment

than fragments of other clonal benthic invertebrates (Wulff, 1985). In addition, and perhaps more importantly, sponges are unique in several ways that could influence their success at asexual propagation: they are extremely simple and homogeneous in their construction, and individual cells within a sponge are highly mobile. Simplicity of design is illustrated not only by a complete lack of organ systems, but also by a lack of clear means for coordination within a sponge. Mechanisms of physiological integration within a sponge are still somewhat mysterious (review in Simpson, 1984), but is clear that they have no vessels by which metabolites could be transported from one part of a sponge to another or nerve cells by which signals could be transmitted. Thus two major advantages of physiological confluence among portions of a clone, (1) aid of portions in sub-optimal microhabitats and (2) integration for defense, do not apply to sponges. Another aspect of the simplicity of sponges is their extreme homogeneity. Subunits, such as the zooids or polyps of colonial bryozoans and cnidarians and the rosettes of plants, cannot be consistently identified either among sponges of different growth forms or over time in a single specimen (Hartman & Reiswig, 1973). The consequence of this homogeneity, with respect to fragmentation, is that even very small fragments taken from nearly any part of a sponge are able to live independently and regenerate entire individuals. Classic experiments, in which investigators have dissociated sponge cells and studied their subsequent reaggregation into a functioning individual, have demonstrated this extreme fragmentability of sponges (Wilson, 1907; review by Simpson, 1984). These classic experiments also illustrate the high mobility of sponge cells, which allows them to reaggregate and to rearrange themselves rapidly. For sponges in nature, the ability of the cells to reorganize rapidly has three important consequences for success of asexual fragments: (1) sponges are able to heal themselves rapidly after damage (e.g., Wilson, 1910; Boury-Esnault, 1976; Storr, 1976; Jackson & Palumbi, 1979), decreasing colonization by pathogens of wounds received in fragmentation; (2) loose fragments are able to reattach rapidly to solid substrata, gaining the stability requisite to successful establishment as independent individuals (Wulff, 1984); and (3) stabilized fragments can rapidly reorganize their cells for efficiency of water pumping in their new shape and orientation (e.g., Hartman & Reiswig, 1973). In the context of these attributes of sponges, their extreme success at and focus on asexual propagation, even at the expense of sexual reproduction, is no surprise.

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