

DISPERSAL AND SURVIVAL OF FRAGMENTS OF CORAL REEF SPONGES

DISPERSION ET SURVIE DES FRAGMENTS D'ÉPONGES RECIFALES

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ABSTRACT

Fragments of the branching Caribbean demosponge species Iotrochota birotulata Higgin, Haliclona rubens (Pallas), and Aplysina (=Verongia) fulva (Pallas) can be dispersed quickly over suitable terrain.

Experiments were designed to mimic natural fragment dispersal over a substratum of small massive corals and rubble from corals in San Blas, Panama. Sponge fragments (100 of each species) were labeled and released at several places on a shallow (-2.1 m) plane and on a slope (-2.3 to -5.0 m). Subsequent distributions of the fragments were then mapped at intervals.

After four weeks, 17% (16/93) of the fragments recovered on the flat plane remained within 0.25 m of their original locations, but the others had dispersed a mean distance of 8.85 m, with 37% (34/93) recovered between 10 and 19 m away. On the slope, 29% (28/98) of the fragments remained undispersed. The mean distance dispersed by the others was 2.60 m, with 11% (11/98) dispersing 5-10 m. Because most of the dispersal occurred during a 2-day storm in the third week of the experiment, net dispersal at the end of four weeks was in the direction of the storm current on the plane and in directions represented by various vector sums of the slope and current directions on the slope.

Fragments of these species survive well in this habitat. After one year, 30% (91/300) of the fragments were found alive and many had adhered to hard substrata and increased in size. Clones in these populations may, therefore, have scattered distributions, arising from frequent establishment of fragments as physiologically independent and distant parts of the sponges from which they became severed.

RESUME

Sur un terrain approprié, les fragments de Iotrochota birotulata Higgin, Haliclona rubens (Pallas) et Aplysina (=Verongia) fulva (Pallas), Démospoges branchues des Caraïbes, peuvent être dispersées rapidement.

Des expériences furent imaginées dans le but d'imiter la dispersion naturelle des fragments sur un substrat de petits coraux massifs et de débris coralliens, à San Blas, Panama. Des fragments d'éponge (100 de chaque espèce) furent marqués puis libérés à plusieurs endroits sur un plan peu profond (-2.1m) et le long d'une pente (-2.3 à -5.0 m). Les distributions successives des fragments furent ensuite cartographiées à différents intervalles de temps.

Après quatre semaines, 17% (16/93) des fragments récupérés sur le plan se trouvaient à moins de 0.25m de leur point d'origine, tandis que les autres fragments s'étaient dispersés sur une distance moyenne de 8.85m avec 37% (34/93) retrouvés entre 10 et 19m du point de départ. Sur la pente, 29% (28/98) des fragments restaient en place. La distance moyenne parcourue par les autres fragments s'élevait à 2.60m, avec 11% (11/98) s'étalant entre 5 et 10m. Comme la plus grande partie de la dispersion s'est située pendant les deux jours d'un orage, dans la troisième semaine de l'expérience, la dispersion nette au bout de quatre semaines suivait le sens du courant de tempête, sur le plan, et sur la pente, des directions intégrant celles de la pente et du courant.

Les fragments de ces espèces survivent bien dans cet habitat. Au bout d'une année, 30% (91/300) des fragments étaient toujours vivants et beaucoup d'entre eux avaient grandi et adhéré à un substrat dur. Par conséquent, les clones dans ces populations, peuvent avoir des distributions en mosaïque, résultant de la fréquente fixation de fragments provenant d'éléments séparés et physiologiquement autonomes à partir des éponges mères.

INTRODUCTION

Propagule dispersal is an important link between life history stages, but is one of the least known aspects of the ecology of most species. Many sessile reef invertebrates propagate by asexual fragments (e.g., Glynn, et al., 1972; Bothwell, 1981; Tunnicliffe, 1981; Highsmith, 1982; Lasker, 1984) which, for some species, can be dispersed before becoming established as independent individuals. Dispersal of asexual fragments affects clone structure and dynamics within populations, exchange among populations, colonization of new substrata, and recolonization of devastated reefs. Information that is central to understanding the ecology and evolution of fragmenting species therefore includes: 1) distances dispersed by fragments, 2) the proportion of fragments that survive and become established as independent individuals, and 3) the environmental circumstances that affect fragment dispersal and survival.

Demosponges are one sessile group for which asexual fragments may be important dispersing propagules. Here I present results of an experimental study of dispersal and survival of fragments of sponges for which asexual fragmentation is the primary mode of propagation. Fragments of three Caribbean species of branching demosponges, representing different orders, were studied in two habitats of contrasting topography and in two years of contrasting weather.

METHODS

Experiments were designed to mimic natural dispersal of fragments of the branching Caribbean demosponge species *Iotrochota birotulata* Higgin, *Haliclona rubens* (Pallas) [= *H. (Amphimedon) compressa* D & M, see Wiedenmayer (1977)], and *Aplysina* (= *Verongia*) *fulva* (Pallas) [see van Soest (1978)]. The experiments were established on Guigala Tupo reef, near the San Blas Field Station of the Smithsonian Tropical Research Institute in Panama. This reef is on the leeward side of a string of small islands that lie, in turn, behind a system of windward reefs. The sponges are most abundant on a substratum of scattered small to medium-sized (up to 1 m in diameter) massive corals and abundant coral rubble.

Fragments, 8 cm in length, were cut from branches, 0.8-1.8 cm in diameter, of healthy sponges and labeled with small pieces of colored plastic. Cut surfaces healed within one day. The labeled fragments were placed in 5 groups on a shallow (-2.1 m) plane and 5 groups near the top of a shallow (-2.3 m to -5 m) slope. Each group included 10 fragments of each species (300 fragments in all). Subsequent positions of each marked fragment were mapped by triangulation from fixed markers after 2 weeks, 4 weeks, and 1 year. The experiment was repeated the following year, using a total of 240 fragments and mapping fragment positions every 10 days for 7 weeks. All fragments were examined for damage, growth, and reattachment to solid substrata. In both years, the experiments were initiated in January, which is early in the dry season, the period of greatest swell in the southern Caribbean. A storm, of a magnitude matched by only 1 to 2 storms per year in the San Blas, swept through for 2 days in the third week of the experiment in 1983. In 1984, the weather remained calm throughout the seven

weeks of the experiment.

Reattachment of errant fragments to suitable substrata, generally coral skeletons, is an important aspect of successful propagation by dispersing fragments. The length of time for which a sponge fragment must remain in contact with a piece of solid carbonate in order to adhere was estimated by tying sponge fragments, 4 cm in length, to pieces of dead rubble from the ramose coral *Porites furcata* Lamarck. Progress of attachment was checked every 5 days.

RESULTS

Distances dispersed by fragments

Distances dispersed by experimental fragments were influenced by weather and habitat, and fragments of the three species dispersed differently (data and statistical comparisons summarized in Tables 1,2). After the first two weeks in both years, many of the fragments recovered (46% in 1983 and 69% in 1984) remained within 0.25 m of their origin points and were considered not to have dispersed. The other fragments dispersed mean distances of 0.56 m in 1983 and 0.55 m in 1984. In 1984, the fragments continued to disperse slowly (Fig. 1) until, after 7 weeks, 55% remained undispersed and the others had dispersed a mean of 0.75 m. In 1983, however, fragments dispersed very differently (Figs. 1,2). During a two day storm in the third week of the experiment, the current reversed direction with the wind, from the usual northerly to southerly, and increased in strength. Fragments recovered after the storm had been dispersed up to 18.75 m from their origins. Some fragments remained undispersed (17% of those recovered on the plane and 29% on the slope), but the others had dispersed a mean distance of 8.85 m on the plane and 2.6 m on the slope (Figs. 1,2; Tables 1,2).

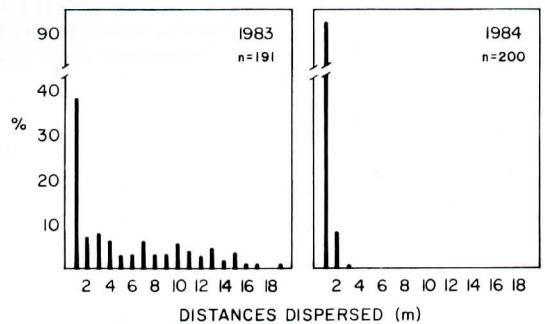


Figure 1. Frequency distributions of dispersal distances of fragments after 4 weeks for experiments in 1983 (storm in 3rd week) and 1984 (calm).

After a year, the mean distances dispersed by fragments of each of the three species were no different from what they were after 4 weeks in both habitats (Tables 1,2). Of the fragments recovered after a year, 31% remained undispersed.

Fragments of all species dispersed significantly farther on the very shallow plane than on the slope after the 1983 storm, but dispersal distances in the two habitats did not differ in relatively calm 1984 (Tables 1,2).

Fragments of the three species dispersed differently. After 4 weeks, significantly more fragments of *I. birotulata* than of the other species remained undispersed. In addition, distances dispersed by *I. birotulata* fragments were significantly less than distances dispersed

by *H. rubens* fragments in both habitats in 1983 and on the shallow plane in 1984. *A. fulva* fragments dispersed farther than *I. birotulata* fragments in 1983 and farther than those of either of the other species in 1984 (Tables 1,2).

Spatial patterns of fragment dispersal

Bottom topography and current direction both affected the spatial patterns of fragment dispersal. After the 1983 storm most fragments recovered on the shallow plane had been dispersed in the direction of the storm current (towards the upper left of Fig. 2), whereas the fragments on the slope had been dispersed various vector sums of slope and current direction. Two fragments from the slope were dispersed up onto the plane, whereupon their dispersal was influenced almost entirely by the storm current (Fig. 2).

Trajectories followed by many fragments were affected by micro-topography as well, and many fragments clustered in slight depressions. Fragments also accumulated at the edge of the acceptable habitat, where their further dispersal was discouraged by the raised edge of a *Thalassia* meadow (upper left corner in Fig. 2) or by clusters of corals (lower sides in Fig. 2) bordering the rubble in some places.

Fragment survival

After one year, a total of 30% (91/300) of the experimental fragments were recovered. This is a minimum estimate of survival, since other surviving fragments may have been buried in rubble, obscuring their tags, or been dispersed out of the area searched. In two cases, a fragment was found that had been temporarily

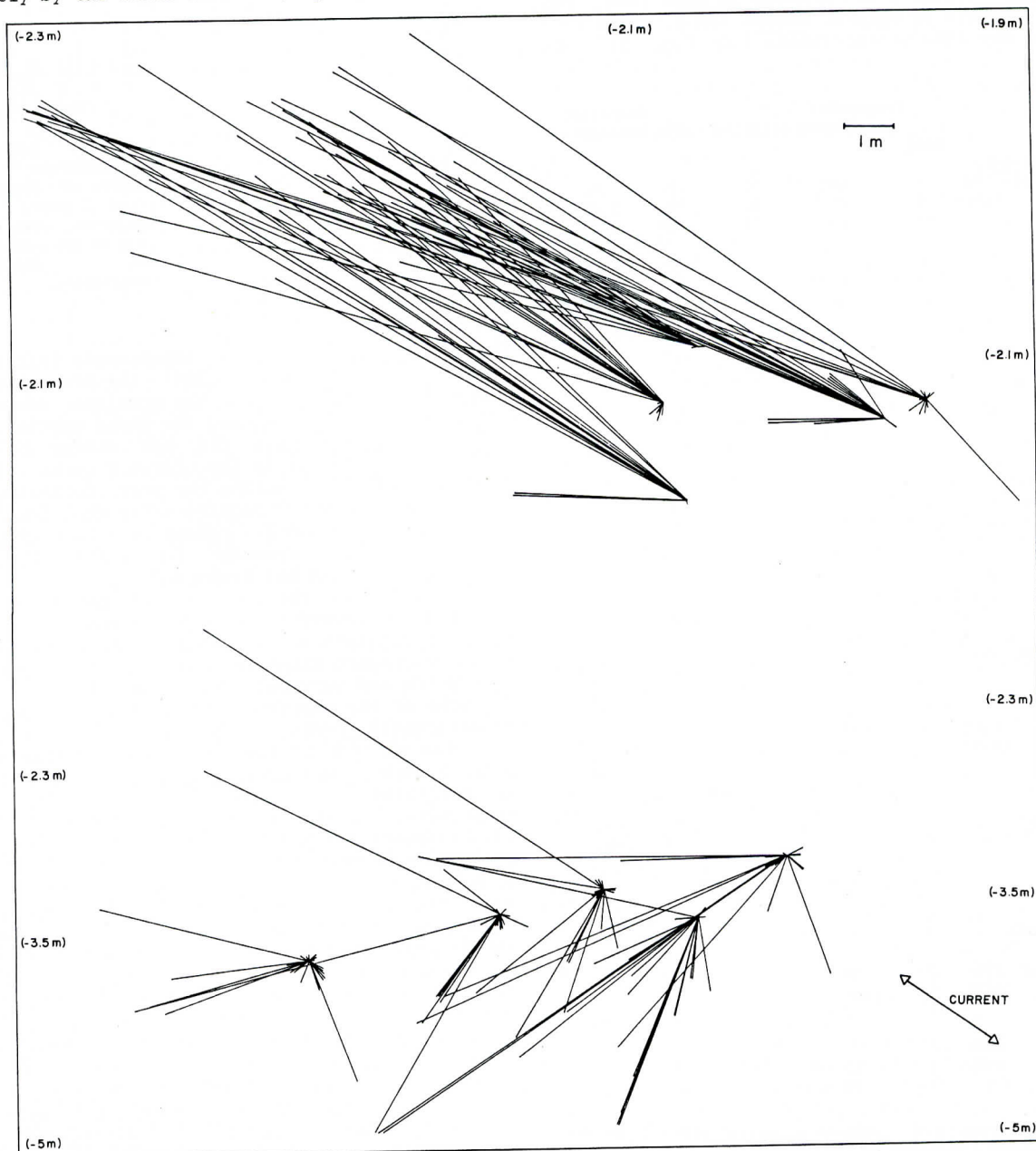


Figure 2. Map of the 20 m x 23 m area in which fragments dispersed from the 10 origin points in 1983. Each line represents the dispersal trajectory of one fragment after 4 weeks. The direction of storm currents in the third week of

the experiment was towards the upper left, the reverse of the usual direction. The upper half of the map represents a flat plane of -2.1 m in depth below MLW and the lower half represents a slope of from -2.3 m to -5 m in depth below MLW.

buried and therefore missed in a previous census. Further dispersal in some directions would place fragments in less suitable habitats. A *Thalassia* meadow surrounded about 10% of the perimeter, and clusters of foliaceous corals, between which flocculent sediment accumulates, were scattered along another 20% of the perimeter. Survival of fragments in these peripheral habitats is not impossible, but depends on their rapid attachment to occasional emergent hard substrata in the seagrass meadow or to the often vertical sides of live corals.

Fragments of the three species survived differently (Fig. 3). Almost all fragments of *I. birotulata* and *H. rubens* survived the first 2 weeks of experimental dispersal in both years, but significant numbers of *A. fulva* fragments were lost (Fig. 3). This same pattern of fragment loss continued between 2 and 4 weeks in calm 1984, but many fragments of both *H. rubens* and *A. fulva* were lost in the 1983 storm (Tables 1,2; Fig. 3). By

TABLE 1

	week	fragments:			dispersal	
		recovered	attached	<.25m distances		
<i>I. birotulata</i>						
plane	1983 2	48	16	28	.56	
	(n=50) 4	41	16	10	5.47	
	52	14	14	3	7.14	
1984	2	40	21	30	.34	
	(n=40) 4	40	24	27	.37	
	7	39	29	27	.52	
slope	1983 2	49	20	26	.42	
	(n=50) 4	45	32	16	1.83	
	52	30	30	16	1.53	
1984	2	39	23	36	.37	
	(n=40) 4	38	26	29	.49	
	7	39	28	30	.59	
<i>H. rubens</i>						
plane	1983 2	49	0	20	.67	
	(n=50) 4	37	0	0	11.35	
	52	16	9	0	11.38	
1984	2	40	15	22	.75	
	(n=40) 4	40	18	18	.88	
	7	38	21	16	.97	
slope	1983 2	50	3	18	.53	
	(n=50) 4	31	7	3	3.19	
	52	17	17	2	3.94	
1984	2	40	9	30	.44	
	(n=40) 4	40	16	14	.49	
	7	38	10	13	.69	
<i>A. fulva</i>						
plane	1983 2	29	6	10	.56	
	(n=50) 4	15	7	6	10.22	
	52	2	2	0	.63	
1984	2	27	10	14	.53	
	(n=40) 4	19	18	10	.77	
	7	21	16	10	.75	
slope	1983 2	33	9	16	.59	
	(n=50) 4	22	15	9	3.04	
	52	12	12	7	1.52	
1984	2	27	9	15	.59	
	(n=40) 4	23	21	12	.81	
	7	23	17	13	.82	

Table 1. Summary of fragment dispersal experiments for three sponge species in two habitats of contrasting topography and two years of contrasting weather. All entries are numbers of individual fragments, except for dispersal distances, which are means of distances (m) dispersed by all fragments that moved more than 0.25 m.

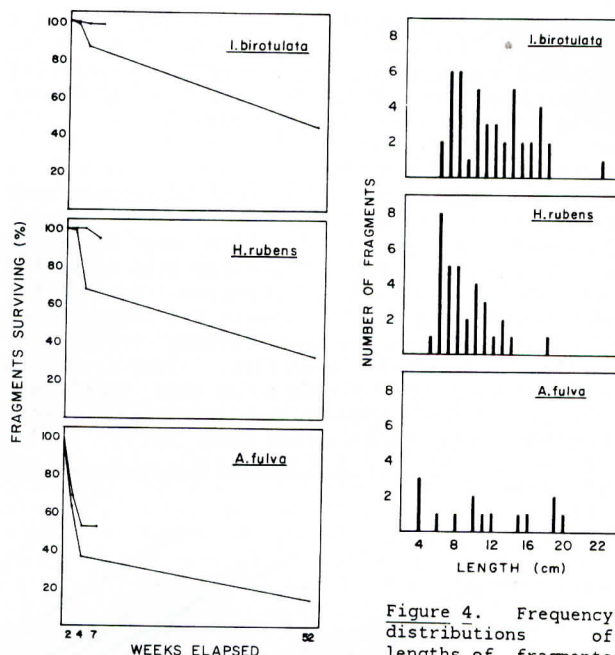


Figure 3. Survival of fragments in the dispersal experiments for 1 year (1983) and for 7 weeks (1984). For each species, n=50 in 1983 and n=40 in 1984.

Figure 4. Frequency distributions of lengths of fragments after 1 year. All fragments were 8 cm long at the start of the dispersal experiment.

the final census in both experiments (after 52 weeks in 1983, 7 weeks in 1984) the proportion of fragments surviving since the previous census (4 weeks) did not differ among the three species.

Loss of fragments did not differ between habitats in 1984 or in the first 2 weeks of the 1983 experiment. During the year following the 1983 storm, however, significantly more fragments of *I. birotulata* and *H. rubens* were lost from the shallow plane than from the slope (Tables 1,2).

Fragments that had dispersed <0.5 m, 0.5-5 m, or >5 m during the storm, did not differ in proportional survival between 4 weeks and 1 year for *I. birotulata* or *H. rubens*. However, for *A. fulva*, increased dispersal distance was associated with decreased survival (G-test, p<.01).

Some of the recovered fragments were damaged. Significantly fewer fragments of *I. birotulata* were damaged than of the other species (Table 2). After 2 weeks, the number of damaged fragments of *I. birotulata*, *H. rubens*, and *A. fulva* were, respectively, 1, 12, 12; and after 4 weeks were 3, 13, 11 (years and habitats combined). Damage to *H. rubens* fragments was almost invariably in the form of patches of 1/4 to 2/3 of the total volume where tissue had been macerated from the skeleton, leaving uncovered fibers. For *A. fulva* fragments, damage consisted of loss of 1/3 to 2/3 of the total volume of both tissue and skeleton. Of the 91 fragments recovered after a year, only 1, an unattached fragment of *H. rubens*, was damaged.

Over half (53/91) of the fragments recovered after a year had increased in size from the original length of 8 cm. Final sizes ranged from 4 cm to 22 cm. Maximum lengths of recovered fragments after a year for *I. birotulata*, *H. rubens*, and *A. fulva* were, respectively, 22, 18, and 20.5 cm and mean lengths were, respectively, 11.7, 8.9, and 11.3 cm (Fig. 4). Half of the recovered fragments (48/91) had developed one or more branches.

Reattachment of fragments

After 5 days, 6/10 *I. birotulata* fragments and 7/10 fragments of each of the other species had become firmly attached to the pieces of rubble to which they were tied. These results differ from those of an earlier experiment in which all fragments of these species became attached to rubble in 5 days (Wulff, 1984). Those experiments were designed to mimic sponge adhesion to newly generated or storm-scoured rubble, and therefore the rubble surfaces were clean. In the new experiment, however, patches of sediment were often caught between the carbonate surfaces and sponge tissue and appeared to interfere with firm attachment. Nevertheless, after 16 days, all 10 *I. birotulata* fragments were firmly attached, and 8/10 fragments of each of the other species were attached. The unattached fragments of *H. rubens* had developed macerated patches next to the rubble and those of *A. fulva* had developed necrotic patches where tied to the rubble, causing them to fragment and vanish. These data do not indicate a statistically significant difference in attachment success among these species, but the suggested superiority of *I. birotulata* in rapid reattachment to rubble is corroborated by behavior of loose fragments in the dispersal experiments.

Loose fragments of the three species differed in the rates at which they attached to solid substrata (Tables 1,2). Significantly more *I. birotulata* fragments had attached to solid carbonate after 2 weeks and after 4 weeks in both years than of either of the other species. Fragments of *H. rubens* attached significantly less than those of the other species at every census in both years. Fragments of *A. fulva* were intermediate in attachment success. Of the 91 fragments recovered after a year, all were attached to solid carbonate substrata except for 7 fragments of *H. rubens*.

DISCUSSION

Dispersing fragments and population structure

Clone structure of populations of fragmenting sponges is determined by patterns of dispersal and survival of asexual fragments. My experiments illustrate the influences on these patterns of weather, habitat, microtopography, and time.

Weather, as manifested in current strength and direction, had the most dramatic effect on fragments. During the stormy weather of 1983, distances dispersed were greater, directions of dispersal more strongly influenced by current, effects of habitat on dispersal distances and directions most strong, and fragment survival lowest.

Habitat, in this case a contrast of a very shallow plane and a slightly deeper slope, influenced dispersal and survival by modifying effects of stormy weather. Dispersal trajectories of fragments on the slope were influenced such that many were at right angles to the strong, unidirectional storm current, whereas on the plane, trajectories matched the storm current direction. Survival of fragments was higher on the slope than on the plane in the year following the storm. No significant differences between habitats in dispersal distances, directions, or survival were found in calmer 1984.

Microtopography affected dispersal by causing accumulations of fragments in slight depressions within suitable habitat and at the edges of suitable habitat, possibly decreasing fragment

TABLE 2

Distances dispersed by fragments (W)				
1983	I,H,A	plane >> slope	1983	plane slope H,A >> I slope H > I
1984	I,H,A	plane = slope	1984	plane slope H > I slope A > I,H
I,H,A 1983 >> 1984			1983 4 weeks = 1 year	
Undispersed fragments (G)		Damaged fragments (G)		
4 weeks				
1983	I >> H	2 weeks	H,A >> I	
1984	I >> H,A	4 weeks	H,A >> I	
Reattachment of fragments to solid substrata (G)				
2 weeks		4 weeks		
1983	I >> A >> H	I >> A >> H		
1984	I >> H,A	I > H		
Fragment survival relative to previous census (G)				
2 weeks		4 weeks		7 weeks 1 year
1983	I,H >> A	I >> H,A		I = H = A
1984	I,H >> A	I,H >> A		I = H = A
1983	slope = plane		slope >> plane	
1984	slope = plane		slope = plane	

Table 2. Comparisons of fragment dispersal, reattachment, and survival among species, habitats, weather conditions, and over time. Statistical tests were by the G-test (G) or Wilcoxon rank sum (W). Significance levels are indicated by "=" for $p > .05$, ">" for $.05 > p > .01$, and ">>" for $.01 > p > .0001$. Species are indicated by the first letter of genus names (I,H,A).

mortality by enforcing a kind of passive habitat selection.

Dispersal and survival of fragments were not constant over time. Fragments of all three species were dispersed far in 4 weeks in 1983, but mean dispersal distances then did not change between 4 weeks and 1 year. Only 1 of the 91 fragments recovered after a year was damaged and only 7 remained unattached, contrasting with 15 damaged and 114 unattached of the 191 fragments recovered after 4 weeks. Differences among the species also decreased with time. In both experiments the proportion of individuals surviving from 4 weeks to the final census (1 year in 1983, 7 weeks in 1984) did not differ among species, in spite of significant differences in survival among species prior to 4 weeks. Thus, most important influences on dispersal and survival appear to act in the first few weeks after a fragment is generated.

These data illustrate the potential importance of distant dispersal and successful establishment of asexual fragments in shaping populations of these species. Fragments were moved up to 18.75 m in two days of stormy weather and, after this rather violent dispersal, 30% of the fragments survived the subsequent year and became established as independent individuals. Currents may have played an unusually important role in this situation because of the very shallow (-2.1 m to -5 m) water. However, Guigala Tupo reef is well protected in the lee of both a string of islands and a system of outer reefs. Furthermore, Panamanian reefs do not experience especially violent storms such as hurricanes, which can fragment and disperse sponges living on fore reef slopes as deep as -10 m to -25 m (pers. observ., 1980). Even if dispersal and survival of the magnitudes demonstrated by these experiments do not occur normally, these data cover only one year. Continued growth of this cohort of

fragments, followed by further fragmentation and dispersal, could scatter representatives of these genotypes throughout a continuous reef system. Clearly clones of sponges are able to spread rapidly over large areas.

In recent studies of tissue compatibility of coral reef sponges, distances between tissue-compatible individuals have been used as evidence in evaluating whether fusion indicates clonal identity. An assumption of limited vegetative spread by sponges has contributed to conclusions that tissue-compatible individuals are not necessarily clone-mates (Kaye and Ortiz, 1981) and also that tissue compatibility does identify clone-mates (Neigel and Avise, 1983; Neigel and Schmahl, 1984). Some reconciliation among these divergent conclusions might be made if patterns of fragment dispersal were known for the populations studied, all of which are congeneric (*Aplysina*) or conspecific (*I. birotulata*) with those in the study presented here. Limited dispersal of asexual fragments, and consequent limited areal extent of clones, does not appear to be an appropriate assumption for these Caribbean demosponges of branching morphology.

Characteristics of successful dispersing fragments

Comparison of fragment dispersal and survival among the three species in this study (Table 2) may help to identify characteristics that contribute to successful propagation by dispersing fragments. Fragments of *I. birotulata* dispersed less, were damaged less, and survived better than fragments of the other species, especially in stormy conditions. These attributes may be related to the stabilization of loose fragments by the especially rapid reattachment of this species to solid substrata. Fragments of *H. rubens* successfully disperse far, perhaps because they survive in spite of their slower reattachment. Fragments of *A. fulva* appear to be most easily dispersed, but least likely to survive dispersal. All experimental fragments were cut to the same length in order to standardize both size and shape. However, narrower branches of *A. fulva* (the mean diameter of 30 naturally generated fragments was 0.8 cm, compared to 1.1 cm and 1.5 cm for *I. birotulata* and *H. rubens*) result in average fragment volumes that are only a half to a third of those of the other species. Smaller fragment volumes may be reflected in increased susceptibility to dispersal and in greatly reduced survival.

Effects of fragment size and shape were not directly addressed in this study. Larger size might increase survival, but decrease dispersal. Branches on fragments might curtail dispersal by snagging on the bottom, or increase dispersal by presenting a larger surface to currents. Branches may increase fragment survival, as has been suggested for the scleractinian *Acropora cervicornis* (Tunncliffe, 1981). Further field studies are needed to understand effects of size, shape, branches, and special characteristics of individual species on fragment dispersal and survival.

Demosponges and scleractinian corals may be compared with respect to characteristics affecting propagation by dispersing fragments. Relatively dense carbonate skeletons of corals may decrease susceptibility of fragments to dispersal in calm weather and increase their susceptibility to damage when dispersed violently. Their more brittle skeletons are also more likely to break

during dispersal. Some protection may be afforded to coral fragments of some species by mucous produced after fragmentation (Bothwell, 1981). However, if the thin layer of tissue over a scleractinian skeleton is damaged, an unprotected patch of carbonate surface may be left open to recruitment by fouling or excavating organisms. By contrast, demosponge skeletons, made of a relatively delicate framework of spongin or of spicules and spongin, make fragments light in weight and readily dispersed. In addition, the homogeneous interspersing of tissue with skeleton that is characteristic of demosponges may increase success of dispersing fragments by allowing rapid reattachment to solid substrata and rapid healing of tissue surfaces damaged in dispersal. Thus, these unique characteristics of demosponges may enable them to be especially successful at propagation by dispersing fragments.

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