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SIZE-DEPENDENT GROWTH IN TWO ZOANTHID SPECIES: A CONTRAST IN CLONAL STRATEGIES¹

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Abstract. The widespread occurrence of genet fragmentation among modular, clonal organisms results in size-dependent life history patterns that are often independent of clonal age. In this study the size dependence of clonal growth rates was experimentally evaluated using two common coral reef cnidarians that inhabit shallow reef environments at Discovery Bay, Jamaica. As a result of the turbulent conditions associated with storms, these organisms commonly undergo fragmentation. The growth of aggregations of these clonal fragments in three small size classes (ranging over three orders of magnitude) was statistically evaluated against a null, exponential model that predicts that relative growth rates of small aggregations are size independent. Growth rates for *Zoanthus solanderi* were consistent with this model. *Z. sociatus*, on the other hand, exhibited size-dependent relative growth rates. The smallest aggregations of this species had the highest relative growth rates, which were sufficiently high to more than compensate for losses due to mortality.

These results are consistent with other life history and distributional differences between these two species. *Zoanthus sociatus* has a higher rate of mortality, does not undergo sexual reproduction until reaching a larger aggregation size, and commonly has a higher vertical distribution (which may represent a spatial refuge from subtidal predators) than does *Z. solanderi*. The comparatively rapid relative growth rates of small aggregations of *Z. sociatus* may be the result of spatial constraints on growth in large aggregations and/or of higher relative energy allocations to growth in small aggregations.

The incorporation of fragmentation into the life history strategy of clonal organisms has a range of predicted consequences. Among some organisms, fragmentation and associated adaptations may be rare and of little consequence. Among organisms that frequently fragment as a result of physical disturbances, natural selection should favor repair and regenerative processes as well as resistance to this source of mortality. At the extreme, fragmentation need not be associated with death and injury. Adaptations at the developmental and physiological level may involve genetically programmed production of asexual fragments and size-dependent shifts in energy allocations to growth, sexual reproduction, and energy reserves. The degree of interdependence of the processes controlling the dynamics of genets and fragmented modules may well depend on the relative importance of such adaptations.

Key words: clones; colonial fission; compensatory growth; energy allocation; fragmentation; growth rates; life histories; modules; population dynamics; size-dependent demography.

INTRODUCTION

The complex population structure of clonal invertebrates has several levels of organization. These populations have age and size-frequency distributions that can be described in terms of numbers of individuals (i.e., zooids, polyps, etc.), colonies, and clones; additional complexity can be attributed to the presence of highly fragmented colonies composed of many small groups of individuals as in the Zoanthidea (Karlson 1986) and to the aggregation of many monoclonal or even polyclonal colonies into very large groups. Using terminology that originated in the plant literature, we can designate a clone as a genet (White 1979, Bell and Tomlinson 1980, Harper 1985, Jackson et al. 1985), a colony as a ramet (modified after White 1979) that is

one of several types of modules, and an individual as the smallest modular unit (Harper and White 1974, Harper 1977, White 1979, Bell and Tomlinson 1980, Bell 1984, Hughes and Jackson 1985, Jackson et al. 1985, Jackson and Hughes 1985).

By definition, an individual genet is all the asexually produced offspring of a single zygote or seed (Harper and White 1974, Harper 1977, White 1979, Bell and Tomlinson 1980, Hughes and Jackson 1985, Jackson et al. 1985). A ramet, according to White (1979), is a single module (or "sequence of modules") of a genet that is conveniently enumerated, is not strictly defined morphologically, and may be attached to the genet or become detached and independent (see also Bell 1984). In practice, the ramet is usually a separated vegetative part of the genet (Harper and White 1974, Harper 1977, Bell and Tomlinson 1980). The evolutionary survival of a species is highly dependent on the demographic

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processes regulating genet numbers and diversity (Bell and Tomlinson 1980) while the short-term ecological success of a clonal species depends on the vegetative spread of ramets. Harper and White (1974) say it another way: "Reproduction by seed permits the multiplication of genets, genetic variation, and dispersal. Growth at the subpopulation level allows a proven successful genotype to exploit a proven successful environment."

Life history variation among clonal plants and animals is often size dependent, rather than age dependent, especially in organisms in which age and size are not significantly correlated. Supportive evidence for the size dependence of plant life histories appears in Sarukhan and Harper (1973), Harper and White (1974), Werner (1975), Harper (1977), Werner and Caswell (1977), White (1979), Sarukhan et al. (1984), and elsewhere. The basic life history attributes of clonal animals have been shown to be highly dependent on colony size by several authors (e.g., Connell 1973, Buss 1980a, 1981, Hughes and Jackson 1980, 1985, Sebens 1982a, Wahle 1983, Hughes 1984, Karlson 1986, Hughes and Connell 1987). Generally, the benefits of large colony size include higher survivorship, enhanced competitive ability, and greater reproductive success (e.g., higher fecundity, more successful matings, or greater chance of successful fertilization) (Buss 1980a, 1981, Sebens 1982a). Organisms may achieve these benefits through growth, aggregation, or fusion with clonemates (Hughes and Jackson 1980), siblings (Ivker 1972), or even unrelated conspecifics (Teissier 1929, Stephenson 1931, Schijfsma 1939, Heyward and Stoddart 1985, Grosberg and Quinn 1986). Small colony size results from young age, crowding, fission, partial mortality, and shrinkage. Usually there is a greater risk of mortality among small colonies, but the production and dispersal of many small "daughter" colonies can spread the risk of mortality (den Boer 1968, Highsmith 1982). Among clonal organisms, such small offspring can originate sexually (e.g., as gametes, zygotes, larvae, seeds), asexually (e.g., as medusae, amictic ova, vegetative fission products), or from external disturbances (e.g., as broken fragments).

Zoanthus sociatus and *Z. solanderi* are two very abundant clonal animals that produce small offspring by all three of the above processes. They have a larval dispersal stage, undergo vegetative fission through the degeneration of stolonal connections, and fragment during storms (Karlson 1981, 1983, 1985, 1986, Fadlallah et al. 1984). They form loosely organized colonies composed of small groups of stolonally connected polyps. Below I refer to these colonies as aggregations (sensu Larwood and Rosen 1979) and to the small groups as polyp clusters. Although these zoanthids most commonly occur in shallow, relatively protected Caribbean reef environments (Goreau 1959, Kinzie 1973, Karlson 1980, Sebens 1982b), they occasionally are exposed to catastrophic storms or extreme tidal con-

ditions (Woodley et al. 1981, Karlson 1983, Fadlallah et al. 1984). Such exposure can result in fragmentation, changes in the sizes of aggregations, and shifts in size-dependent life history attributes.

Among the life history predictions for fragmenting clonal organisms is the energy allocation argument that small groups of individuals delay sexual reproduction in favor of more rapid growth to escape size-dependent mortality (Highsmith 1982, Hughes and Jackson 1985). Previous analyses of sexual reproduction and size-dependent mortality support the predictions of delayed sexual reproduction and disproportionately high mortality rates among small zoanthid aggregations (Karlson 1985, 1986); this is especially true for *Zoanthus sociatus*.

In this paper, I evaluate clonal growth rates as a function of aggregation size. I describe two fragmentation experiments in which I simulated storm disruption and dispersal of fragments and monitored their subsequent growth. These experiments document divergent growth patterns in *Zoanthus sociatus* and *Z. solanderi*. The null model I begin with in this analysis is the exponential growth model that commonly is assumed to be valid for a variety of colonial invertebrates (Jackson 1977, 1979, but see Kaufman 1981) and plants (Harper 1977, Causton and Venus 1981) during early growth after exhaustion of yolk or endosperm. *Zoanthus solanderi* growth data fit this model very well while those for *Z. sociatus* do not. I then evaluate three alternative models that suppose that *Z. sociatus* growth deviates from the exponential model because (1) mortality is not proportional to aggregation size, (2) growth occurs only at the ends of stolons (a linear growth model), and (3) growth occurs only at the periphery of sheetlike aggregations (a concentric growth model).

These last two models represent the extremes of how sessile colonial organisms grow over two-dimensional substrata if constrained only by the shape of the colony or aggregation (Jackson 1979). Since the zoanthids examined here exhibit branching stoloniferous growth and an aggregation shape somewhat intermediate between the runner and sheetlike extremes, one might suppose that zoanthid growth rates would fall somewhere between those predicted by these spatial models. The analyses based on these two models will indicate that growth in *Zoanthus sociatus* is not consistent with either model. The implications of these results will be discussed in terms of spatial and energetic constraints on clonal growth and size-dependent life history variation among fragmenting clonal organisms.

STUDY SITES, ANIMALS, AND METHODS

Study sites

On Jamaican coral reefs, the *Zoanthus* zone is typically located subtidally in the lee of the reef crest at depths of 0–2 m (Goreau 1959, Goreau and Goreau 1973). This zone is dominated by *Zoanthus sociatus* (Goreau 1959, Kinzie 1973, Karlson 1983), its con-

WEST BACK REEF

ONE PALM ISLAND

EAST BACK REEF

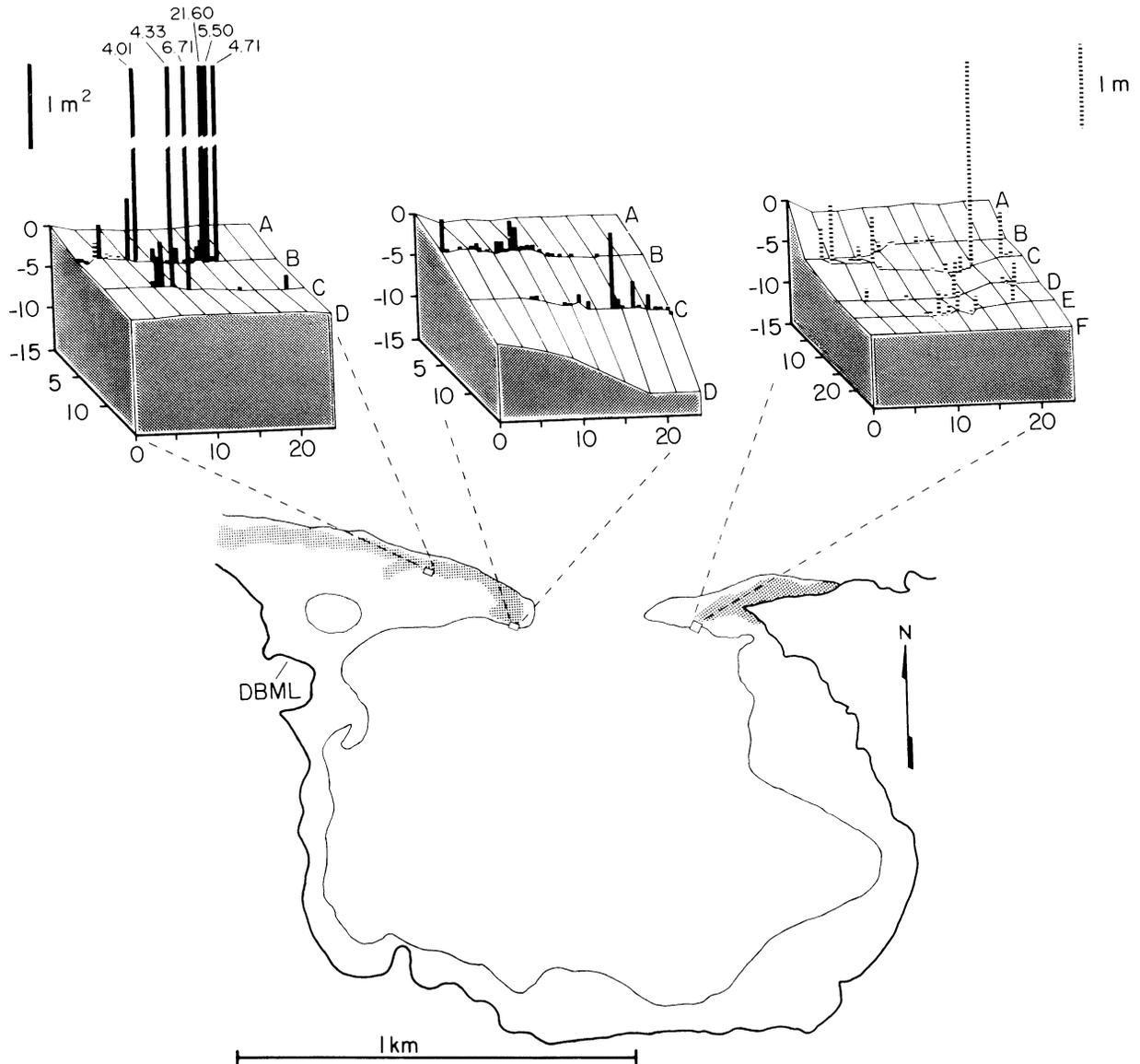


FIG. 1. Map of study sites at Discovery Bay, Jamaica. Transects are designated by letters as in Table 1. Distances are in metres. Transect A was parallel with the reef crest on the northeast side of each site. Vertical lines on three-dimensional graphs indicate aggregation size for *Zoanthus sociatus* (—) and *Z. solanderi* (----). The sizes (in m²) of six large aggregations of *Z. sociatus* at the west back reef are given above the interrupted vertical lines. Shaded area represents shallow reef < 1 m deep and a 5 m depth contour is also indicated. DBML = Discovery Bay Marine Laboratory.

gener *Z. solanderi* (Karlson 1980), and numerous algal species (Karlson 1983 and J. Lang, *personal communication*). Normally it has an "impoverished" coral fauna including 22 species (Goreau and Goreau 1973). At Discovery Bay, Jamaica, this zonation pattern is typical along ≈0.7 km of the west back reef (Fig. 1). Distributional data are provided below for a study site located on the west back reef in the vicinity of sites extensively studied by Kinzie (1973), Karlson (1983), and J. Lang (*personal communication*).

On the steeply sloping bottom in the lee of One Palm

Island (Fig. 1), a second study site was established at a location where the zonation pattern is somewhat different. At this site many zoanthid aggregations occur on largely unconsolidated coral rubble to depths below 10 m. During July 1984, large numbers of sea anemones and some colonies of the gorgonian *Briareum asbestinum* and the coral *Acropora cervicornis* were noted here. The prevalence of these organisms suggests that this site is more protected from turbulent wave action than are other sites along the west back reef (see Woodley et al. 1981, Wahle 1983, 1985).

A third study site was located on the east back reef (Fig. 1). Although some aggregations of *Zoanthus sociatus* can be found here, *Z. solanderi* is much more common (Karlson 1980, 1981), occurring to a depth of 6 m. The opposite pattern holds for the west back reef and One Palm Island sites; *Z. solanderi* is present, but is not very abundant. The east back reef site is generally well protected from waves generated by the prevailing northeasterly winds (Karlson 1980) and was even somewhat protected from Hurricane Allen in 1980 (Williams 1984). Not long after this major storm, B. Keller (*personal communication*) noted that large aggregations of *Zoanthus solanderi* along the east back reef appeared to have been battered, but had survived. Survival of *Z. sociatus* populations along the west back reef was much more variable. Shallow (<1 m) populations in the lee of One Palm Island were totally obliterated during Hurricane Allen, while those in deeper water (10 m) and in shallow water (1–2 m) between One Palm Island and the rest of the west back reef crest (i.e., on the north side of One Palm Island) survived (B. Keller, *personal communication*).

Animals

Zoanthus sociatus and *Z. solanderi* are members of the order Zoanthidea (Cnidaria: Anthozoa). According to Walsh (1967), this order includes three families, seven genera, and 268 species worldwide. Over 60% of these species are members of the family Zoanthidae (*Palythoa*, 102 species; *Zoanthus*, 59 species; and *Isaurus*, 5 species). These three genera are, for the most part, free-living tropical organisms that can be especially prevalent in lower intertidal and upper subtidal zones (e.g., Goreau 1959, Kinzie 1973, Sebens 1982b, Karlson 1983, Ryland et al. 1984).

In contrast to Panamanian populations (Sebens 1982b, Fadlallah et al. 1984), Discovery Bay *Zoanthus* populations are not commonly exposed to intertidal stresses nor do predators severely limit their distributions (Karlson 1983). Instead, one finds distributional patterns affected by gradients in exposure to wave action. Exposed populations experience substratum disruption and fragmentation (Karlson 1983, 1986), while more protected populations experience substratum stability and higher frequencies of encounters with other spatial competitors (Karlson 1980).

Zoanthus sociatus and *Z. solanderi* can form extensive aggregations (Kinzie 1973) as they grow over solid coral rock or unconsolidated rubble and can reach densities in excess of 10^4 polyps/m² (Karlson 1983). Zoanthid polyps vary in size depending, in part, on substratum topography and other microhabitat conditions. For example, in situ measurements of polyp height for *Z. sociatus* at One Palm Island in 1977 averaged 20 mm yet ranged between 5 and 80 mm (R. H. Karlson 1983 and *personal observation*).

Although zoanthids resemble clonal sea anemones, they differ from them by forming groups of polyps in

which stolonial and coenenchymal connections may be maintained following asexual budding. They also lack the well-developed musculature so common among sea anemones and the hard skeletal support system so typical of many other common, coral reef cnidarians (e.g., scleractinian corals, gorgonians, antipatharians, and hydrocorals). These limitations are likely constraints on upright growth in an occasionally turbulent environment; generally, zoanthids are restricted to lateral stoloniferous growth over the substratum.

Sexual reproduction, growth, and physical disturbance are three processes that can affect local population size and the size-frequency distributions of zoanthid aggregations. Although gametogenesis in *Zoanthus sociatus* can result in the production of $>10^7$ ova \cdot m⁻² \cdot yr⁻¹ (Fadlallah et al. 1984), recruitment rates appear to be considerably less than 10 individuals \cdot m⁻² \cdot yr⁻¹ (Karlson 1983). Typical growth of additional polyps occurs by extratentacular budding from stolons (West 1979, Karlson 1983). The degeneration of stolons and the creation of small, interconnected polyp clusters within larger aggregations is a normal part of zoanthid growth (West 1979, Muirhead and Ryland 1985). Fig. 2 depicts the relative frequency distributions of polyp cluster size from a collection of 88 small (≤ 118 polyps) aggregations of *Z. sociatus* and 104 aggregations of *Z. solanderi*; these small aggregations were highly fragmented as has also been found for much larger aggregations (Karlson 1985, 1986). In spite of this high level of fragmentation, both species typically occur as tightly packed aggregations of polyps (i.e., the absence of stolonial connections between polyps is not visually apparent from above). Stolonial elongation, budding, and stolonial degeneration is likely to result in the slow dispersal of genotypes within these loosely organized, multigenet aggregations. Rapid dispersal over somewhat greater distances can result from physical disturbance (Karlson 1983). Dispersed groups of polyps may form small, isolated aggregations or may collect within large aggregations. These zoanthids are capable of extensive regeneration following the disruptive effects of storms (Karlson 1983).

Transects

During January 1984, the distribution and abundance of zoanthids at each of the three study sites were determined along parallel 25-m line transects at 5-m horizontal intervals throughout the *Zoanthus* zone. The initial transect at each site was selected at a representative location in very shallow water parallel to the reef crest just seaward (i.e., northeast) of the *Zoanthus* zone (Fig. 1). Along each transect, the location, depth, length along the transect line, greatest linear dimension (=a), and the greatest linear dimension perpendicular to this last measurement (=b) were recorded for each intersected zoanthid aggregation. The approximate area of each aggregation was estimated using the formula for the area of an ellipse, area = $\pi ab/4$; this general ellip-

tical approximation includes the special case in which aggregations grow as concentric circles. This procedure for estimating area was considered necessary only because of the logistically impossible task of using standard photographic methods on large aggregations in such shallow water. Zoanthid percent cover was estimated using the sum of aggregation lengths along the transect line for each transect. Polyp densities were determined for each transect by counting all polyps within 10, 25-cm² quadrats taken within zoanthid aggregations. These quadrats were dropped haphazardly within aggregations along each transect.

Growth

The effect of aggregation size on zoanthid growth was investigated using two different manipulations designated here as the initial fragmentation and reciprocal transplant experiments. These experiments simulated one disruptive effect of storm-induced fragmentation, namely the creation of small, isolated aggregations.

Initial fragmentation experiment.—In July 1983 aggregations of *Zoanthus sociatus* at One Palm Island and *Z. solanderi* at the east back reef were collected with their coral rubble substrata and trimmed with a scalpel to a size of 1, 10, or between 100 and 200 polyps per aggregation. Each aggregation was centrally located on the rubble substrata. There were 10 aggregations per size class per species yielding a total of 60 aggregations containing 2826 polyps. At each site, all 30 substrata were attached using cable ties to a single, large, 7.6-cm mesh nylon net, which was tied and heavily weighted to the bottom at a depth of 2 m. Due to the nonuniform size and shape of the substrata on which these zoanthids were growing, aggregations were positioned in a haphazard manner on the nets rather than at predetermined, randomly selected locations. There was sufficient space for unimpeded lateral growth on all substrata throughout the experiment. These procedures are very similar to those described by Sebens (1982b) for a series of transplant experiments using these same species but only one small aggregation size class.

During January and July 1984, all 60 aggregations in the initial fragmentation experiment were photographed so that the number of polyps per aggregation could be determined later. Given that the total number of polyps used in this experiment was so large, direct polyp counts were conducted in the field only for small aggregations. Relative growth rates were then calculated on a per-capita (i.e., initial number of polyps) per-month basis for each of the successive 6-mo intervals and each of three aggregation size classes (i.e., class 1 = 1–5 polyps, class 2 = 6–50 polyps, and class 3 = 51–500 polyps). These data were then analyzed for aggregation size and time effects using standard two-way ANOVA (Snedecor and Cochran 1967). Further description of these statistical procedures and the null models being tested appears in Results, below.

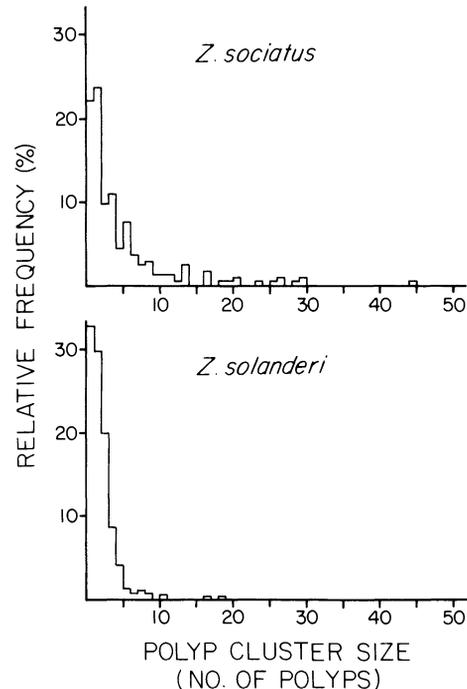


FIG. 2. Relative frequency (%) distributions of polyp cluster size in terms of numbers of polyps for *Zoanthus sociatus* and *Z. solanderi*. There were 249 clusters in 88 aggregations of *Z. sociatus* and 468 clusters in 104 aggregations of *Z. solanderi*.

Reciprocal transplant experiment.—In January 1984, the above procedures were repeated with the following modifications to evaluate habitat-related effects on zoanthid survivorship and growth. Forty-four aggregations of *Zoanthus sociatus* from One Palm Island and the same number of *Z. solanderi* from the east back reef were collected and trimmed into either a 1- or 10-polyp size class. Half of the aggregations from each species and size class was transplanted across the bay to the other site; half remained at the collection site. There were 10–13 aggregations per size class per species per site. In July 1984 polyps in each aggregation were counted directly in the field and relative per-month growth rates were then determined.

RESULTS

Transects

The *Zoanthus* zone at the west back reef site was very similar to that described elsewhere (Goreau 1959, Goreau and Goreau 1973, Kinzie 1973, Karlson 1983). This nearly horizontal zone had a mean slope of only 1.0°, a mean depth of 1.22 m, and a width of <15 m (Table 1). In terms of number of aggregations and percent cover, *Z. sociatus* was far more abundant here than was *Z. solanderi* (Table 1). *Z. sociatus* had an overall mean aggregation size of 1.72 m², a size range of 3.14 cm²–21.60 m² (Fig. 1), an overall mean density of 3.86 polyps/cm², and a range of 2.12–5.20 polyps/

TABLE 1. Summary of zoanthid depth distribution and abundance data. Polyp density and aggregation size data are given as means and standard errors. Letter designations for each transect match those given in Fig. 1.

West Back Reef Transects (mean slope = 1.0°)						
Transect	A	B	C	D		
Horizontal distance (m)	0	5	10	15		
Mean depth (m)	0.71	1.22	1.21	1.02		
<i>Zoanthus sociatus</i>						
Number of aggregations	0	22	7	0		
Aggregation size (m ²)	...	1.72 ± 1.01	1.74 ± 1.01	...		
Cover (%)	0	18.9	26.0	0		
Polyp density (no./cm ²)	...	3.81 ± 0.26	3.91 ± 0.29	...		
<i>Zoanthus solanderi</i>						
Number of aggregations	0	9	1	0		
Aggregation size (m ²)	...	0.04 ± 0.02	0.003	...		
Cover (%)	0	3.9	0.1	0		
Polyp density (no./cm ²)	...	1.35 ± 0.02	0.64 ± 0.16	...		
One Palm Island transects (mean slope = 31.4°)						
Transect	A	B	C	D		
Horizontal distance (m)	0	5	10	15		
Mean depth (m)	0.98	1.79	4.57	9.14		
<i>Zoanthus sociatus</i>						
Number of aggregations	0	29	21	0		
Aggregation size (m ²)	...	0.05 ± 0.02	0.08 ± 0.04	...		
Cover (%)	0	10.6	16.0	0		
Polyp density (no./cm ²)	...	2.79 ± 0.13	3.69 ± 0.31	...		
East Back Reef transects (mean slope = 22.1°)						
Transect	A	B	C	D	E	F
Horizontal distance (m)	0	5	10	15	20	25
Mean depth (m)	1.23	4.26	4.11	5.61	5.55	6.10
<i>Zoanthus sociatus</i>						
Number of aggregations	0	0	0	0	3	0
Aggregation size (m ²)	0.00003 ± 0.00002	...
Cover (%)	0	0	0	0	0.07	0
Polyp density (no./cm ²)	2.51 ± 0.50	...
<i>Zoanthus solanderi</i>						
Number of aggregations	0	9	22	9	27	0
Aggregation size (m ²)	...	0.04 ± 0.01	0.24 ± 0.11	0.08 ± 0.03	0.03 ± 0.01	...
Cover (%)	0	5.2	15.2	5.0	11.0	0
Polyp density (no./cm ²)	...	1.57 ± 0.10	1.38 ± 0.08	1.44 ± 0.11	1.48 ± 0.07	...

cm² within aggregations. Aggregation sizes for *Z. sociatus* were: mean, 6.64×10^4 polyps and range, 1.20×10^1 – 8.34×10^5 polyps.

At One Palm Island, the lower distributional limit of *Zoanthus sociatus* extended below 10 m (R. H. Karlson, *personal observation*). Aggregations of *Z. sociatus* were significantly smaller here than were those at the more typical west back reef ($t = 2.75$, $P < .01$), but there were no significant differences with respect to percent cover per transect ($t = 1.96$, $P > .10$), number of aggregations per transect ($t = 1.24$, $P > .20$), or mean polyp densities ($t = 1.92$, $P > .05$) (Table 1). Aggregation sizes at One Palm Island were: mean, 2.11×10^3 and range, 2.00×10^0 – 2.82×10^4 polyps, respectively. Numerous small aggregations of *Z. solanderi* also were present here, interspersed among larger *Z. sociatus* aggregations. However, none of these occurred along the transects.

Zoanthus solanderi was most abundant at the east back reef where it extended over an almost 25 m wide

band with a mean depth of 4.88 m (Table 1). It had an overall mean aggregation size of 0.11 m², a size range of 0.20 cm²–2.45 m² (Fig. 2), an overall mean density of 1.47 polyps/cm² (Table 1), and a range of 0.92–2.28 polyps/cm². Aggregation sizes for *Z. solanderi* were: mean, 2.20×10^3 and range, 1.00×10^0 – 3.60×10^4 polyps, respectively.

These data clearly establish that the number of polyps in zoanthid aggregations ranged over five orders of magnitude and that most aggregations contained thousands of individuals. The proportion of aggregations having fewer than 100 polyps was 26.8% for *Zoanthus sociatus* and 45.5% for *Z. solanderi*. The data presented below document a disproportionately large contribution to the growth of numbers of individuals by very small aggregations of the former species.

Initial fragmentation experiment

A total of 51 and 57 semiannual growth rate estimates were determined for *Zoanthus sociatus* and *Z.*

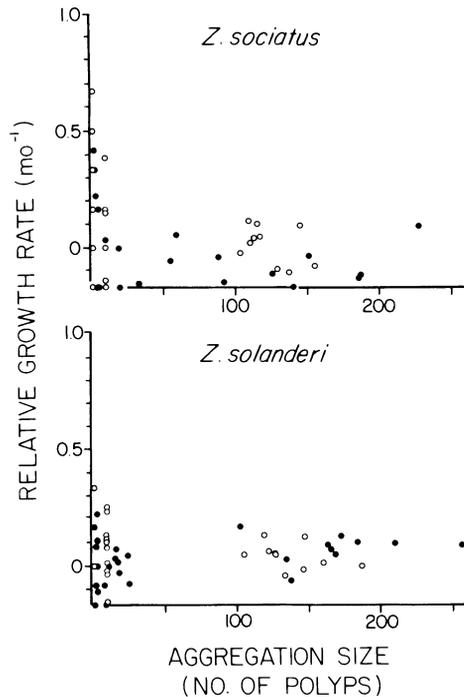


FIG. 3. Net relative growth rates for *Zoanthus sociatus* and *Z. solanderi* vs. aggregation size over two, 6-mo time intervals ending January 1984 (O) and July 1984 (●). Growth rates are given in terms of the proportional net change in polyp number per number of polyps at the start of each interval per month. Aggregations not surviving an interval yielded a minimum rate of -0.167 mo^{-1} .

solanderi, respectively, from the 60 small fragmented aggregations used in this experiment; 12 aggregations died during the first 6 mo. After 12 mo, there were 42 surviving aggregations containing 3496 polyps. Net relative growth rates ranged between -0.17 and 0.67 mo^{-1} (Fig. 3). For *Zoanthus solanderi*, the overall mean growth rate was 0.05 mo^{-1} , and there was no significant variation due to aggregation size (Table 2). Therefore, the exponential model adequately describes clonal

growth in this species. Growth in *Z. sociatus*, on the other hand, did not fit this model. It had an overall mean growth rate of 0.02 mo^{-1} and a significant aggregation size effect on growth (Table 2); its highest relative growth rates occurred among aggregations in the smallest size class (Fig. 3). Relative growth rates of large aggregations (> 10 polyps) appeared to be uniform (i.e., size independent) and thus may have fit the exponential model above this apparent size threshold (Fig. 3). There were no significant time or interaction effects (Table 2).

There are at least three explanations for high relative growth rates of small aggregations of *Zoanthus sociatus*. First, relative (per capita) mortality rates may have been disproportionately high among large aggregations. Second, growth may have been inhibited in large aggregations due to morphological constraints associated with aggregation shape, two-dimensional clonal growth patterns, and crowding. Third, physiological shifts in energy allocations may have favored asexual growth in numbers of polyps among small aggregations and sexual reproduction among large aggregations. Although it is possible that any one of the above explanations could have been solely responsible for the observed deviation from the exponential model, they are not mutually exclusive alternatives. Below, I statistically evaluate the first two alternatives using the data from *Zoanthus sociatus*.

Mortality among these zoanthids is caused by a variety of factors, including physical stress, predation, disturbance, and competitive overgrowth (Karlson 1980, 1983, 1986, Sebens 1982b, Fadlallah et al. 1984). Of the original 60 aggregations in this experiment, 18 had totally disappeared after 12 mo; 67% of these were *Z. sociatus* aggregations in the two smaller size classes (Table 3). In addition, shrinkage (indicating partial mortality and possibly some degree of fragment dispersal) was also prevalent (Table 3). The high frequencies of shrinkage and total mortality of aggregations resulted in several negative net growth rates in all three size classes of *Z. sociatus* (Fig. 3). In an attempt

TABLE 2. Tests of the exponential model using two-way ANOVA of net relative growth rates (per month) for *Zoanthus sociatus* and *Z. solanderi* in each of three size classes and two time intervals.* The data are plotted in Fig. 3.

Species	Source of variation	Degrees of freedom	Sum of squares	Mean square	F
<i>Z. sociatus</i>	Aggregation size	2	0.318	0.159	4.25†
	Time	1	0.010	0.010	0.25 NS
	Interaction	2	0.037	0.018	0.49 NS
	Error	45	1.684	0.037	
	Total	50	2.048		
<i>Z. solanderi</i>	Aggregation size	2	0.021	0.010	0.64 NS
	Time	1	0.032	0.032	1.95 NS
	Interaction	2	0.050	0.025	1.54 NS
	Error	51	0.828	0.016	
	Total	56	0.930		

* Standard data transformation failed to eliminate significant heteroscedasticity: $F_{\max} = 14.06$ ($P < .01$) and 16.68 ($P < .01$) for *Z. sociatus* and *Z. solanderi*, respectively. The sums of squares have been adjusted for disproportionate numbers (Snedecor and Cochran 1967).

† $P < .025$; NS = not significant.

TABLE 3. The fate of aggregations in the initial fragmentation experiment after 6 and 12 mo.

Species	Aggregation size class (no. polyps)	Sample time (mo)	Number of aggregations			
			Growth	No net change	Shrinkage	Death*
<i>Zoanthus sociatus</i>	1-5	6	5	1	0	4
		12	5	0	0	2
	6-50	6	3	1	1	5
		12	1	1	1	1
51-500	6	6	0	4	0	
	12	2	0	7	1	
<i>Z. solanderi</i>	1-5	6	6	1	0	3
		12	4	1	2	1
	6-50	6	7	0	3	0
		12	4	1	3	1
	51-500	6	7	0	3	0
		12	9	0	1	0

* Average mortality rates appear in Karlson (1986).

to remove some of the mortality effects from the analysis of growth in *Z. sociatus*, I conducted a second ANOVA of relative (per capita) growth rates after having eliminated data indicating shrinkage or death (Table 3). Once again this analysis resulted in a significant aggregation size effect (Table 4). The smallest aggregation size class exhibited the highest mean relative growth rate (0.30 mo^{-1}) and the data did not conform with expectations based on the exponential model. Aggregations in the smallest size class grew significantly faster than predicted by this model (i.e., their mean rate of growth was significantly higher than the overall mean across all size classes [0.18 mo^{-1}]). There was over a fourfold difference in the mean relative growth rates between the largest and smallest size classes. There were no significant time or interaction effects (Table 4).

Given that both of the above analyses clearly indicate that relative (per capita) growth rates in *Zoanthus sociatus* did not conform with the exponential model, two alternative clonal growth models were tested. The first was a linear growth model based on the expected growth of runnerlike clones, which do not branch; the second was a concentric growth model based on

TABLE 4. Test of the exponential model using two-way ANOVA on all nonnegative relative growth rates (per month) for *Zoanthus sociatus* in each of three size classes and two time intervals.† The data are plotted in Fig. 3.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Aggregation size	2	0.284	0.142	6.36**
Time	1	0.010	0.010	0.47 NS
Interaction	2	0.023	0.012	0.52 NS
Error	19	0.424	0.022	
Total	24	0.741		

** $P < .01$, NS = not significant.

† Variances are homogeneous: $F_{\max} = 108.57$, 6 groups, 1 df, NS. The sums of squares have been adjusted for disproportionate numbers (Snedecor and Cochran 1967).

growth being restricted to the periphery of circular, sheetlike clones (Jackson 1979). These two models bracket the morphological extremes of encrusting clonal organisms that lack upright growth. Zoanthids are branching stoloniferous forms that should exhibit growth rates within this predicted range, if growth is limited primarily by spatial constraints. Both models are consistent with the observation that relative growth rates are inversely related to aggregation size.

Under the linear growth model, the null hypothesis was that the absolute (i.e., not relative) rate at which new individuals were added to aggregations was independent of aggregation size. ANOVA using all nonnegative growth rates resulted in a highly significant aggregation size effect. Generally, more individual polyps were added per unit time to large aggregations than to small aggregations. These growth rates ranged between 0.17 and 20.5 new polyps per month for aggregations with 1-227 polyps. Mean growth rates were 0.47, 1.22, and 9.38 polyps per month for small, medium, and large aggregation size classes (Table 5). This linear model is rejected as a description of growth in *Zoanthus sociatus*.

Under the concentric growth model, the null hypothesis was that the relative growth rate per unit circumference per month [i.e., $\Delta N / (C_i \Delta t)$, where $C_i = \sqrt{4\pi N_i}$ (an approximation of the number of polyps on the periphery of each aggregation) and N_i = the initial number of polyps in each aggregation] did not vary among size classes. Assumptions under this model were that aggregations were circular, the density of individuals did not vary with aggregation size, and this relative growth rate was proportional to the square root of aggregation size. Mean growth rates in *Zoanthus sociatus* were 0.10, 0.11, and 0.23 mo^{-1} for small, medium, and large aggregation size classes (Table 6). Although these data indicate only a twofold maximum difference in mean growth rates, the means are significantly different and the concentric growth model also is rejected as a description of growth in *Zoanthus sociatus*. There

TABLE 5. Test of the linear model using two-way ANOVA on all nonnegative growth rates (change in polyp number per month) for *Zoanthus sociatus* in each of three size classes (determined at the beginning of each of two time intervals).

A) Growth rates ≥ 0 polyps/mo				
	Time interval	Size class (initial no. polyps)		
		1-5	6-50	51-500
\bar{X}	1	0.306	1.750	8.556
	2	0.667	0.167	11.833
s^2	1	0.062	2.490	23.151
	2	0.042	0.056	150.216
n	1	6	4	6
	2	5	2	2

B) ANOVA on log-transformed growth rates†

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Aggregation size	2	15.486	7.743	32.20***
Time	1	0.002	0.002	0.01 NS
Interaction	2	0.892	0.446	1.86 NS
Error	19	4.569	0.240	
Total	24	20.949		

*** $P < .001$, NS = not significant.

† The logarithmic transformation eliminated significant heteroscedasticity: $F_{\max} = 79.42$, 6 groups, 1 df, NS. The sums of squares have been adjusted for disproportionate numbers (Snedecor and Cochran 1967).

were no significant time or interaction effects (Table 6). Rejection of both of the spatial growth models supports the conclusion that growth was not limited severely by spatial constraints associated with the shape of aggregations or the stoloniferous branching patterns.

Reciprocal transplant experiment

This experiment was designed to evaluate species, size, and habitat-related effects on zoanthid survivorship and growth. After 6 mo, 71.6% of 88 aggregations experienced total mortality, 9.1% shrank, 3.4% did not change size, and only 15.9% grew (Table 7). This heavy mortality resulted from a variety of causes including predation, overgrowth, physical storm damage, and the presence of unusually dense algal populations. Total mortality of aggregations was very high for *Zoanthus sociatus* (88.6%) and for the smaller of the two size classes for *Z. solanderi* (90.5%; Table 7); there was no significant habitat effect on this mortality rate (Karlson 1986). As a direct consequence of high mortality, all but one of the mean net growth rates were negative and that one was not significantly greater than zero (Table 7).

The data from this experiment provide an extremely limited basis for considering species, size, and habitat effects on clonal growth. In fact, only 14 of the original 88 aggregations grew larger over the 6-mo interval (Table 7). However, I include data from this experiment because they provide ancillary support for two conclusions based on the initial fragmentation experiment.

First, maximum relative growth rates were exhibited by clonal fragments begun as single polyps; these rates were 0.67 mo^{-1} for *Zoanthus sociatus* and 0.50 mo^{-1} for *Z. solanderi*; the highest rate achieved by aggregations begun as groups of 10 polyps was 0.28 mo^{-1} for *Z. solanderi* (Table 7). These data are similar in magnitude and indicate a species difference similar to those indicated in Fig. 3. Second, the data from the reciprocal transplant experiment corroborate the existence of a large survivorship difference between the 1- and 10-polyp size classes for *Z. solanderi* (i.e., 90 and 22%, respectively; Table 7) while both experiments suggest that enhanced survivorship in *Z. sociatus* occurs at significantly larger aggregation sizes (Tables 3 and 7).

DISCUSSION

The above analyses indicate that relative (per capita) growth rates of small zoanthid aggregations were independent of aggregation size in *Zoanthus solanderi* (i.e., consistent with an exponential growth model) and were aggregation-size dependent in *Z. sociatus*. Relative growth rates did not vary significantly among aggregations that ranged across three orders of magnitude in *Z. solanderi*; they were inversely related to aggregation size in *Z. sociatus*. After elimination of all data for aggregations that died or shrank from the analysis of growth in *Z. sociatus*, relative growth rates were 4.2 times higher for small aggregations than for those in the largest size class.

The difference in the relationship between aggregation size and growth rates in these two species is con-

TABLE 6. Test of the concentric growth model using two-way ANOVA on all nonnegative relative growth rates (per month) for *Zoanthus sociatus* in each of three size classes (determined at the beginning of each of two time intervals).

A) Growth rates ≥ 0				
	Time interval	Size class (initial no. polyps)		
		1-5	6-50	51-500
\bar{X}	1	0.086	0.156	0.220
	2	0.121	0.015	0.250
s^2	1	0.005	0.020	0.015
	2	0.001	0.001	0.036
n	1	6	4	6
	2	5	2	2

B) ANOVA on growth rates†

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Aggregation size	2	0.079	0.039	3.81*
Time	1	0.001	0.001	0.04 NS
Interaction	2	0.031	0.016	1.50 NS
Error	19	0.196	0.010	
Total	24	0.306		

* $P < .05$, NS = not significant.

† Variances are homogeneous: $F_{\max} = 81.43$, 6 groups, 1 df, NS. The sums of squares have been adjusted for disproportionate numbers (Snedecor and Cochran 1967).

TABLE 7. Results of the reciprocal transplant experiment after 6 mo at East Back Reef (EBR) and One Palm Island (OPI) sites.

Category	<i>Zoanthus sociatus</i>				<i>Zoanthus solanderi</i>			
	EBR		OPI		EBR		OPI	
	Initial aggregation size (no. polyps)							
	1	10	1	10	1	10	1	10
Initial number of aggregations	11	11	11	11	11	13	10	10
Number of aggregations that died	8	9	11	11	11	3	8	2
Number of polyps in surviving aggregations	2, 2, 5	1, 5	2, 6, 8, 10, 10, 11, 17, 17, 19, 23	1, 4	3, 9, 9, 13, 14, 17, 18, 27
Net relative growth rate per mo	\bar{X} -0.030 SE 0.080 n 11	-0.158 0.008 11	-0.167 0.0 11	-0.167 0.0 11	-0.167 0.0 11	-0.009 0.036 13	-0.083 0.067 10	0.017 0.045 10
One-sample comparison against zero growth								$t = 0.38$ NS†
Positive relative growth rate per mo	\bar{X} 0.333 SE 0.167 n 3	0.667 ... 1	0.123 0.032 5	0.500 ... 1	0.130 0.041 5

† NS = not significant.

sistent with other differences in their life histories. It is known that the onset of sexual reproduction is delayed more in *Zoanthus sociatus* than in *Z. solanderi*; small aggregations of *Z. sociatus* are nonreproductive (Karlson 1985, 1986). This implies that there is a greater risk of mortality among small aggregations of *Z. sociatus* than of *Z. solanderi*. This implication, in fact, has been substantiated directly by predation and fragmentation experiments (Sebens 1982b, Karlson 1983, 1986); generally *Z. sociatus* experiences higher mortality rates than does *Z. solanderi*. It is further corroborated by vertical distribution differences between the two species. *Z. sociatus* inhabits an intertidal zone in Panama where it frequently experiences desiccation and occasionally suffers mass mortality from extreme aerial exposure (Sebens 1982b, Fadlallah et al. 1984). *Z. sociatus* is more desiccation resistant than *Z. solanderi* and it has higher survivorship in this intertidal zone than in lower intertidal and subtidal habitats; this intertidal zone probably represents a spatial refuge from subtidal predators (Sebens 1982b).

Zoanthus solanderi typically inhabits a lower vertical zone where it is much more likely to encounter predators and spatial competitors (Karlson 1980, Sebens 1982b) and is more likely to have evolved allelochemical defenses than *Z. sociatus* (Karlson 1980). In general, such defensive compounds are extremely common among sessile epibenthic invertebrates (Bakus 1981, Coll et al. 1982, Sammarco et al. 1985); these organisms have few other adaptive alternatives given their low mobility and their limited suite of behavioral responses. The occurrence of powerful allelochemicals in zoanthids has long been recognized (Scheuer 1964, Attaway 1968, Hashimoto et al. 1969, Moore and Scheuer 1971, Cha et al. 1982, Moore et al. 1982);

detailed studies have indicated extremely high levels of toxicity associated with the presence of eggs in *Palmytha tuberculosa* (Kimura et al. 1972).

In lieu of effective allelochemical defenses among small nonreproductive aggregations (as indicated by their high relative susceptibility to predators), *Zoanthus sociatus* may escape significant levels of size-dependent mortality by exploiting the intertidal refuge mentioned above and/or by diverting energy resources to support high relative growth rates rather than sexual reproduction among small aggregations. Given that polyp biomass in *Zoanthus sociatus* is approximately one-third that of *Z. solanderi* (Sebens 1977), this energy diversion towards growth represents less of an energy investment per polyp in the former species. Growth of the larger, better defended polyps of the latter species requires more energy per polyp and therefore represents a more costly alternative to sexual reproduction.

The intertidal refuge hypothesis may be further evaluated by examining dispersal and habitat selection by the sexual and asexual propagules of this zoanthid. Location of the intertidal refuge might involve active behavioral adaptations among larvae (e.g., Grosberg 1982) or more passive dispersal properties affecting, for example, the specific gravity of dislodged colonial fragments. Sufficient data for an adequate evaluation of habitat selection in this species are not currently available.

The energy reallocation hypothesis attributes size-dependent growth rates in *Zoanthus sociatus* to shifts in the energy allocations for growth. This implies that energy is generally in limited supply (Jackson and Hughes 1985), that there is a size threshold above which survivorship is significantly increased, and that size-

related stimuli initiate the shift in energy allocations. There is considerable evidence suggesting the generality of energy as well as spatial limitations on clonal organisms growing on coral reefs (e.g., Jackson 1977, Muscatine and Porter 1977, Buss and Jackson 1981, Jackson and Hughes 1985). As pointed out by Buss (1980b), the utilization of space and the acquisition of energy resources (by heterotrophy, phototrophy, or chemotrophy) by such sessile organisms are highly interdependent processes. Furthermore, there is evidence that growth form and rates can vary directly in response to limited food (e.g., Crowell 1957, Berrill 1961, Winston 1976) and space (e.g., Buss 1979, Karlson 1980). The interdependence between these two parameters may link proximal spatial or chemical stimuli (e.g., crowding effects, contact events at clonal edges, carbon dioxide tension [Loomis 1957], and nutritional condition [Berrill 1961]) to the physiological changes regulating shifts in energy allocations. Physiological regulation of energy allocations may also be controlled to some degree by internal morphogenetic processes (i.e., clonal fragmentation and size-dependent shifts in energy allocations may be genetically programmed).

There is an enormous range of fragmenting clonal organisms on coral reefs (Glynn 1976, Loya 1976a, b, Highsmith et al. 1980, Hughes and Jackson 1980, 1985, Tunnicliffe 1981, Highsmith 1982, Wahle 1983, 1985, Walker and Bull 1983, Lasker 1984, Karlson 1985, 1986, Wulff 1985). Fragmentation due to both external disturbance and to normal, endogenously controlled fission promotes the local spread of genotypes across highly disturbed reef flats and deeper (35 m), less disturbed reef environments (Hughes and Jackson 1985). Part of the cost of this spreading of risk among small fragments is relatively high size-dependent mortality; sexually produced larvae generally experience even higher mortality rates (Highsmith 1982). The analysis of relative growth rates in *Zoanthus sociatus* suggests that the loss of individual polyps due to high size-dependent mortality can be more than compensated for by the rapid growth of small aggregations (Fig. 3). The maximum relative growth rate in the smallest size class was 0.67 mo^{-1} or 400% over 6 mo (Fig. 3); Sebens (1982b) reported a similar maximum growth rate for *Z. sociatus* in Panama.

This maximum growth rate is equivalent to an annual relative growth rate of 2400%, which exceeds some rates recently reported for 15 coral species from Heron Island, Australia. Hughes and Connell (1987) found maximum relative growth rates of 500–2000%/yr for small (<10 cm²), young (<1 yr) corals. Although the ages of *Zoanthus* aggregations used in the present study were unknown, each aggregation was created as a fragment of a larger aggregation and therefore was older than comparably sized aggregations that might have grown from recently recruited, sexually produced propagules. The rapid relative growth of small, asexually produced fragments of *Z. sociatus* suggests that this

species may have evolved exceptionally well-developed adaptations associated with fragmentation. At the developmental level such adaptations include the endogenous control of stolonal degeneration (e.g., West 1979, Muirhead and Ryland 1985). At the physiological level, they include the regulatory mechanisms controlling energy allocations.

The following predictions represent some potentially important, yet not previously recognized, evolutionary consequences of clonal fragmentation. Because of the advantages generally associated with large size and rapid growth among small colonies, fragments, or aggregations (Connell 1973, Highsmith 1982), natural selection should favor adaptations promoting physiological plasticity and facilitation of rapid shifts in energy allocations in response to changes in size. Rapid growth of small, asexually produced clonal fragments should not only affect the energy allocation for sexual reproduction (Williams 1975, Highsmith 1982), but also that for energy reserves. Like the endosperm and yolk carried by sexually produced propagules in plants and animals, respectively, energy reserves are likely to be necessary for rapid growth should individuals within large aggregations become isolated as small clonal fragments. Fragmenting species that are vulnerable to size-dependent mortality should contain or be able to mobilize more energy reserves per unit body mass than nonfragmenting species, and these energy reserves, like other life history attributes, should vary in a size-dependent manner. Such reserves in clonal fragments should be most important to species that undergo fission as a normal part of clonal growth, less so among species that experience fragmentation only as a result of physical disturbance, and least among species that rarely fragment.

The above arguments regarding energy may be generally applicable to a variety of clonal invertebrates, protists, fungi, and plants exhibiting fission and size-dependent life histories (e.g., Sarukhan et al. 1984, Hughes and Jackson 1985, Hughes and Connell 1987). The analysis of clonal growth rates in *Zoanthus sociatus* and *Z. solanderi* illustrates the importance of considering such attributes as components of an integrated life history. The interpretation of growth rate data required knowledge of how survivorship varied with aggregation size; departure from the exponential growth model occurred in a species that experienced disproportionately high mortality rates in the smallest aggregation size class. Furthermore, the existence of a size threshold above which survivorship was significantly enhanced indicates the importance of examining clonal life histories across a range of size classes. Such studies may be descriptive, involving the monitoring of large numbers of naturally occurring clones over long periods of time (e.g., Hughes and Jackson 1985, Hughes and Connell 1987), or experimental, involving controlled size manipulations to address specific hypotheses (e.g., Wahle 1983, Karlson 1986).

Interdependence of genet and module demographics?

As noted in the introduction, clonal organisms have a complex population structure that can be described simultaneously at several levels of organization. They have age and size-frequency distributions of genets and modules with the latter being defined at several levels (e.g., polyps, leaves, rosettes, colonies, fragments, ramets, aggregations, etc.). Harper and his coworkers have been very strong supporters of the notion that we distinguish the demographic processes controlling "birth" and "death" rates at these different levels of organization (Harper and White 1974, Harper and Bell 1979, Harper 1981). Two major reasons for this are that (1) quite different biological processes can be involved and (2) the density of modules and genets can be independent of one another. But just how independent are they and might they not be more closely linked under certain conditions? And what are the consequences of tight vs. loose linkage between levels? Might we not anticipate that tight linkage between module and genet demographics is more likely among clonal organisms that do not undergo extensive fragmentation as opposed to those that do? Might not programmed fragmentation under genetic and/or developmental control lead to higher levels of dependence between levels of organization than comparable levels of fragmentation due to some stochastic environmental process?

The answers to the above questions will improve our understanding of the ecological and evolutionary success of clonal species. The linkage between levels of organization may occur at both time scales. For example, the coupling of vegetative and sexual processes has led to the successful radiation of rhizomatous angiosperms since the Cretaceous; this is one of the major recent evolutionary trends among clonal land plants (Tiffney and Niklas 1985). On shorter time scales, we may find significant interdependent processes affecting clonal population dynamics. Using the zoanthid example, we may find that genetic or developmental control of stolonal degeneration directly affects future fragment dispersal, which, in turn, affects the size-frequency distribution of aggregations and their size-dependent life histories.

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