

Growth Rates and Growth Strategy in a Clonal Marine Invertebrate, the Caribbean Octocoral *Briareum asbestinum*

DANIEL A. BRAZEAU¹ AND HOWARD R. LASKER

Department of Biological Sciences, State University of New York, Buffalo, NY 14260

Abstract. Colony form directly effects colony reproductive output among colonial benthic invertebrates. The relationship between reproductive effort, colony form, and growth rate in colonies of the Caribbean octocoral *Briareum asbestinum* were examined by measuring the growth rates of 118 tagged colonies on Pinnacles and House Reef in the San Blas Islands, Panama. Colony growth rates, individual branch growth rates, and branch addition rates were measured over six month intervals from July 1986 to July 1988.

Colonies grew at a net rate of 16.6 cm/year and added 1.2 branches/year. Individual branch measurements yielded a net rate of growth of 2.02 cm/year/branch. Positive growth rates, which provide a measure of minimum potential growth, were 71.3 cm/year, and 8.7 branches/year for colonies and 6.21 cm/year for individual branches. Net growth rates and branch addition rates were 76 and 85% less than potential growth rates indicating large losses to fragmentation and predation. Calculated mean longevity of individual colonies (ramets) is short (10.6 years), given observed rates of growth and loss. However, since fragmented branches can reattach and initiate new colonies, losses due to fragmentation contribute to the asexual expansion of the genet.

In July 1987, 783 branches on the tagged colonies were individually mapped in order to characterize the relationship between branch size and the number of bifurcations (tips), and growth rates. The best predictor of growth rate was the number of tips per branch ($r^2 = 0.46$; $P < .0001$). No relationship was found between branch growth and branch size, consequently branch growth per

unit length decreased as branch size increased. The independence of branch growth and size may reflect the diversion of energy away from growth toward reproduction. As a consequence of this pattern, bifurcating growth forms will, on a colony basis, grow more rapidly and amass more reproductive tissue than simple linear extension. However, the short longevity of ramets of *Briareum asbestinum* limits the advantage to be gained from accumulating reproductive tissue by rapid branch bifurcation.

Introduction

One of the fundamental components of the interaction between an organism and its environment is the organism's morphology. Among colonial invertebrates "form" takes on multiple interpretations corresponding to the multiple levels of individuality. The individual zooid or polyp, the colony which those polyps form, and the collection of genetically identical colonies can all be considered to have a form that to differing degrees contributes to the fitness of the genotype (or genet). In this paper we examine growth of a Caribbean gorgonian coral and show how the pattern of growth generates colony form and how that affects one element of fitness: colony reproductive output.

Colony form among benthic invertebrates influences virtually all aspects of the organism's interaction with the environment. Colony morphology affects resistance to wave and current action (Wainwright and Dillon, 1969; Chamberlain and Graus, 1975; Velimirov, 1976; Graus, *et al.*, 1977; Tunnicliffe, 1982; Vosberg, 1982), feeding (Leversee, 1976; McKinney, 1981; Ryland and Warner, 1986), competitive interactions, and even the susceptibility to predation (Kaufmann, 1973; Jackson, 1979). All of these factors should have clear repercussions on fitness, but perhaps the most direct effect of colony morphology

Received 16 September 1991; accepted 7 July 1992.

¹ Present address: Department of Biology, University of Houston, Houston, TX 77204-5513.

is on reproduction. Colonial benthic invertebrates grow by adding new individuals (*i.e.*, polyps or zooids) to the colony. Among many species, each of these individuals is capable of producing gametes. However, in many cases individuals at or near the growing colony edge or tip are either not reproductive or produce fewer gametes than individuals further removed from the growing edge (Rinkevich and Loya, 1979; Wallace, 1985; Chornesky and Peters, 1987; Brazeau and Lasker, 1990). Thus, both total colony size and colony form determine gamete production. Many benthic species also propagate via fragmentation, thus colony growth rate and form also affects the size, survivability, and generation rate of asexual propagules (Walker and Bull, 1983; Lasker, 1984, 1990). Since the pattern and rate of growth of a colony affects both colony size and form, the pattern of growth becomes a key element in the reproductive strategies of benthic species.

In this paper we use data on the form and growth rates of the arborescent form of the Caribbean gorgonian *Briareum asbestinum* to examine the relationship between growth and reproduction. Among arborescent colonies growth can be partitioned into three components, the generation of new branches, extension of existing branch tips, and the production of gametes. Polyps of *B. asbestinum* that are near the growing branch tip produce fewer gametes than those five cm or more behind the growing tip (Brazeau and Lasker, 1990). Thus the distribution of growth between extension of existing branches and the formation of new branches will have key effects on the colony's reproductive output. *Briareum asbestinum* is an excellent species for such a study as it has a sufficiently simple morphology to allow accurate assessments of form and growth.

Materials and Methods

Colonies of *Briareum asbestinum* are common throughout the Caribbean and occur over a wide depth range (1–20 m). Colonies consist of moderate sized polyps (1 mm diameter) that grow in encrusting and/or simple branching morphologies. Reproductive colonies of *B. asbestinum* are gonochoric brooders (Brazeau and Lasker, 1990). Sexual maturity is determined by size (branch length) for both sexes. All branches greater than 20 cm in length contain gametes prior to spawning.

Data on colony growth were collected as part of a larger study examining fecundity and reproductive success of colonies of *B. asbestinum* at Pinnacles and House Reef in the San Blas Point area near the Smithsonian Tropical Research Institute field station in the San Blas Islands, Panama (Fig. 1). House Reef is a shallow reef rising from *Thalassia* beds at a depth of 6 m to <0.5 m. The reef slope consists almost entirely of the stony corals, *Agarcia*

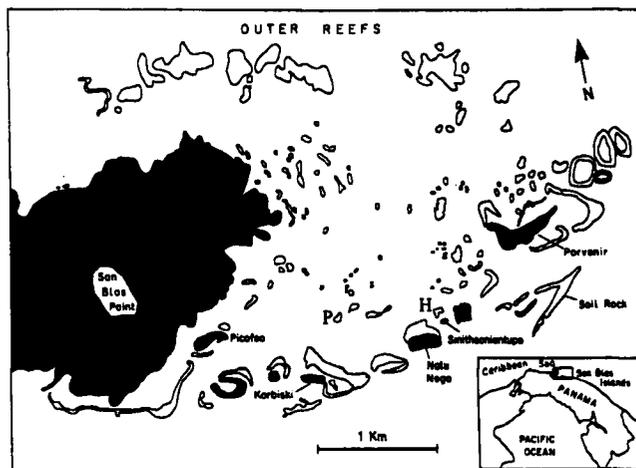


Figure 1. San Blas point region in the San Blas Islands, Panama. Open areas designate reefs: P-Pinnacles Reef and H-House Reef.

spp. and *Porites furcata*, and the hydrocoral, *Millepora complanata*. Colonies of *B. asbestinum* are common along the entire depth gradient. Pinnacles is a patch reef complex extending from 0.5 to 8 m depth. It has higher coral and gorgonian diversity than House. Unlike House Reef, the hard substrate at Pinnacles Reef is broken by many sand patches and channels. Colonies of *B. asbestinum* are found throughout the patch reef, but are most common at depths of 5–8 m.

In July of 1986, 46 colonies at Pinnacles and 60 colonies at House Reef were tagged by attaching aluminum tags to the substratum at the base of each colony. Colonies were chosen haphazardly, the only requirement being that colonies be of reproductive size (have at least one branch 20 cm in length). The length of all branches for each colony were measured to the nearest 0.5 cm. Approximately every six months (Jan 7–Feb 13; May 31–July 29, 1987; Jan 19–Feb 16; May 22–Aug 26, 1988) all colonies that could be positively identified (tags could be found) were remeasured. In July of 1987, 31 colonies at Pinnacles were added to the colonies remaining from the previous year. In all, 118 colonies on the two reefs were monitored for at least one six-month interval. For 65 of these colonies, there are measurements for all four six-month intervals.

In July of 1987 it became apparent that colony size was highly variable due to the loss of branches due to colony fragmentation. In order to obtain a more accurate measure of colony growth, 45 colonies at each reef were arbitrarily selected from the tagged colonies and the lengths of each branch individually recorded on colony diagrams. The individual branches were then identified and measured in subsequent surveys. These data provide more accurate growth measurements for 783 individually identified branches. To determine if there is a lateral or horizontal component to colony growth in *B. asbestinum*,

all branches that had been knocked down, but were still attached to the colonies, were also recorded on colony diagrams and measured over each interval.

Whole colony measurements were used to calculate two measures of colony growth rates: (1) branch specific colony growth, that is total colony growth divided by the number of branches per colony present at the end of each interval (cm/branch/year); and (2) change in number of branches/colony. Sample variances were large and heterogeneous despite log or cubic transformation therefore differences in colony and individual branch growth data were tested using the nonparametric Mann-Whitney U test (SPSS-X release 2.2; Hull and Nie, 1981). In order to reduce the probability of a type I error due to the multiple statistical tests, significance levels were determined using the Bonferroni procedure (for L tests the corrected significance level $\{\alpha'\}$ is, $\alpha' = \alpha/L$).

Results

General colony characteristics

Mean colony size and number of branches/colony for the tagged colonies of *B. asbestinum* of reproductive size on Pinnacles and House Reef increased in each year of the study (Fig. 2). At the beginning of the study the average colony had 9.5 branches (S.E. = 0.7, n = 101) and a total length of 176.7 cm (S.E. = 14.0, n = 101). Mean branch length was 19.1 cm (S.E. = 0.6, n = 716). Colonies had an average of 0.67 (S.E. = 0.09, n = 119) horizontal branches, 14.3 cm (S.E. = 2.3, n = 119) in length. Colonies at Pinnacles were significantly larger than colonies at House Reef in total length (Mann-Whitney U test, $P = .003$, n = 101). There were no significant differences in the number of branches/colony, though branch size at Pinnacles was significantly larger than at House Reef (Mann-Whitney U test, $P = .001$, n = 709).

Colony growth

There was no distinct horizontal component to colony growth for colonies of *B. asbestinum*. Of 119 horizontal branches, none grew horizontally in length, though many turned upward and grew or gave rise to new branches which then grew vertically. Consequently, colony growth can be characterized entirely in terms of branch addition or loss, and changes in total colony height.

Losses in colony size were caused by: (1) fragmentation, (2) predation, primarily by the snail *Cyphoma gibbosum* and the polychaete *Hermodice carunculata* (pers. obs.), and (3) death. Fragmentation was particularly important, resulting in the loss of whole branches or sections of colony. These losses caused much of the variation seen in colony growth. In order to obtain a more accurate estimate of colony growth rates, positive growth rates were calcu-

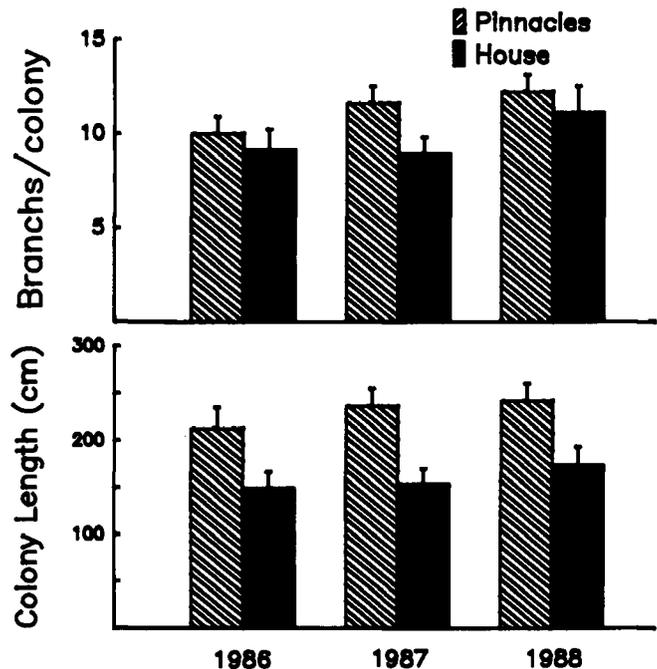


Figure 2. Bar graphs of mean colony size and number of branches/colony of *Briareum asbestinum* for the years 1986, 1987, and 1988. Error bars designate one standard error.

lated by excluding from the data set all colonies that decreased in size. The growth rates calculated in this way provide a minimum estimate of colony growth potential when free of losses due to predation and fragmentation.

During the period from July 1986 to July 1988 colonies of *B. asbestinum* increased in total size by 14.3 cm/year (S.E. = 1.0, n = 89) and added 1.23 branches/year (S.E. = 0.4, n = 89) in the two populations studied (Table I). Excluding cases of negative growth yields positive growth rates of 71.3 cm/year/colony (S.E. = 9.2, n = 59) and 8.7 branches/year/colony (S.E. = 0.7, n = 59). Figure 3 shows colony growth in terms of specific growth and addition rates of branches. There were no significant differences between reefs in net colony growth rates for any of the three measures (Table II). There were, however, significant differences in positive growth rates between reefs, indicating that during some intervals potential growth rates were higher at House Reef than at Pinnacles (Table II).

Growth rates of individual branches

Growth rates of individual branches, for both net and positive growth, from 1987 to 1988 are shown in Table III. There were significant differences in growth rates of branches between reefs. Net branch growth rate was significantly higher at House Reef in Jul. 87–Jan. 88 and Jan.–Jul. 1988 (Table III). Similarly, positive growth rates of branches at House Reef were significantly higher than those at Pinnacles over both interval (Table III).

Table I

Net and positive monthly colony growth rates for *Briareum asbestinum* for each six-month interval July 1986 through July 1987

Reef date	Colony growth rates cm/month					
	n	Net mean	S.E.	n	Positive mean	S.E.
Pinnacles						
Jul 86-Jan 87	33	1.48	1.3	25	4.98	0.6
Jan 87-Jul 87	28	2.28	1.1	18	5.55	1.1
Jul 87-Jan 88	64	2.81	1.3	44	7.30	0.9
Jan 88-Jul 88	72	-1.10	1.2	42	3.56	1.1
House						
Jul 86-Jan 87	35	1.85	0.8	23	4.51	0.7
Jan 87-Jul 87	32	2.30	1.7	21	7.65	1.2
Jul 87-Jan 88	47	2.15	1.9	30	8.88	1.7
Jan 88-Jul 88	46	-0.60	1.6	29	5.40	0.9
Both						
Jul 86-Jan 87	68	1.66	0.7	48	4.75	0.4
Jan 87-Jul 87	60	2.30	1.0	39	6.71	0.8
Jul 87-Jan 88	111	2.53	1.1	74	7.96	0.9
Jan 88-Jul 88	118	-0.90	0.9	71	4.31	0.7

Growth rates are for vertical growth only. Negative numbers indicate tissue or branch loss.

One of the advantages of following the growth of individual branches is that it allows one to examine the relationship between branch growth (and, therefore, colony growth) and branch characteristics like initial length and number of bifurcations (branch tips). Positive growth rates of branches were independent of branch size ($r^2 = 0.005$; $P > 0.153$), indicating that small and large branches had similar growth rates (Fig. 4). Positive growth rates of branches were positively correlated with the number of branch tips ($r^2 = 0.455$; $P < 0.0001$). Thus, growth rates of branches are determined by the number of growing tips, not by branch size (Fig. 5). The slope of the regression line for positive branch growth *versus* number of branch tips, yields a growth rate of 5.93 cm/year/tip (S.E. = 0.39).

Discussion

Rate of growth

The best estimate of growth rate of colonies of *B. asbestinum* comes from the measurement of individual branches. These data yield a net growth rate of 2.02 cm/year/branch. This value is less than the branch growth rates reported by Gladfelter *et al.* (1978) for scleractinians with branching morphologies (*Acropora cervicornis*, 7.1 cm/year; *A. prolifera*, 5.9–8.2 cm/year; and *A. palmata*,

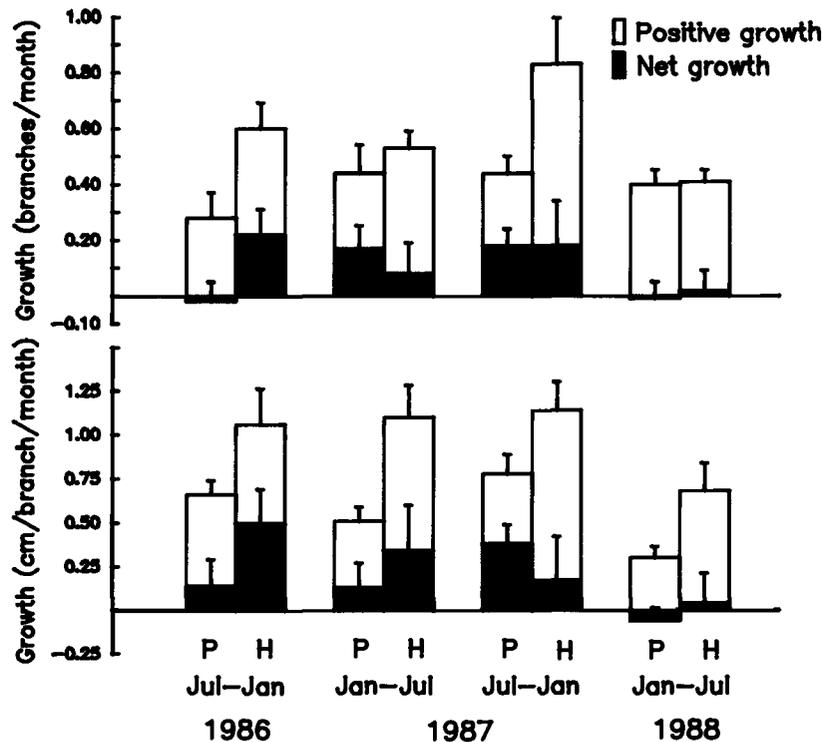


Figure 3. Mean growth rates in cm/branch and branches/colony for colonies of *Briareum asbestinum* on Pinnacles (P) and House Reef (H). Growth rates are shown for each six-month period beginning July 1986 to July 1988. Values for n are given in Table I. Error bars designate one standard error.

Table II

Results of Mann-Whitney U test comparing net and positive growth rates of colonies of *Briarium asbestinum* between Pinnacles and House Reefs for each six-month interval

Factor	n ₁	n ₂	Colony growth measures					
			cm/month		cm/branch/month		branches/month	
			U	SL	U	SL	U	SL
Net growth:								
Jul 86–Jan 87	33	35	524.5	0.515	563.0	0.859	428.0	0.765
Jan 87–Jul 87	28	32	448.0	0.692	387.0	0.208	466.5	0.892
Jul 87–Jan 88	64	47	1448.0	0.385	1559.0	0.815	1520.0	0.646
Jan 88–Jul 88	72	46	1467.0	0.162	1423.5	0.103	1624.0	0.566
Positive growth:								
Jul 86–Jan 87	25	23	259.5	0.563	226.0	0.204	75.7	0.010
Jan 87–Jul 87	18	21	154.0	0.232	92.0	0.004	96.0	0.145
Jul 87–Jan 88	44	30	684.0	0.833	501.5	0.033	340.0	0.061
Jan 88–Jul 88	42	29	362.5	0.004	282.5	<0.001	201.5	0.496

U-statistic and significance level shown for each colony growth measure. Significant differences ($\alpha = 0.05/3 = 0.016$) indicated by bold print. SL = level of significance.

4.7–9.9 cm/year), though the positive individual branch growth rates of colonies of *B. asbestinum* (6.21 cm/year) are similar to scleractinian growth rates. Growth rates of branches for colonies of *B. asbestinum* appeared similar to those reported for other Caribbean gorgonians (Kinzie, 1970; Lasker, 1990; Yoshioka and Yoshioka, 1991). However, it should be noted that these studies reported growth rates based upon changes in colony height (not true branch growth) and in one case (Kinzie, 1970) were given as the means of positive growth only. The most comparable value from this study would be the branch specific growth rates of positive colony growth. This value for colonies of *B. asbestinum* (9.25 cm/year, Fig. 3) is greater than that reported for most gorgonians.

Average colony size of colonies of *B. asbestinum* increased over both years of the study on both reefs, though both populations experienced very low or negative growth in the period from January to July of 1988. Total colony length and number of branches/colony increased 20 and 24%, respectively, from July 1986 to July 1988. However, positive colony growth rates, which provide an estimate of the minimum growth potential of colonies, indicate that colonies of *B. asbestinum* can potentially increase 71.3 cm/year in length and add 8.7 branches/year. This is a potential yearly increase of 40% in colony length and 91% in branch number relative to mean colony size. A similar comparison of net and positive growth rates of individual branches indicated that net growth rates were only 32.5% of positive growth rates. This disparity between the minimum potential growth and the realized or net growth suggests that colonies (ramets) of *B. asbestinum* sustain large losses due to predation, colony fragmentation, and disease. Because fragmentation often results in

the establishment of new colonies, the loss to the genet is certainly less. Lasker (1983) found that 24–60% of the colonies of *B. asbestinum* at nearby Marsarkantupo reef in the San Blas Islands originated from nearby colonies. Similarly 18–67% of the colonies of *B. asbestinum* examined at Carrie Bow Cay, Belize resulted from colony fragmentation (Lasker, 1983). In this study, 62% of the colonies of *B. asbestinum* monitored had at least one branch that had been knocked down and reattached to the substrate. Thus, colony fragmentation (*i.e.* branch loss), while detrimental to the ramet, potentially increases clonal spread to the benefit of the genet.

While genet longevity may be increased by routine colony fragmentation, ramets will be relatively transitory given this strategy. Ramet age can be estimated from the data collected here by dividing total colony size by the net colony growth rate to yield an age of 10.6 years for an average reproductive colony (largest colony estimated age, 50.1 years). This value over estimates average ramet age because colonies too small to be reproductive were not included in this study. This suggests that most ramets of *B. asbestinum* are short-lived when compared to scleractinians (Connell, 1973; Buddemeir and Kinzie, 1976) and some gorgonians (Grigg, 1977; Lasker, 1990). While individual mean ramet longevity may have little importance when considered from the level of the genet it is important from the standpoint of sexual reproduction in that ramet longevity must be sufficient to allow ramets to reach reproductive size. In this regard, the small size of colonies of *Briareum asbestinum* at first reproduction, as compared to other scleractinians and gorgonians (Brazeau and Lasker, 1990), agrees well with the transitory nature of ramets.

Table III

Net and positive growth rates of branches of *Briareum asbestinum* for the period July 1987 to July 1988

Reef	Jul 87–Jan 88 (cm/month)			Jan 88–Jul 88 (cm/month)			Jul 87–Jul 88 (cm/year)		
	n	Mean	S.D.	Mean	S.D.	Mean	S.D.		
<i>Net growth</i>									
Pinnacles	424	0.31	0.74	-0.04	1.11	1.64	1.27		
House	359	0.41	1.30	0.01	1.18	2.46	10.57		
Both	783	0.36	1.04	-0.02	1.15	2.02	9.11		
Mann-Whitney U Tests: Pinnacles vs. House Reef									
$N_1:N_2$	424:359			424:359			424:359		
U	63626.5			69599.0			65483.0		
SL	<0.00001			0.038			0.0008		
Reef	Jul 87–Jan 88 (cm/month)			Jan 88–Jul 88 (cm/month)			Jul 87–Jul 88 (cm/year)		
	n	Mean	S.D.	n	Mean	S.D.	n	Mean	S.D.
<i>Positive growth</i>									
Pinnacles	307	0.62	0.43	253	0.48	0.40	285	5.43	3.61
House	259	0.93	0.67	222	0.58	0.41	262	7.05	5.03
Both	566	0.76	0.57	475	0.53	0.41	547	6.21	4.41
Mann-Whitney U Tests: Pinnacles vs. House Reef									
$N_1:N_2$	307:259			253:222			285:262		
U	27090.0			22891.5			30212.0		
SL	<0.00001			0.0005			0.0001		

Growth rates determined from measurements of individually mapped branches. Mann-Whitney U test results show a significant difference in net branch growth rates between reefs for all intervals. SL = level of significance.

Net rates of colony growth were on average 18% (per 6-month interval) greater on House Reef than at Pinnacles. Growth rates of individual branches were 33% higher on House Reef. While this study design cannot address the cause of these differences, these data do indicate that growth rates of some clonal marine invertebrates may be extremely site specific. Given the high growth rates at House Reef, it is interesting that colony size was greater at Pinnacles. These data show that colony size tells very little about a colony's growth rate, and that the factors that cause tissue and/or branch loss are higher at House Reef than at Pinnacles. However, as noted above, branches lost *via* fragmentation may reattach. Thus, whereas ramets may decrease in size or disappear entirely, the genet may potentially increase in areal extent *via* this process. This is particularly important for colonies of *B. asbestinum* on reefs like House Reef where success at sexual reproduction at least locally seems to be very low (as measured by the number of embryos released, Brazeau and Lasker, in press). In contrast, growth rates at Pinnacles are lower,

but success at sexual reproduction is higher (Brazeau and Lasker, in press). These differences between reefs (low sexual reproduction with high potential for asexual reproduction vs. higher success at sexual reproduction with low potential for asexual reproduction) may result in populations with greatly different levels of genetic diversity. Interestingly, the factors that presumably enhance fragmentation (*i.e.*, high turbulence) may also greatly reduce sexual reproduction in populations of *B. asbestinum* (Brazeau and Lasker, in press).

Pattern of growth

The ability to measure the entire colony allows one to examine the nature of growth in ramets of *B. asbestinum*. Growth rates in ramets of *B. asbestinum* are independent of colony or branch size. This seems to be the rule for many scleractinians (Bak *et al.*, 1977; Hughes and Jackson, 1985) and at least one other gorgonian (Wahle, 1983), though Chornesky and Peters (1987) have found that rates of vertical and lateral growth in colonies of *Porites astreoides* increases with colony surface area. Growth in colonies of *B. asbestinum* was found to be determined by the number of branch tips. This suggests that most of the polyps on a branch are not involved with branch growth, only those near the tip. This agrees with the reproductive biology of colonies of *B. asbestinum*. Reproductive effort (number and volume of gonads/polyp) increases away from the tip and base of the branch (Brazeau and Lasker, 1990). Thus as branch size and, therefore, the number of polyps away from the tip increases, growth rates remain the same while average reproductive effort per polyp increases.

The relationship between reproductive effort and branch growth and its implications for clonal growth strategies are shown in Figure 6. The graph shows that by bifurcating, branches increase reproductive tissue exponentially compared to the linear rate of increase for a branch with a single growing tip. This relationship stems from the exponential rate of increase of tissue in continually branching systems and in this regard is not too surprising. However, the graph illustrates two important points: (1) upright branching colonies should be arborescent, and (2) the benefit of arborescent growth becomes most important with age (colony or ramet longevity). The model agrees well with the growth forms observed among gorgonians. Unlike many gorgonians, however, ramets of *B. asbestinum* are not highly arborescent. Sixty-two percent of all branches measured in this study had a single tip. This incongruity is resolved by considering overall growth strategy of colonies of *B. asbestinum*. Site tenacity of ramets of *B. asbestinum* is low. Most branches never reach a size where the reproductive benefits of an arborescent strategy greatly exceed that of a single growing tip.

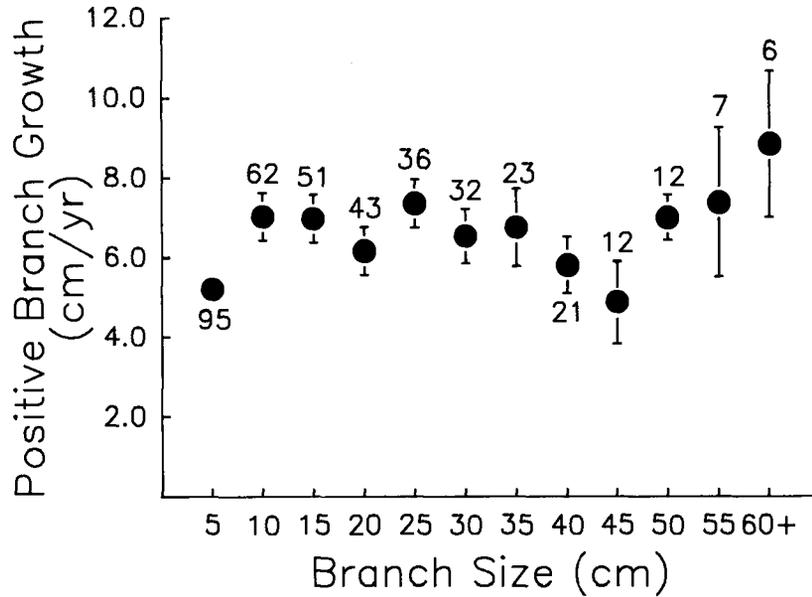


Figure 4. The relationship between positive branch growth and initial branch size ($r^2 = 0.005$; $P = 0.153$). Number of branches in each size class indicated above points. Error bars are \pm one standard error. In a number of cases the error bars are smaller than the dots.

Average branch size in ramets of *B. asbestinum* is 19.1 cm, which corresponds to 3–5 years of age. As shown in Figure 6, the difference between the growth strategies in this period is slight. In addition, the arborescent growth strategy would increase drag forces on the branches and further increase the probability of branches being lost. This simple graphical model predicts that branching species with high site tenacity will be arborescent. Species like *B. asbestinum* with low site tenacity, will reach re-

productive age early, and should have branches with few bifurcations.

Acknowledgments

We thank the Kuna Indians and the Republic of Panama for permission to work in the San Blas Islands and the Smithsonian Tropical Research Institute for the use of its facilities. M. A. Coffroth assisted with the fieldwork

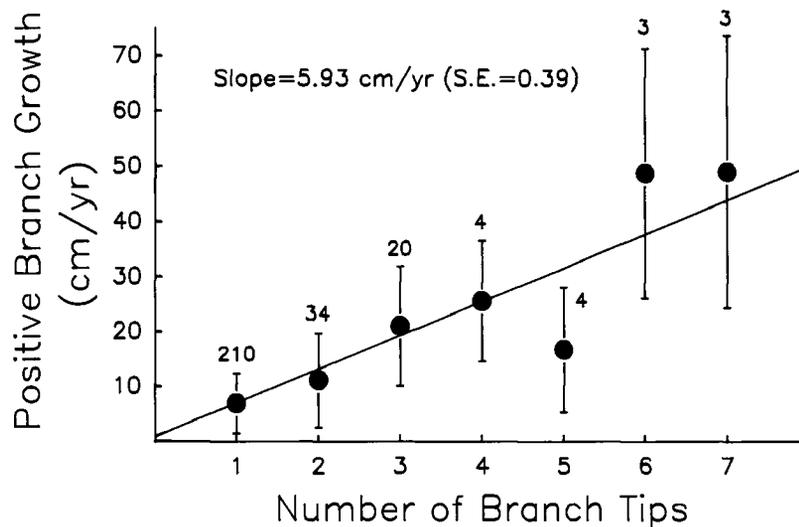


Figure 5. The relationship between positive branch growth and the number of tips/branch ($r^2 = 0.455$; $P < 0.0001$). Number of branches in each class indicated above points. Error bars are \pm one standard error.

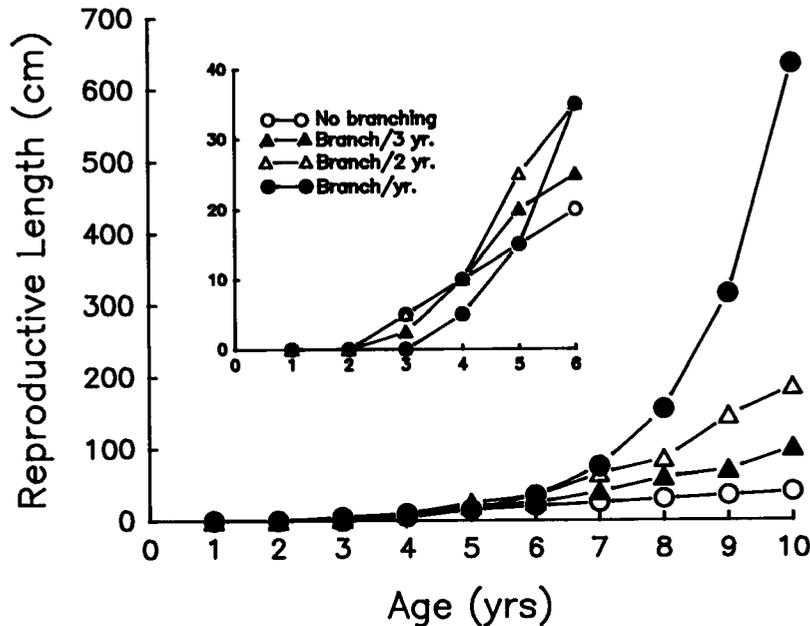


Figure 6. Increase in reproductive tissue for different growth strategies ranging from colonies whose branches never bifurcate to colonies with branches that bifurcate every year. Growth rate and amount of reproductive tissue follow the growth pattern of colonies of *Briareum asbestinum*. Growth rate is tip dependent (5.9 cm/tip/year). Reproductive tissue is calculated assuming losses of 5 cm to base and each growing tip. Inset shows an expanded view of the first six years.

and provided comments on the manuscript. This research was supported by NSF grant OCE-8521684.

Literature Cited

- Bak, R. P., J. J. Brouns, and F. M. Heys. 1977. Regeneration and aspects of spatial competition in the scleractinian corals *Agaricia agaricities* and *Montastrea annularis*. *Proc. Third Int. Coral Reef Symp.* 1: 143-148.
- Brazeau, D. A., and H. R. Lasker. 1990. Sexual reproduction and external brooding by the Caribbean gorgonian, *Briareum asbestinum*. *Mar. Biol.* 104: 465-474.
- Brazeau, D. A., and H. R. Lasker. in press. Reproductive success in a marine benthic invertebrate, the Caribbean octocoral *Briareum asbestinum*. *Mar. Biol.* 000: 000-000.
- Buddemeir, R. W., and R. A. Kinzie. 1976. Coral growth. *Oceanogr. Mar. Biol. Annu. Rev.* 14: 183-225.
- Chamberlain, J. A., and R. R. Graus. 1975. Water flow and hydro-mechanical adaptations of branched reef corals. *Bull. Mar. Sci.* 25: 112-125.
- Chornesky, E. A., and E. C. Peters. 1987. Sexual reproduction and colony growth in the scleractinian coral *Porites astreoides*. *Biol. Bull.* 172: 161-177.
- Connell, J. H. 1973. Population ecology of reef-building corals. Pp. 205-245 in *Biology and Geology of Coral Reefs*, Vol II, O. A. Jones and R. Endean eds. Academic Press, New York.
- Gladfelter, E. H., R. K. Monahan, and W. B. Gladfelter. 1978. Growth rates of five reef-building corals in the northeastern Caribbean. *Bull. Mar. Sci.* 28: 728-734.
- Graus, R. R., J. A. Chamberlain, J. A., and A. M. Boker. 1977. Structural modification of corals in relation to waves and currents. Pp. 135-153 in *Reefs and Related Carbonates—Ecology and Sedimentology*. *Studies in Geology* 4, S. H. Frost, M. P. Weiss, and J. B. Saunders, eds. Am. Assoc. Petrol. Geol. Tulsa, Oklahoma.
- Grigg, R. W. 1977. Population dynamics of two gorgonian corals. *Ecology* 58: 278-290.
- Hughes, T. P., and J. B. C. Jackson. 1985. Population dynamics and life histories of foliaceous corals. *Ecol. Monogr.* 55: 141-166.
- Hull, C. H., and N. H. Nie. 1981. *SPSS Update 7-9. New Procedures and Facilities for Release 7-9*. McGraw-Hill Book Co. New York.
- Jackson, J. B. C. 1979. Morphological strategies of sessile animals. Pp. 499-555 in *Biology and Systematics of Colonial Organisms*, G. Larwood and B. R. Rosen, eds. Syst. Assoc. Spec. vol. 11. Academic Press, London.
- Kaufmann, K. W. 1973. The effect of colony morphology on the life-history parameters of colonial animals. In *Animal Colonies*, R. S. Boardman, A. H. Cheetham, and W. A. Oliver, eds. Dowden, Hutchinson and Ross. Pennsylvania.
- Kinzie, R. A. 1970. *The ecology of the gorgonians (Cnidaria, Octocorallia) of Discovery Bay, Jamaica*. Ph.D. Thesis, Yale University.
- Lasker, H. R. 1983. Vegetative reproduction in the octocoral, *Briareum asbestinum* (Pallas). *J. Exp. Mar. Biol. Ecol.* 72: 157-169.
- Lasker, H. R. 1984. Asexual reproduction, fragmentation, and skeletal morphology of a plexaurid gorgonian. *Mar. Ecol. Prog. Ser.* 19: 261-268.
- Lasker, H. R. 1990. Clonal propagation and population dynamics of a gorgonian coral. *Ecology* 71: 1578-1589.
- Leversee, G. J. 1976. Flow and feeding in fan-shaped colonies of the gorgonian coral, *Leptogorgia*. *Biol. Bull.* 151: 344-356.
- McKinney, F. K. 1981. Planar branch systems in colonial suspension feeders. *Paleobiology* 7: 344-354.
- Rinkevich, B., and Y. Loya. 1979. The reproduction of the Red Sea coral *Stylophora pistillata*. II. Synchronization in breeding and seasonality of planulae shedding. *Mar. Ecol. Prog. Ser.* 1: 145-152.

- Ryland, J. S., and G. F. Warner. 1986. Growth and form in modular animals: ideas on the size and arrangement of zooids. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* **313**: 53-76.
- Tunncliffe, V. 1982. The effects of wave induced flow on a reef coral. *J. Exp. Mar. Biol. Ecol.* **64**: 1-10.
- Velimirov, B. 1976. Variations in growth forms of *Eunicella cavolinii* Koch (octocorallia) related to intensity of water movement. *J. Exp. Mar. Biol.* **21**: 109-117.
- Vosberg, F. 1982. *Acropora reticulata*: structure, mechanics, and ecology of a reef coral. *Proc. R. Soc. Lond. Ser. B* **214**: 481-499.
- Wahle, C. M. 1983. The roles of age, size and injury in sexual reproduction among Jamaican gorgonians. *Am. Zool.* **23**: 961.
- Wainwright, S. A., and J. R. Dillon. 1969. On the orientation of sea fans (Genus *Gorgonia*). *Biol. Bull.* **136**: 130-139.
- Walker, T. A., and G. D. Bull. 1983. A newly discovered method of reproduction in gorgonian coral. *Mar. Ecol. Prog. Ser.* **12**: 137-143.
- Wallace, C. C. 1985. Reproduction, recruitment and fragmentation in nine sympatric species of the coral genus *Acropora*. *Mar. Biol.* **88**: 217-233.
- Yoshioka, P. M., and B. B. Yoshioka. 1991. A comparison of the survivorship and growth of shallow-water gorgonians species of Puerto Rico. *Mar. Ecol. Prog. Ser.* **69**: 253-260.