

## DETERMINANTS OF RECRUITMENT, JUVENILE GROWTH, AND SPATIAL DISTRIBUTION OF A SHALLOW-WATER GORGONIAN<sup>1</sup>

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*Abstract.* In the northern Gulf of Mexico, the gorgonian *Leptogorgia virgulata* (Cnidaria: Octocorallia) recruited onto a shallow limestone outcropping that was covered by sand of various depths. To test the hypothesis that sand limited the recruitment of *L. virgulata* at this site, I placed cement patio stones as settlement surfaces in different microhabitats.

Sand scour reduced recruitment by 50% on buried stones compared with unburied controls. Recruitment was also inhibited by the presence of an algal mat on unburied controls. Initial recruitment patterns persisted for 10 mo on artificial substrata. By that time, dead, intact skeletons were more common on buried than on raised stones. Overall mortality rates did not differ between raised and buried treatments.

In a 55-d transplant experiment, buried juvenile colonies grew significantly more than unburied colonies. Rapid growth may enhance survival of buried colonies by raising polyps out of the sand.

I mapped the microhabitats in an untouched 24-m<sup>2</sup> plot and constructed an index of habitat quality for each contiguous 1-m<sup>2</sup> block. This index was highly correlated with numbers of both adult and juvenile *Leptogorgia virgulata* colonies. Sixty-seven percent of the 1984 recruitment cohort died the following year, but the spatial pattern established at the time of recruitment persisted. Although the abundance of recruits was correlated with habitat quality, there was no relationship between recruitment and adult abundance or the percent cover of encrusting organisms. Finally, recruitment was highest and least variable in patches of clean limestone compared with recruitment in randomly selected patches.

On both natural and artificial substrata, the recruitment of *Leptogorgia virgulata* was affected by the distribution of sand. In spite of heavy 1st-yr mortality, the spatial pattern established at the time of recruitment persisted in the adult population. Mortality after recruitment did not modify the distribution of colonies to any great extent.

*Key words:* Cnidaria; disturbance; Florida; gorgonian; growth; Gulf of Mexico; juvenile; mortality; Octocorallia; recruitment; sand; spatial pattern; transplant.

### INTRODUCTION

For sessile plants and animals, the distribution of seeds or larvae is often the primary determinant of small-scale spatial pattern. In many plant communities, for example, spatial pattern is determined by the initial distribution of seeds (e.g., Rabinowitz 1978) or by early mortality of seeds and seedlings (e.g., Louda 1982, Augspurger 1984). Harper (1977:112) envisions recruitment as successful passage through a sieve, "an environmental lattice of safe and unsafe sites." Variable recruitment can also permit the coexistence of space competitors (Skellam 1951, Warner and Chesson 1985), generate oscillations in local populations (Roughgarden et al. 1985), and determine the outcome of succession (Connell and Slatyer 1977) and the species composition of mature assemblages (Sutherland 1974).

The importance of recruitment in marine benthic communities is widely recognized (Thorson 1950, Meadows and Campbell 1972, Underwood and Denley 1984). In some cases, the spatial pattern of recruitment largely determines spatial pattern in the adult population (Ryland 1959, Grosberg 1982). If mortality following recruitment is constant in space, the distribution of adults will match the distribution of recruits. In other examples, mortality is consistently greater in some places than in others (as envisioned by Colman 1933), and the initial recruitment distribution is modified with time by processes such as competition, predation, and disturbance (Connell 1961, 1978, Dayton 1971, Paine 1974, 1984, Luckenbach 1984). In either case, the importance of recruitment cannot be decided by examining only the recruitment stage, no matter how carefully this is done (e.g., Caffey 1985). Instead, what is needed is a comparison of the spatial pattern of recruits with the spatial pattern of adults (see especially Fig. 5 in Connell 1961 and Figs. 1 and 2 in Grosberg 1982).

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TABLE 1. Percent cover of different microhabitats in a 24-m<sup>2</sup> plot ( $N = 24$  contiguous 1-m<sup>2</sup> quadrats).

Unburied limestone			Shallow sand (1–3 mm)			Deep sand (>3 mm)			Encrusting animals		
$\bar{X}$	SD	Range	$\bar{X}$	SD	Range	$\bar{X}$	SD	Range	$\bar{X}$	SD	Range
26.58	14.22	10–61	12.75	6.17	2–28	36.38	21.42	4–87	24.29	23.11	0–75

In this paper, I present experimental and correlative evidence on the role of recruitment in determining the spatial distribution of the gorgonian *Leptogorgia virgulata*. Recent work has focused on recruitment variation among patches of similar microhabitat (e.g., Kay and Keough 1981, Caffey 1985), but in this study, such within-habitat variation was relatively small. Instead, the recruitment of *L. virgulata* was influenced primarily by spatial variation in microhabitat, particularly variation in the presence of sand.

Sand may limit recruitment in two ways. First, larvae could be unwilling or unable to settle in patches with sand. Second, larvae that settled on hard substrata could be buried or abraded by moving sand (e.g., Daly and Mathieson 1977). Using artificial substrata, I experimentally controlled sand exposure and monitored the recruitment, subsequent mortality, and juvenile growth of *L. virgulata* in different microhabitats. These experiments revealed the nature of “safe sites” (sensu Harper 1977) for *L. virgulata* recruitment. I used the results of the recruitment experiment to construct an index of habitat quality for contiguous patches of natural substrata in an unmanipulated plot. This index successfully predicted the spatial distributions both of recruits and of adult colonies of *L. virgulata*.

#### MATERIALS AND METHODS

##### *Life history of Leptogorgia virgulata*

*Leptogorgia virgulata* (Cnidaria: Octocorallia) is an arborescent, shallow-water gorgonian. Colonies are dioecious, with external fertilization and subsequent development. The planula stage develops in 24 h and remains in the plankton for 2–3 d before settlement and metamorphosis, although settlement can be delayed for as long as 19 d after fertilization (Adams 1980). Unlike some gorgonian species, *L. virgulata* shows no evidence of asexual reproduction. I did not find any juveniles that appeared to have originated by vegetative reproduction (Lasker 1983) or fragmentation (Walker and Bull 1983). Therefore, juvenile colonies are presumably derived from the settlement of planktonic larvae. Larvae do not move after settlement and metamorphosis, so the settlement site can be inferred from the point of attachment of the colony base. Early colony growth is rapid: 20 d after settlement, colonies are 6 mm high (Adams 1980), which was the minimum size of recruits I detected in monthly field censuses. *L. virgulata* reaches reproductive maturity in 2 yr, which is rapid for octocorals (cf. Grigg 1977). In field censuses, I distinguished among three color morphs

of *L. virgulata*: yellow, purple, and orange (details in Gotelli 1985). Colony color of *L. virgulata* is a heritable trait (Adams 1980), and color morphs could show differential recruitment responses.

##### *Study site*

The study site was an isolated limestone outcropping at 1.5 m depth, 50 m offshore of Wilson Beach, Franklin County, Florida. Complete site descriptions are given in Gotelli (1985, 1987). The outcropping was  $\approx 1$ –2 ha in area. There are no other inshore areas of exposed limestone in this part of the Gulf of Mexico. The site was exposed briefly to air once or twice a year, in the fall and winter, when strong north winds coincided with extreme low tides.

There was moderate small-scale variation in habitat on the outcropping. The spatial scale of microhabitat variation was fairly small: contiguous 1-m<sup>2</sup> quadrats often differed significantly in the percentages of different microhabitats. Table 1 gives the distribution of various microhabitats in a 24-m<sup>2</sup> plot. This plot was selected for long-term monitoring because it had a relatively high abundance of *Leptogorgia virgulata* ( $\bar{X} = 1.3$  colonies/m<sup>2</sup>). The plot also included a typical array of microhabitats. Every 1-m<sup>2</sup> quadrat in the plot contained at least some areas of unburied limestone and some areas of shallow (1–3 mm depth) and deep (>3 mm depth) sand. Sand accumulated in shallow rock depressions and low-lying areas. Maximum vertical relief on the rock reef was  $\approx 20$  cm, although most patches did not vary by >5–10 cm in vertical relief. Although I do not have data on temporal changes in microhabitat, sand movement at this site must have been fairly common, because the bases of many large *L. virgulata* colonies were buried by a centimetre or more of sand. A field experiment with patches of brightly colored aquarium gravel also demonstrated the potential for particle transport on the outcropping (Gotelli 1985).

##### *Microhabitat recruitment experiment*

I tested the null hypothesis that *Leptogorgia virgulata* recruitment is not affected by the presence of sand. Because *L. virgulata* planulae settle readily on cement surfaces (Adams 1980), I used round cement patio stones (40 cm in diameter, 5 cm thick) as recruitment substrata. Thirty numbered stones were inscribed with a set of crosshairs on the top for mapping colonies. I placed 10 stones in each of three microhabitat treatments: raised on limestone, raised on sand, and buried

in sand (Fig. 1). The surface of each buried stone was flush with the adjacent sand. Each stone was >1 m from its nearest neighbor. I haphazardly interspersed replicates, so that the two sand treatments were not spatially isolated from the limestone treatment.

The raised stones settled 4–6 mm after their initial placement, but I never found them covered by sand. Within 3 wk of placement, an algal mat formed on stones in the two raised treatments. The appearance and thickness of the algal mat was similar to that found on raised patches of natural substrata at the site. This algal mat did not accumulate on buried stones, which were always covered by 1–2 mm of fine sand. I fanned this sand away at each recruitment census, but the sand cover returned within 2–3 h. One buried stone became exposed and had abnormally high recruitment (Gotelli 1985). I deleted these data from the analyses and substituted median data from the other replicates in the buried treatment.

I established treatments on 14 March 1984 and, with weekly spot checks, detected the first *Leptogorgia virgulata* recruits on 7 June 1984. Census dates were 7 June, 4 July, 14 August, 8 September, 6 November 1984, and 11 May 1985. At each census, I recorded the  $x$ - $y$  coordinate location on the stone, color, and total branch length (measured in millimetres) of every *L. virgulata* colony. New recruits could be reliably distinguished from previously recorded colonies on the basis of coordinate locations and colony size and color.

On the 11 May 1985 census, I did not record stone identification numbers and was unable to relocate all of the replicates. At that time I harvested all living colonies and dead colony skeletons from each of the three treatments. Colonies were air-dried, and total branch lengths were measured to the nearest millimetre with a HIPAD digitizer.

The analyses of cumulative abundance and recruitment rate followed a repeated-measures design (Winer 1971). Data from the 11 May 1985 census were analyzed separately with a one-way ANOVA. All data were normalized with a square-root transformation. In addition, I converted the recruitment data to rates, the number of new colonies per 49 d (the longest interval between any two successive censuses).

The analysis of mortality rate could not be handled with the same statistical model, because some replicates had no colonies present that could go extinct. I collapsed one of the factors (either time or color morph) and performed a repeated-measures analysis of mortality rate on the remaining two factors. I also performed contingency table analyses on mortality rate for the different factors. All of these analyses produced similar results.

#### *Algae removal experiment*

After harvesting the 1984 recruitment experiment, I used the raised patio stones to test the null hypothesis that the presence of the algal mat had no effect on the

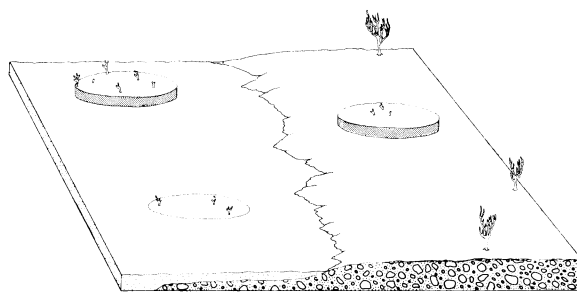


FIG. 1. Placement of patio stones in the three microhabitats: raised on limestone (right), raised on sand, and buried in sand. Small colonies represent *Leptogorgia virgulata* recruits, in the observed relative abundance.

recruitment of *Leptogorgia virgulata*. On 14 May 1985 I moved seven patio stones, which I left unscraped as controls, from the raised limestone onto sand. I used a putty knife and wire brush to scrape clean seven patio stones from the raised sand treatment. None of the stones from the buried treatment were used in this experiment, and I assume there were no residual treatment effects on the raised stones. The scraped and unscraped stones were censused on 31 May 1985, when recruits were first detected. After this census, I removed all of the recruits and repeated the scraping treatment. I censused the experiment again on 7 June 1985, but found no new recruits.

#### *Juvenile transplant experiment*

To measure the effect of sand on early colony growth, I collected juvenile gorgonians from natural rock surfaces, cemented them onto cinder blocks, and transplanted them into appropriate microhabitats. On 7 September 1984, I collected 64 small, healthy *Leptogorgia virgulata* colonies by carefully detaching each colony base with a sharp knife point. Colony branch length was 3–5 cm at the start of the experiment; colonies of this size were probably 8–16 wk old.

Four randomly chosen colonies, two yellow and two purple, were cemented under water to each of 16 small ( $\approx 120$  cm<sup>2</sup> surface area) cinderblock fragments with a few grams of SOS epoxy putty. Cemented colonies were left untouched for 24 h and appeared undamaged by the treatment; the polyps were usually re-extended 20 min after cementing, and all of the colonies appeared healthy at the start and end of the experiment.

I placed eight such cinderblock fragments on top of the sand, and buried eight others, so that only the upper 5 mm of each colony branch tip was exposed. I measured the total branch length of each colony at the start (8 September 1984) and the end (30 October 1984) of the experiment. Treatments were maintained for 55 d.

I analyzed the logarithm (base 10) of the growth ratio (final size/initial size) of each individual colony. During the experiment, 13 colonies became detached, and one cinderblock was lost, so the original split-plot de-

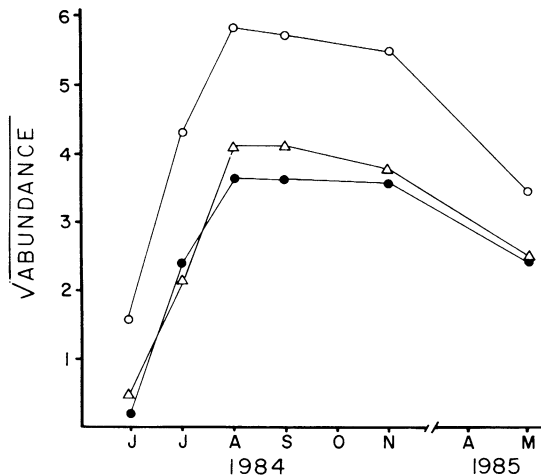


FIG. 2. Average cumulative abundance (colonies per stone) of *Leptogorgia virgulata* in the three treatments: ○ = raised on sand; ● = buried in sand; △ = raised on limestone.

sign could not be analyzed. In an initial test, I ignored the blocks and performed a two-way ANOVA (microhabitat and color morph) on the growth ratios. This analysis revealed no significant color morph or interaction effects. Therefore, I averaged the growth ratios for all colonies of a single block, and compared log mean ratios of raised and buried treatments with a *t* test. Results were similar to those of the two-way ANOVA test for treatment effect.

#### Recruitment data from natural surfaces

I monitored the recruitment of *Leptogorgia virgulata* on natural substrata in three different plots. In October 1983, I cleared a 6 × 1 m plot of all encrusting animals and *L. virgulata* colonies. Within a few weeks of the initial clearing, low-lying bare rock surfaces were inundated by sand, and raised surfaces were colonized by microalgae. Monthly, through July 1985, I counted and removed all juvenile *L. virgulata* colonies (and juveniles of the compound ascidian *Aplidium stellatum* [Gotelli 1987]). These censuses established the temporal pattern of *L. virgulata* recruitment.

In August 1983, I began monitoring recruitment in an unmanipulated 12 × 2 m plot divided into 24 1-m<sup>2</sup> blocks for censuses. This plot was chosen randomly with respect to microhabitat variation and contained the full array of microhabitats present on the outcropping. Monthly, from August 1983 to July 1985, I recorded the maximum height, color, and *x-y* coordinates of every *L. virgulata* colony in the plot. These data gave an accurate spatial map of both juvenile and adult distributions.

In July 1984, during the recruitment peak, I mapped the microhabitats in the 24-m<sup>2</sup> plot. In each 1-m<sup>2</sup> block, I categorized the substrata under an evenly spaced array of 100 points into four classes: (1) unburied rock; (2) shallow sand (1–3 mm depth); (3) deep sand (>3

mm depth); and (4) encrusting animals (mostly the compound ascidian *Aplidium stellatum*, the boring sponge *Cliona cellata*, and other encrusting sponges) (Table 1). Most areas of unburied rock were covered by an algal mat, which was ubiquitous at this site. I used these data to create a quantitative habitat index. Each substratum measurement was assigned a score as follows: unburied rock, 2; shallow sand, 1; deep sand, 0; encrusting animals, 0.

The sum of the 100 scores for each 1-m<sup>2</sup> block gave a numeric habitat index that ranged from 0 to 200. I assigned a score of 2 to unburied rock and a score of 1 to shallow sand to reflect the experimental result that shallow sand reduced *L. virgulata* recruitment by ≈ 50% (Fig. 2). I assigned a score of 0 to deep sand and encrusting animals because these surfaces were probably not available for larval settlement. The usefulness of this index is seen when it is plotted against the number of recruits or adult colonies in a block. These comparisons are critical because the recruitment experiments were conducted on artificial substrata. The habitat index correlations show whether the same patterns hold on natural substrata.

The third measurement of natural recruitment comes from a set of plots that was used in a field experiment. The experiment tested for effects of fish predation and the presence of adult colonies on recruitment of *Leptogorgia virgulata*. Adult colonies were removed from half of the plots, and fish predators were excluded from half of the plots with large-mesh wire roofs. Neither treatment had significant effects on recruitment, and the results are described elsewhere (Gotelli 1985). For our purposes, the data can be used to assess the effects of habitat quality on recruitment. Fourteen 0.36-m<sup>2</sup> plots were established on patches of clean limestone that I judged to be optimal habitat for recruitment. Each plot had at least one adult *L. virgulata* colony originally present, and no sand or encrusting animals.

TABLE 2. Repeated-measures ANOVA for cumulative abundance of *Leptogorgia virgulata* colonies in three experimental microhabitat treatments: raised stones on limestone, raised stones on sand, and stones buried flush with sand surface.

Source of variation	SS	df	MS	F ratio
Microhabitat	34.48	2	17.24	11.11**
Error	41.91	27	1.55	
Time	110.10	4	27.52	86.61**
Time × microhabitat	2.20	8	0.27	0.86
Error	34.42	108	0.32	
Color	144.90	2	72.45	68.90**
Color × microhabitat	1.10	4	0.27	0.26
Error	56.78	54	1.05	
Color × time	24.82	8	3.10	16.02**
Color × time × microhabitat	1.88	16	0.12	0.61
Error	41.81	216	0.19	

\*\* *P* < .01.

The plots and treatments were established on 6 June 1984 and marked on four corners by bricks. I censused for recruitment of *L. virgulata* on 7 July 1984. Recruitment in these preselected plots was compared with recruitment in the 24-m<sup>2</sup> plot, which contained a more typical array of microhabitats.

The 6-m<sup>2</sup> recruitment plot ran parallel to, and 10 m east of, the 24-m<sup>2</sup> census plot. The 30 patio stones and 14 preselected plots were interspersed between these two strips, 2–20 m from the nearest census line. Although larval abundance and settlement are known to vary on this spatial scale (Caffey 1985, Gaines et al. 1985), it is difficult to imagine that this spatial arrangement of plots led to any consistent biases. In all analyses, I have assumed that the supply of larvae was similar (though not necessarily identical) among the different treatments and census plots.

RESULTS

*Effects of microhabitat on recruitment*

The cumulative abundance of *Leptogorgia virgulata* differed significantly among the three treatments (Table 2). Abundance was highest on the raised stones on the sand and ≈50% lower for both buried sand and raised limestone treatments (Fig. 2). There was no interaction between time and treatments (Table 2); although abundance peaked in August and declined through the fall, relative numbers in the three treatments remained the same. By May 1985, abundance had declined substantially from the previous summer. However, the treatments still differed significantly ( $F_{2,24} = 4.91, P < .05$ ) and in the same rank order as before.

The pattern in Fig. 2 is generated by two processes: increases caused by recruitment of new juveniles and decreases caused by mortality of established colonies.

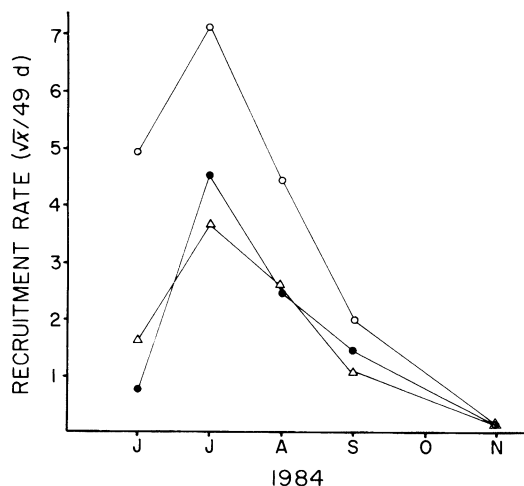


FIG. 3. Average recruitment rate (colonies per stone; square root (x)/49 d) of *Leptogorgia virgulata* in the three treatments. Symbols as in Fig. 2.

TABLE 3. Repeated-measures ANOVA for juvenile recruitment rate of *Leptogorgia virgulata* in three experimental microhabitat treatments.

Source of variation	ss	df	MS	F ratio
Microhabitat	32.08	2	18.54	20.59**
Error	24.31	27	0.90	
Time	140.04	4	35.01	23.40**
Time × microhabitat	26.62	8	3.33	2.22*
Error	161.62	108	1.50	
Color	97.40	2	48.70	55.78**
Color × microhabitat	1.77	4	0.44	0.51
Error	47.14	54	0.87	
Color × time	35.43	8	4.43	3.76**
Color × time × microhabitat	11.36	16	0.71	0.60
Error	254.18	216	1.18	

\*  $P < .05$ .  
\*\*  $P < .01$ .

These processes can be distinguished because the fate of individual *Leptogorgia virgulata* colonies was recorded through 1984.

The recruitment pattern, that is, the rate of new colony appearance in each time period (Fig. 3), among the three treatments was consistent with the pattern of cumulative abundance: the highest recruitment rate was always for the raised sand treatment. There was an interaction between treatments and time (Table 3), but this arose primarily because recruitment in the November 1984 sample was near zero in all treatments.

In contrast to the abundance and recruitment data, average mortality rates were similar among treatments (raised sand  $\bar{X} = 10.02\%$  mortality per census; buried sand  $\bar{X} = 10.24\%$ ; raised limestone  $\bar{X} = 10.79\%$ ;  $F_{2,27} = 0.02, P > .90$ ). This pattern is consistent with the peaked abundance curve of Fig. 2: abundance increased steadily during the recruitment season, then declined in the fall, as dead colonies were no longer replaced by new juveniles.

In addition to effects of microhabitat and time, there were differences in recruitment of the three color morphs. There was some interaction with time (Table 3), but in most censuses the yellow morph recruited in the greatest abundance ( $\bar{X} = 4.39$  colonies per stone; [square root {x}/49 d]-transformation). The orange morph was the rarest ( $\bar{X} = 1.05$ ), and the purple morph was intermediate in abundance ( $\bar{X} = 2.10$ ). As with the three microhabitats, mortality rates of the three color morphs were similar.

Figure 4 gives the size-frequency distributions of all colonies collected from the patio stones in May 1985. Mean colony sizes were similar ( $F_{2,211} = 1.93, P = .15$ , for  $\log_{10}$  transformed data), although the largest colonies were collected from the buried treatment. Living colonies were significantly larger than dead skeletons (buried treatment,  $t_{68} = 4.96, P < .01$ ). Of the buried colonies, 17% were dead, compared with only 2.4 and

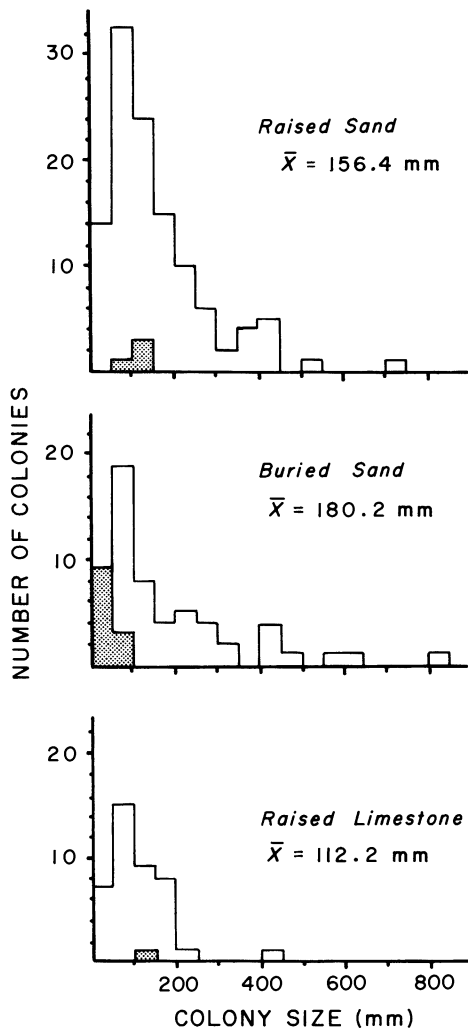


FIG. 4. Size frequency histograms of total colony branch length (in millimetres) of *Leptogorgia virgulata* colonies harvested from the three experimental treatments. Open bars are for living colonies; shaded bars are for dead colony skeletons. Mean sizes are for living colonies only.

3.4% of colonies from the raised sand and limestone treatments, respectively ( $\chi^2_2 = 14.2$ ,  $P < .01$ ).

#### *Effects of algae on recruitment*

Benthic algae and the associated sediment mat inhibited *Leptogorgia virgulata* recruitment. After 15 d, scraped stones had significantly more colonies ( $\bar{X} = 1.43$ ) than unscraped stones ( $\bar{X} = 0.11$ ;  $t_{14} = 3.81$ ,  $P < .01$ ).

Because it was easier to find juveniles on bare cement than in the algal mat, low recruitment in the algal mat could reflect a sampling bias rather than a treatment effect. To check for a sampling bias, I removed all juveniles I could find in both treatments, waited a week, and censused the experiment again on 7 June 1985. In the interim, colonies hidden in the algal mat presum-

ably would have grown to a detectable size. However, no additional colonies were found in either treatment during the second census. So the difference in recruitment on scraped and unscraped stones cannot be attributed to a sampling bias.

#### *Effects of sand on juvenile growth*

Burial by sand enhanced the growth of juvenile *Leptogorgia virgulata* colonies. The average growth ratio ( $\log_{10}$  transformed) of buried colonies was 0.355 compared with only 0.217 for raised colonies ( $t_{13} = 7.26$ ,  $P < .01$ ). There was no significant difference in the probability of new branch formation between these two conditions ( $\chi^2_1 = 1.12$ ,  $P > .10$ ). Growth rates of purple and yellow colonies were similar (Table 4).

#### *Correlates of spatial pattern in juvenile and adult populations*

In June and July 1984, *Leptogorgia virgulata* recruited in large numbers to the reef (Fig. 5). In the 24-m<sup>2</sup> plot, the number of recruits in each 1-m<sup>2</sup> block was positively correlated ( $r^2 = 0.48$ ,  $P < .01$ ) with the habitat index (Fig. 6). The significance of this relationship is unchanged by exclusion of the three points in the upper right-hand corner of the figure ( $r^2 = 0.25$ ,  $P < .01$ ). Nor is the pattern affected by exclusion of those blocks with a relatively high (>25%) cover of encrusting animals ( $r^2 = 0.51$ ,  $P < .01$ ). Abundance of adult *Leptogorgia virgulata* colonies in a block also correlated with the habitat index (Fig. 7;  $r^2 = 0.35$ ,  $P < .01$ ). Between August 1983 and May 1984 there was essentially no recruitment (Fig. 5), so these adult colonies were a minimum of 10 mo old.

Although the habitat index was correlated with both juvenile and adult abundance, these two variables were uncorrelated with each other. That is, there was no relationship between the number of adult colonies in a particular plot and the number of recruits that appeared there ( $r^2 = 0.09$ ,  $P > .10$ ). Finally, numbers of *Leptogorgia virgulata* recruits and adults were uncorrelated with percent cover of encrusting animals ( $r^2 = 0.03$  and  $0.06$ , respectively;  $P > .10$ ).

The spatial pattern of recruitment in 1984 was repeated in 1985. Although recruitment in 1985 was generally low (Fig. 5), the number of recruits in each 1-m<sup>2</sup> block of the 24-m<sup>2</sup> plot correlated significantly between years ( $r^2 = 0.52$ ,  $P < .01$ ).

TABLE 4. Two-way ANOVA for effects of microhabitat and colony color on juvenile growth of transplanted *Leptogorgia virgulata* colonies.

Source of variation	SS	df	MS	F ratio
Microhabitat	0.0991	1	0.0991	6.64*
Color	0.0001	1	0.0001	0.01
Microhabitat $\times$ color	0.0208	1	0.0208	1.39
Error	0.6417	43	0.0149	

\*  $P < .05$ .

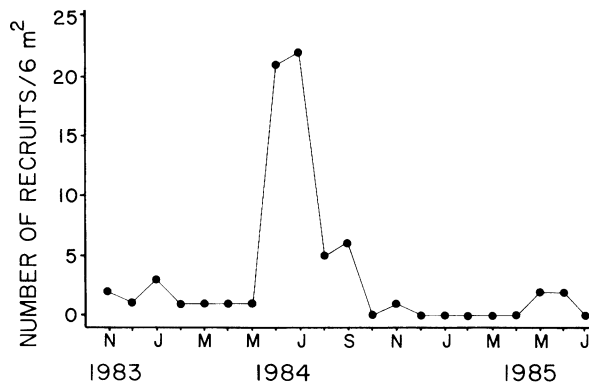


FIG. 5. Monthly recruitment of *Leptogorgia virgulata* in a cleared 6-m<sup>2</sup> plot. All new recruits were removed monthly.

Microhabitat quality affected not only the mean, but the variance in recruitment (Table 5). All of the pre-selected plots of clean limestone had at least some recruitment, whereas only half of the randomly selected plots had recruitment during the same time period. Recruitment into preselected plots was three times as great as into randomly selected plots, and almost four-fold less variable. These patterns probably reflect the greater variance of microhabitat quality in the randomly selected plots. Variation in recruitment cannot be attributed to the differences in quadrat size of the two samples. Indeed, the smaller preselected quadrats should generate greater variances, other things being equal (Williams 1964).

## DISCUSSION

### *Effects of sand on recruitment*

The experiments showed that the presence of sand reduced *Leptogorgia virgulata* recruitment on artificial substrata; relative abundances in the three treatments persisted for at least 10 mo. Sand also appeared to reduce recruitment on natural substrata, and the spatial distribution of adult colonies matched that of juveniles. The correlation ( $r^2$ ) between recruitment and the habitat index was 0.48, whereas the correlation between adult abundance and the habitat index was only 0.35. The weaker correlation for adults may be caused by shifting microhabitats, spatial variation in mortality after recruitment, and errors in the quantification of microhabitats and the estimation of abundance.

Nevertheless, it is clear that the initial spatial pattern on natural substrata was sustained during the following year. For each 1-m<sup>2</sup> block of the 24-m<sup>2</sup> plot, the number of surviving juveniles in August 1985 was correlated with the number of original recruits that had appeared in June and July of 1984 ( $r^2 = 0.52$ ,  $P < .01$ ; Fig. 8). Although 67% of the 1984 cohort died during the year, the original spatial pattern persisted. On both natural and artificial substrata, spatial patterns established at the time of recruitment persisted through time

and were not obscured by mortality following recruitment.

Although some organisms thrive in areas of high sand scour (Ricketts et al. 1968, Daly and Mathieson 1977), the presence of sand is usually detrimental to invertebrate recruitment (Daly and Mathieson 1977, Grigg 1977, Taylor and Littler 1982, McGuinness 1984). In terms of community organization, habitats exposed to sand may be chronically disturbed; they occupy a position in the lower right hand corner of the species-richness vs. disturbance graph of Connell (1978). These kinds of habitats have been overlooked in comparison with more accessible and well-studied rocky coasts (Dayton 1984).

### *Recruitment vs. juvenile growth*

The presence of sand reduced recruitment of *Leptogorgia virgulata*, but enhanced the growth of established juveniles. Could these patterns be related? If sand were an important mortality factor for juvenile gorgonians, enhanced growth might increase colony survival by raising polyps out of the zone of contact. Regeneration and early growth may have important ecological consequences for colonies that become established in different microhabitats (Wahle 1983).

Colonies in the transplant experiment appeared healthy after 55 d, but colonies harvested from the recruitment experiment (Fig. 4) showed long-term effects of exposure to sand. Although total mortality rates were comparable in the three treatments, the fraction of dead standing skeletons was much higher in the buried treatment. And the average size of living colonies in the buried treatment was largest. These patterns are all consistent with the ideas that sand is an

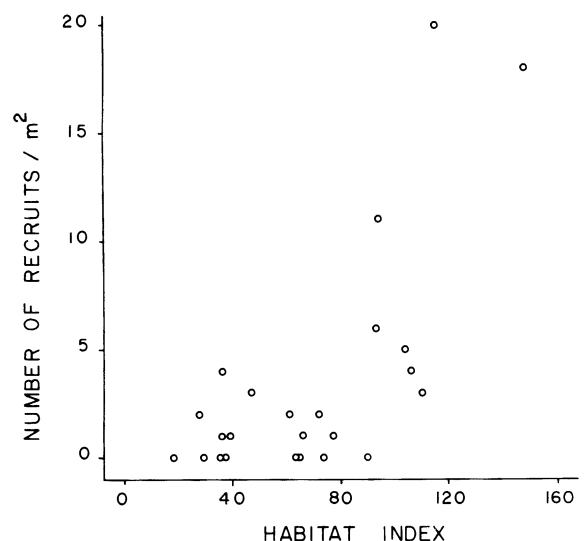


FIG. 6. Numbers of *Leptogorgia virgulata* recruits per square metre detected during June and July of 1984 vs. the habitat index in each contiguous 1-m<sup>2</sup> block of an untouched 24-m<sup>2</sup> plot.  $r^2 = 0.48$ ,  $P < .01$ .

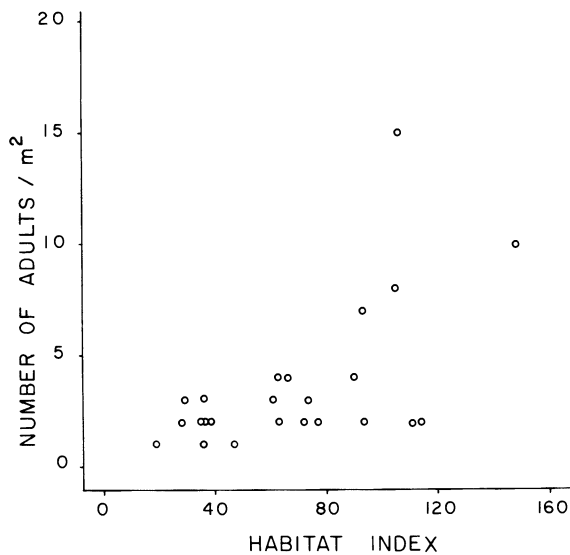


FIG. 7. Numbers of adult *Leptogorgia virgulata* colonies per square metre vs. the habitat index.  $r^2 = 0.35$ ,  $P < .01$ .

important source of juvenile mortality, and that an increased growth rate of buried colonies enhances survival in this microhabitat.

An explanation for enhanced growth is unknown, but might involve shifts in skeletal architecture or polyp density. For terrestrial plants, similar increases in growth are a common response to herbivory (Simberloff et al. 1978, Belsky 1986, Paige and Whitham 1987).

#### Alternative interpretations

In spite of the concordance between the experimental and nonexperimental data, results of this study must be interpreted cautiously. Because the settlement stage could not be observed in the field, there is no way of knowing whether the recruitment patterns were caused by larval settlement (Gaines et al. 1985), early juvenile mortality (Luckenbach 1984), or both (Young and Chia 1984). Nor is there any obvious explanation for reduced recruitment in the raised limestone treatment compared with the raised sand treatment (Fig. 3). Patch isolation (Keough 1984) or refuges from mortality (Connell 1975) may be important here.

Any factor that covaried with sand might also be responsible for the recruitment patterns. For example, one alternative hypothesis is that enhanced recruitment on raised surfaces occurred because larvae settled preferentially on the algal mat (e.g., Strathmann et al. 1981). But the scraping experiment showed that the presence of algae decreased, not increased, recruitment (see also Breitbart 1984). So, the difference between the treatments cannot be attributed to the fact that raised surfaces had an algal mat and buried surfaces did not. The small-scale flow regime may also differ between treatments. This factor is known to affect recruitment in soft-bottom communities (Eckman 1983,

TABLE 5. Recruitment in randomly selected and preselected plots of high-quality microhabitat.

	N	Number with no recruits	No. recruits/m <sup>2</sup>		
			$\bar{X}$	s	cv
Randomly selected plots	24	13	2.50	4.97	1.99
Preselected plots	14	0	7.74	4.24	0.55

Hannan 1984) and is difficult to control in field experiments (Dayton and Oliver 1980). On the other hand, I measured one aspect of flow in the field, the dispersion time of a 1-cc cloud of milk, and found no significant differences among treatments (Gotelli 1985).

Two alternative explanations for the habitat-index correlations are enhanced recruitment in the presence of adult colonies (e.g., Scheltema et al. 1981) and competition for attachment space with encrusting animals (e.g. Menge 1976). However, neither of these mechanisms generated statistically significant correlations. Numbers of adults and recruits were independent, although both were correlated with the habitat index. Moreover, in the recruitment experiment, there was no relationship between the number of colonies on the stones in one time period and the number that recruited in the next ( $P > .10$ , three positive slopes, one negative slope).

Competition for attachment space is unlikely in this system, simply because the percent cover of encrusting animals was so low (Table 1; cf. Buss and Jackson 1979, Sebens 1986). Also, I have removed encrusting animals from limestone and noticed that sand often inundated the exposed areas. Thus, encrusting animals may not always have been pre-empting high-quality recruitment sites for *Leptogorgia virgulata*. The compound ascidian *Aplidium stellatum* occasionally overgrew the



FIG. 8. Numbers of surviving juvenile colonies in July of 1985 vs. the numbers of original recruits per block in June and July of 1984.  $r^2 = 0.52$ ,  $P < .01$ . Empty square = one point; half-filled square = two points; solid square = three points.



bases of established *L. virgulata* colonies (cf. Sebens 1982), but the area of overgrowth did not appear to change over a 2-yr period (N. J. Gotelli, *personal observation*).

In sum, the presence of sand had important consequences for the recruitment, juvenile growth, and spatial pattern of a local population of the gorgonian *Lepetogorgia virgulata*. Because these patterns persisted through time, the spatial distribution of adult colonies cannot be understood without an examination of recruitment processes. For sessile organisms with low settlement rates, recruitment may be the primary determinant of spatial pattern. Unfortunately, the larval stages of many marine invertebrates are difficult to manipulate in the field, which limits the usefulness of recruitment studies. Further experiments on larval settlement behavior (Scheltema 1974) and transplants of newly settled juveniles into field microhabitats (Young and Chia 1984) are necessary to determine the ultimate causes of spatial variation in recruitment.

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#### LITERATURE CITED

- Adams, R. O. 1980. Investigations of color, morphology and development of the sea whip *Leptogorgia virgulata* (Lamarck) (Cnidaria: Octocorallia: Gorgonacea). Dissertation, Florida State University, Tallahassee, Florida, USA.
- Augsburger, C. K. 1984. Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. *Ecology* **65**:1705-1712.
- Belsky, A. J. 1986. Does herbivory benefit plants? A review of the evidence. *American Naturalist* **127**:870-892.
- Breitburg, D. 1984. Residual effects of grazing: inhibition of competitor recruitment by encrusting coralline algae. *Ecology* **65**:1136-1143.
- Buss, L. W., and J. B. C. Jackson. 1979. Competitive networks: nontransitive competitive relationships in cryptic coral reef communitites. *American Naturalist* **113**:223-234.
- Caffey, H. M. 1985. Spatial and temporal variation in settlement and recruitment of intertidal barnacles. *Ecological Monographs* **55**:313-332.
- Colman, J. 1933. The nature of the intertidal zonation of plants and animals. *Journal of the Marine Biological Association of the United Kingdom* **28**:435-476.
- Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* **42**:710-723.
- . 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. Pages 460-490 in M. L. Cody and J. M. Diamond, editors. *Ecology and evolution of communities*. Harvard University Press, Cambridge, Massachusetts, USA.
- . 1978. Diversity in tropical rain forests and coral reefs. *Science* **199**:1302-1310.
- Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* **111**:1119-1144.
- Daly, M. A., and A. C. Mathieson. 1977. The effects of sand movement on intertidal seaweeds and selected invertebrates at Bound Rock, New Hampshire, U.S.A. *Marine Biology* **43**:45-55.
- Dayton, P. K. 1971. Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* **41**:351-389.
- . 1984. Processes structuring some marine communities: are they general? Pages 181-197 in D. R. Strong, Jr., D. Simberloff, L. G. Abele, and A. B. Thistle, editors. *Ecological communities: conceptual issues and the evidence*. Princeton University Press, Princeton, New Jersey, USA.
- Dayton, P. K., and J. S. Oliver. 1980. An evaluation of the experimental analyses of population and community patterns in benthic marine environments. Pages 93-120 in K. R. Tenore and B. C. Coull, editors. *Marine benthic dynamics*. University of South Carolina Press, Columbia, South Carolina, USA.
- Eckman, J. E. 1983. Hydrodynamic processes affecting benthic recruitment. *Limnology and Oceanography* **28**:241-257.
- Gaines, S., S. Brown, and J. Roughgarden. 1985. Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. *Oecologia (Berlin)* **67**:267-272.
- Gotelli, N. J. 1985. Factors influencing the recruitment of two subtidal invertebrates. Dissertation, Florida State University, Tallahassee, Florida, USA.
- . 1987. Spatial and temporal patterns of reproduction, larval settlement, and recruitment of the compound ascidian *Aplidium stellatum*. *Marine Biology* **94**:45-51.
- Grigg, R. W. 1977. Population dynamics of two gorgonian corals. *Ecology* **58**:278-290.
- Grosberg, R. K. 1982. Intertidal zonation of barnacles: the influence of planktonic zonation of larvae on vertical distribution of adults. *Ecology* **63**:894-899.
- Hannan, C. A. 1984. Initial settlement of marine invertebrate larvae: the role of passing sinking in a near-bottom turbulent flow environment. Dissertation, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, USA.
- Harper, J. L. 1977. *Population biology of plants*. Academic Press, London, England.
- Kay, A. M., and M. J. Keough. 1981. Occupation of patches in the epifaunal communities on pier pilings and the bivalve *Pinna bicolor* at Edithburgh, South Australia. *Oecologia (Berlin)* **48**:123-130.
- Keough, M. J. 1984. Effects of patch size on the abundance of sessile marine invertebrates. *Ecology* **65**:423-437.
- Lasker, H. R. 1983. Vegetative reproduction in the octocoral *Briarum asebustum* (Pallas). *Journal of Experimental Marine Biology and Ecology* **72**:157-169.
- Louda, S. M. 1982. Distribution ecology: variation in plant recruitment over a gradient in relation to insect seed predation. *Ecological Monographs* **52**:25-41.
- Luckenbach, M. W. 1984. Settlement and early post-settlement survival in the recruitment of *Mulinia lateralis* (Bivalvia). *Marine Ecology Progress Series* **17**:245-250.
- McGuinness, K. A. 1984. *Communities of organisms on intertidal boulders: the effects of disturbance and other factors*. Dissertation, University of Sydney, Sydney, Australia.
- Meadows, P. S., and J. I. Campbell. 1972. Habitat selection by aquatic invertebrates. *Advances in Marine Biology* **10**:271-382.
- Menge, B. A. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and

- environmental heterogeneity. *Ecological Monographs* **46**:353–393.
- Paige, K. N., and T. G. Whitham. 1987. Overcompensation in response to mammalian herbivory: the advantage of being eaten. *American Naturalist* **129**:407–416.
- Paine, R. T. 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia (Berlin)* **15**:93–120.
- . 1984. Ecological determinism in the competition for space. *Ecology* **65**:1339–1348.
- Rabinowitz, D. 1978. Early growth of mangrove seedlings in Panama, and an hypothesis concerning the relationship of dispersal and zonation. *Journal of Biogeography* **5**:113–133.
- Ricketts, E. F., J. Calvin, and J. W. Hedgepeth. 1968. Between Pacific tides. Fourth edition. Stanford University Press, Stanford, California, USA.
- Roughgarden, J., Y. Iwasa, and C. Baxter. 1985. Demographic theory for an open marine population with space-limited recruitment. *Ecology* **66**:54–67.
- Ryland, J. S. 1959. Experiments on the selection of algal substrates by polyzoan larvae. *Journal of Experimental Biology* **36**:613–631.
- Scheltema, R. S. 1974. Biological interactions determining settlement of marine invertebrates. *Thalassia Jugoslavica* **10**:263–296.
- Scheltema, R. S., I. P. Williams, M. A. Shaw, and C. Loudon. 1981. Gregarious settlement by the larvae of *Hydroides dianthus* (Polychaeta: Serpulidae). *Marine Ecology Progress Series* **5**:69–74.
- Sebens, K. P. 1982. Competition for space: growth rate, reproductive output and escape in size. *American Naturalist* **120**:189–197.
- . 1986. Spatial relationships among encrusting marine organisms in the New England subtidal zone. *Ecological Monographs* **56**:73–96.
- Simberloff, D., B. J. Brown, and S. Lowrie. 1978. Isopod and insect root borers may benefit Florida mangroves. *Science* **201**:630–632.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. *Biometrika* **38**:196–218.
- Strathmann, R. R., E. S. Branscomb, and K. Vedder. 1981. Fatal errors in set as a cost of dispersal and the influence of intertidal flora on set of barnacles. *Oecologia (Berlin)* **48**:13–18.
- Sutherland, J. P. 1974. Multiple stable points in natural communities. *American Naturalist* **108**:859–873.
- Taylor, P. R., and M. M. Littler. 1982. The roles of compensatory mortality, physical disturbance, and substrate retention in the development and organization of a sand-influenced rocky-intertidal community. *Ecology* **63**:135–146.
- Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biological Review* **25**:1–45.
- Underwood, A. J., and E. J. Denley. 1984. Paradigms, explanations and generalizations in models for the structure of intertidal communities on rocky shores. Pages 151–180 in D. R. Strong, D. Simberloff, L. G. Abele, and A. B. Thistle, editors. *Ecological communities: conceptual issues and the evidence*. Princeton University Press, Princeton, New Jersey, USA.
- Wahle, C. M. 1983. Regeneration of injuries among Jamaican gorgonians: the role of colony physiology and environment. *Biological Bulletin* **165**:778–790.
- Walker, T. A., and G. D. Bull. 1983. A newly discovered method of reproduction in a gorgonian coral. *Marine Ecology Progress Series* **12**:137–143.
- Warner, R. W., and P. L. Chesson. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. *American Naturalist* **125**:769–787.
- Williams, C. B. 1964. *Patterns in the balance of nature*. Academic Press, London, England.
- Winer, B. J. 1971. *Statistical principles in experimental design*. McGraw-Hill, Kogakusha, Tokyo, Japan.
- Young, C. M., and F.-S. Chia. 1984. Microhabitat-associated variability in survival and growth of subtidal solitary ascidians during the first 21 days after settlement. *Marine Biology* **81**:61–68.