

# Quantifying spatial patterns of overgrowth in epibenthic communities

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**ABSTRACT:** A method is presented that allows rapid and accurate measurement of changes in the spatial pattern of space occupation in encrusting organisms. The boundaries of organisms are represented as polygons, and geometric difference calculations are used to establish the perimeters of the areas gained or vacated between sampling dates. The influence of interspecific interactions on occupation of space is also quantified: geometric intersection calculations are used to define the perimeters of the areas gained or lost in overgrowth interactions. A method is presented for estimating the sampling frequency necessary for detection of significant changes in occupation of space. The method provides a means of quantifying not only changes in percent cover and diversity but also the dynamics of colony movement and the rates and outcomes of competitive interactions.

## INTRODUCTION

Marine epibenthic assemblages are often space-limited, with intense competition for space. In sessile organisms, the mechanism of interference competition may be the overgrowth of one organism by another (Jackson 1979). The results of local overgrowth can include (1) reduced fecundity or growth, (2) death and/or (3) local extinction of the overgrown species (Connell & Keough 1985). Community diversity can be influenced by the form of the competitive interactions. If the species form a competitive hierarchy (competitive transitivity), domination by a single species is predicted in the absence of disturbance (Paine 1966). Coexistence of species is predicted if there is a competitive network (competitive intransitivity) and no disturbance (Jackson & Buss 1975, Buss & Jackson 1979, Jackson 1979, Karlson & Jackson 1981, Rubin 1982, Karlson & Buss 1984). The conditions under which 'perfect intransitivity' and permanent coexistence are likely to occur are so stringent as to make them unlikely. However, local coexistence may be prolonged in systems with networks relative to comparable systems with hierarchies.

Networks are the result of reversals of the outcome of competition or equality of the species competing for the same space or possibly ecological 'confusion' generated by disturbance or selective predation (Paine 1984). When no apparent winner is seen, the result is termed a standoff or delay/tie (Connell 1976, Russ

1982) or the 2 species may be defined as competitively equivalent (Kay & Keough 1981). Many mechanisms influence the occurrence of competitive hierarchies or networks in particular assemblages. Toxic allelochemical poisoning of the dominant species by a subordinate may yield reversals (Jackson & Buss 1975). A faster growth rate in a normally subordinate species may allow it to become the top competitor in certain circumstances (Buss 1980). Large colony size may allow species lower in a hierarchy to win in encounters with smaller individuals of the supposed dominant (Day 1977, Buss 1980). Directionality of growth can also alter the expected outcome. In most frontal encounters a particular species may win, whereas it may lose when it meets a competitor on its flank or rear (Jackson 1979, Buss 1982, Rubin 1982). Spatial heterogeneity may also reverse the expected outcome. A colony that is slightly elevated may obtain an initial advantage in overgrowing neighbors (Russ 1982, Paine 1984, Connell & Keough 1985, Walters & Wethey 1986). Grazing by predators may also affect the outcome (Day & Osman 1981, Paine 1984). In these epibenthic assemblages, an understanding of the dynamics of the system thus requires knowledge of the rates, directions and spatial patterns of interactions of the component species, as well as the consistency of the outcomes.

Here we present a method for measuring the spatial pattern of competitive interactions of sessile encrusting organisms. The method allows quantification of the

dynamics and spatial pattern of space occupation, and the influence of inter- and intraspecific interactions on space occupation. In addition we provide a method for determining the appropriate frequency at which to sample a system in order to detect changes in occupation of space. The method defines colony boundaries as polygons, allowing calculation of the geometric difference between colony boundaries in consecutive samples.

### METHODS

Since encrusting organisms are for the most part 2-dimensional, they can be represented as sets of polygons. Our method of analysing spatial patterns of growth and overgrowth among these organisms takes advantage of this 2-dimensionality. By calculating the geometric difference between the polygon which defines the perimeter of a colony on one date and the polygon which defines the perimeter on another date, it is possible to determine the outline of the area vacated and the new area gained by the colony (Fig. 1). The general scheme for such geometric calculations is

outlined in the Appendix. This method is potentially very powerful because it uses all of the spatial information about 2-dimensional organisms in defining the dynamics of space occupation.

To test the utility of geometric difference calculations in quantifying the spatial pattern of overgrowth in encrusting organisms, we analysed series of photographs taken of subtidal settling plates which were colonized by colonial ascidians and sponges. Photographs of this sort are easily obtainable and are an example of the kind of data set that has often been collected by field ecologists interested in the dynamics of such assemblages (e.g. Connell 1976, Sutherland & Karlson 1977, Paine 1984, Ryland et al. 1984, Hughes & Jackson 1985). Two replicate plates (L19 and L20) were measured.

Daily photographs were taken of settlement plates placed subtidally on a floating dock in Long Island Sound at the Yale Peabody Museum Field Station in Guilford Connecticut, USA (41° 16' N, 72° 44' W). The plates were submerged on August 10, 1983 and daily photographs were taken from August 15, 1983 to October 10, 1983. The settling plates were removed from the water for approximately 3 min each day while

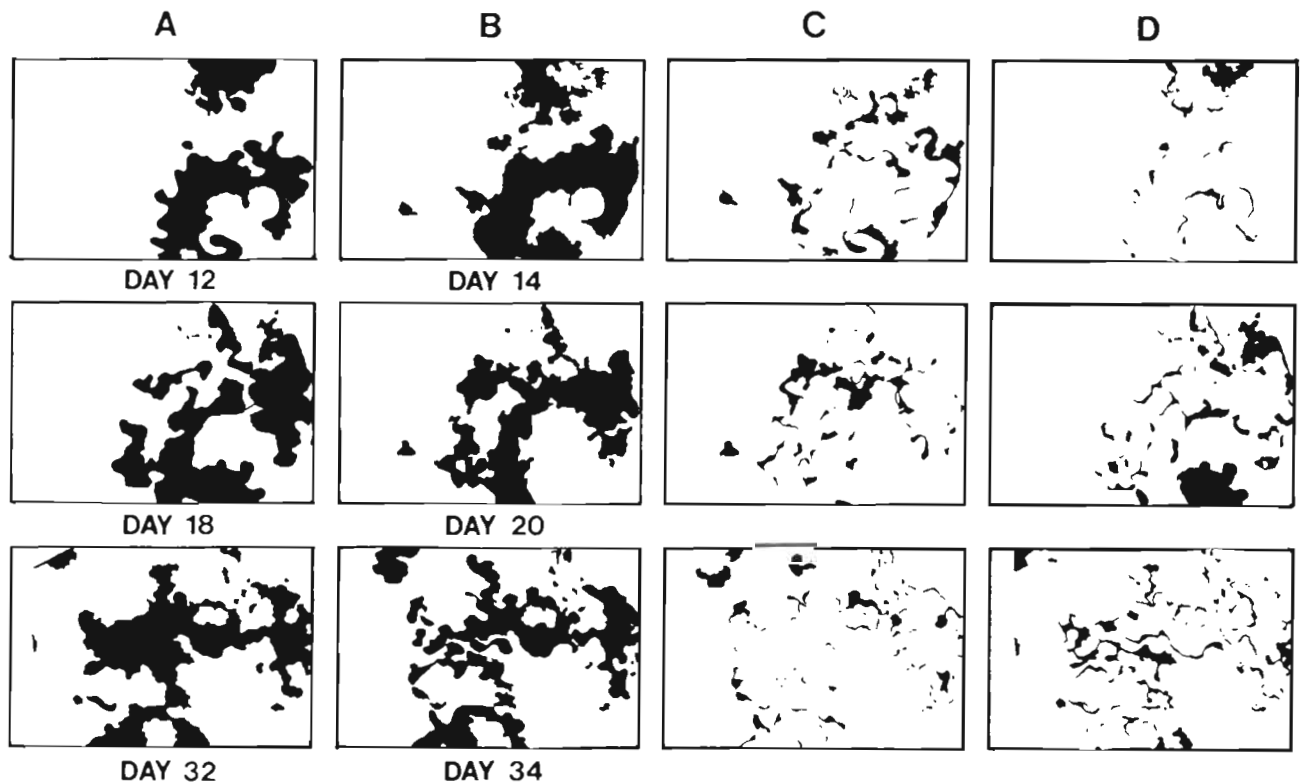


Fig. 1. Examples of results of area growth and loss calculations on the L20 plate. In each row the first 2 panels (A, B) show the area occupied by *Botryllus schlosseri* colonies in consecutive samples separated by 2 d. Third panel (C): new area gained, from polygon calculation.  $C = B - A$ . Fourth panel (D): area lost over the 2 d from the polygon calculation.  $D = A - B$ . See Appendix for method of calculation. Colonies lose area along one set of boundaries and gain area along other boundaries. Total colony area may change very little, as the colony 'crawls' from one place to another

they were photographed. We assume this had no effect on their growth rates. Flash-lit photographs were taken with a 2:1 extension ring on a 35 mm camera. A focal framer on the camera and screws on the settling plates provided precise registration of camera position from day to day. A ruler on the framer ensured a constant scale. Enlargements of the negatives (20 × 24 cm) from approximately every other day were mapped with a graphics tablet interfaced with a minicomputer (Wethey 1984). The coordinates of points around the perimeter of each organism were measured with an accuracy of 0.1 mm. The coordinate systems of the photographs were superimposed by rotation, translation and scaling (least squares fit). All maps had the same boundaries after superimposition.

The positions of points around the perimeter of the colonial ascidian *Botryllus schlosseri* (Pallas) and the

growth (Table 2). Thus not only was the gain and loss of space quantified (Table 1), but also its spatial pattern (Fig. 1). The spatial pattern is very important in colonies that vacate space along one set of boundaries and gain space along others. In such species total colony area or percent cover may change very little as the colony 'crawls' from one place to another (Birke-land et al. 1981, Ryland et al. 1984).

In order to examine the influence of sampling frequency on rate estimates, we compared the results of calculations made from the samples taken every 2 d with results obtained from samples spaced every 4, 6, 8 or 10 d. Estimates made from 4, 6, 8 and 10 d intervals were made by dropping the intervening samples from the analysis. If sampling frequency had no effect on the analysis, then the growth and loss of space calculated by comparing samples collected 10 d apart should

Table 1. Correlations of growth and area loss against colony area and perimeter. The correlation coefficient ( $r$ ) and  $p$  (the probability that the slope is 1) are shown for regressions on *Haliclona loosanoffi* and *Botryllus schlosseri* on the L19 and the L20 plates. Correlations significant at  $p < 0.05$  level are marked with \* N = 15

Correlation	<i>Haliclona loosanoffi</i> L19			<i>Botryllus schlosseri</i> L19		
	$r$	$p$	Sig.	$r$	$p$	Sig.
Growth/day vs loss/day	-0.21	.470		0.78	.001	*
Growth/day vs area	-0.13	.670		0.78	.001	*
Loss/day vs area	0.70	.006	*	0.83	.000	*
Growth/day vs perimeter	-0.23	.420		0.69	.007	*
Loss/day vs perimeter	0.74	.002	*	0.71	.004	*
Correlation	<i>Haliclona loosanoffi</i> L20			<i>Botryllus schlosseri</i> L20		
	$r$	$p$	Sig.	$r$	$p$	Sig.
Growth/day vs loss/day	-0.03	.932		0.80	.001	*
Growth/day vs area	-0.16	.643		0.53	.052	*
Loss/day vs area	0.74	.009	*	0.57	.032	*
Growth/day vs perimeter	-0.24	.476		0.41	.143	
Loss/day vs perimeter	0.70	.017	*	0.39	.165	

sponge *Haliclona loosanoffi* Hartman were recorded as polygons. Calculations of the geometric unions, intersections and differences among the polygons were used to measure area gains (growth), area losses, and overgrowth relations of the 2 species (Fig. 1, Table 1) following a method developed by Turner & Borkin (see Appendix). The change in area of a colony between 2 dates was calculated as the geometric difference between the perimeters on the 2 dates (Fig. 1). Growth by one colony that resulted in loss of space by another species (overgrowth) was calculated as the geometric intersection of the loser's perimeter before overgrowth with the perimeter of the area gained by the winner during the period of overgrowth. The importance of overgrowth in the system was estimated as the percent of total areal gain or loss that was the result of over-

equal the sum of the growth or loss of space over the intervening dates. This was tested by calculating the linear regression of values determined from infrequent sampling against the sum of the values from the samples taken every 2 d. The regressions were forced through the origin. If the slope of the line is 1.0, then there is a perfect correspondence between the results obtained from frequent and infrequent sampling. The slope of the regression is a measure of the percent of the actual area change (as measured by the 2 d samples) that was detected by the infrequent sampling. If the slope is 0.85, then 85 % of the actual area change is measurable by infrequent sampling. Daily measurements were not used because the area change over 24 h was often no greater than our digitizing error of 2 to 3 %.

## RESULTS

Several questions regarding space occupation in encrusting organisms were addressed in this study. We estimated the effectiveness of the polygon difference calculations in quantifying the following: (1) the dynamics and spatial pattern of space occupation; (2) the influence of inter- and intraspecific interactions

on space occupation; (3) the amount and importance of information lost by infrequent sampling.

In order to test the utility of the method in determining the dynamics of space occupation we plotted colony area against time from Day 0 to Day 36 (Fig. 2). Area changes were easily detected, both in large and small colonies. Although the sponges were much smaller than the ascidians, both were seen to increase

Table 2. Effect of sampling frequency on the detection of area change. Regressions of total growth, amount of growth that was due to overgrowing the competitor, total area loss and area loss due to being overgrown are shown for the 4 data sets comparing the results from sampling every 2 d with sampling frequencies of every 4, 6, 8, and 10 d. Freq.: frequency of sampling in days; SE: standard error of the slope; DF: degrees of freedom; Sig.: slopes of regressions significantly different from 1.0 at  $p < 0.05$  are marked with \*

Freq.	Slope	SE	DF	Sig.	Freq.	Slope	SE	DF	Sig.
<b><i>Haliclona loosanoffi</i> L19</b>					<b><i>Haliclona loosanoffi</i> L20</b>				
TOTAL GROWTH (new area gained)					TOTAL GROWTH (new area gained)				
4	.899	.019	7	*	4	.737	.085	5	*
6	.846	.045	5	*	6	.620	.126	3	
8	.808	.065	3		8	.571	.231	2	
10	.724	.081	2		10	.652	.085	1	
OVERGROWTH					OVERGROWTH				
4	.898	.132	3		4	.916	.069	5	
6	.594	.083	2	*	6	.774	.152	3	
8	.660	.145	1		8	.534	.310	2	
10	.675	.296	1		10	.279	.021	1	*
TOTAL LOSS (area vacated)					TOTAL LOSS (area vacated)				
4	.824	.038	7	*	4	.819	.053	5	*
6	.717	.066	5	*	6	.506	.040	3	*
8	.623	.080	3	*	8	.194	.084	2	*
10	.294	.064	2	*	10	.200	.030	1	*
LOSS FROM OVERGROWTH					LOSS FROM OVERGROWTH				
4	.958	.133	3		4	.681	.064	5	*
6	.400	.066	3	*	6	.482	.055	3	*
8	.125	.065	2	*	8	.181	.106	2	*
10	.067	.296	1		10	.277	.020	1	*
<b><i>Botryllus schlosseri</i> L19</b>					<b><i>Botryllus schlosseri</i> L20</b>				
TOTAL GROWTH (new area gained)					TOTAL GROWTH (new area gained)				
4	.654	.089	7	*	4	.752	.050	7	*
6	.848	.102	5	*	6	.738	.045	5	*
8	.567	.113	3	*	8	.620	.069	3	*
10	.556	.059	2	*	10	.533	.104	2	*
OVERGROWTH					OVERGROWTH				
4	.870	.191	3		4	.558	.095	4	*
6	.355	.116	3	*	6	.449	.072	3	*
8	.097	.071	2	*	8	.184	.060	2	*
10	.877	.065	1		10	.157	.013	1	*
TOTAL LOSS (area vacated)					TOTAL LOSS (area vacated)				
4	.423	.063	7	*	4	.669	.033	7	*
6	.373	.038	5	*	6	.639	.034	5	*
8	.296	.065	3	*	8	.476	.057	3	*
10	.315	.092	2	*	10	.327	.070	2	*
LOSS FROM OVERGROWTH					LOSS FROM OVERGROWTH				
4	.656	.225	3		4	.810	.080	5	*
6	.433	.171	3	*	6	.679	.079	3	*
8	.599	.014	2	*	8	.476	.057	3	*
10	.877	.065	1		10	.992	.163	1	

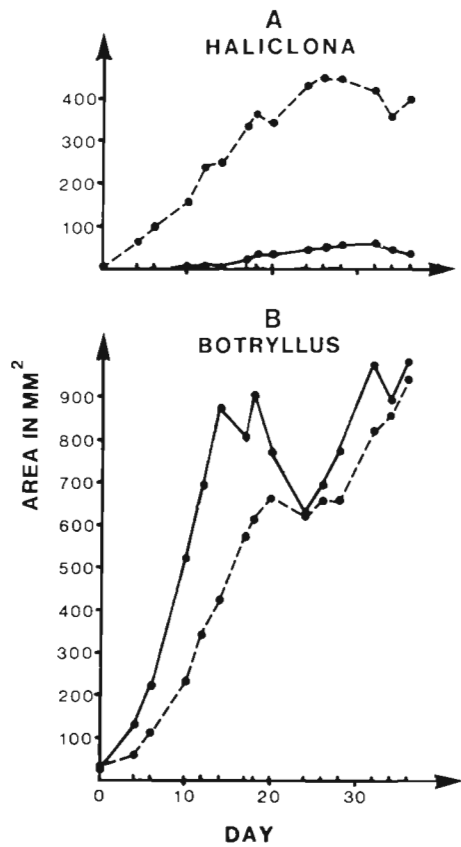


Fig. 2. Overall colony area plotted against time (d) for the *Haliclona loosanoffi* (A) and the *Botryllus schlosseri* (B) colonies on the L19 (---) and L20 (—) plates

rapidly in size initially, then slow down, showing both positive and negative changes in area (Fig. 2).

To test the utility of the method in determining the spatial pattern of space occupation, we calculated the locations of areas gained and lost. The method was very effective. We documented that early in growth (Days 12 to 14) the *Botryllus schlosseri* colonies grew at almost all locations around their perimeters (Fig. 1). Later (Days 18 to 20; 32 to 34), colonies lost area from both their centers and perimeters and grew only slightly at their edges (Fig. 1). This corresponds to the pattern of *B. schlosseri* senescence documented by Grosberg (1982), and was observed on a 20 d cycle comparable to what he reported. Thus it was possible to measure the timing and spatial pattern of changes in space occupation in detail (Fig. 1).

To determine the effectiveness of the method in measuring the influence of competition on space occupation, growth and overgrowth over competitors (both as percent of colony area) were plotted against time for *Botryllus schlosseri* and *Haliclona loosanoffi* (Fig. 3 A, B). Area loss and area loss resulting from being overgrown (both as percent of colony area) were also plotted against time (Fig. 3 C, D). The slopes of the lines in

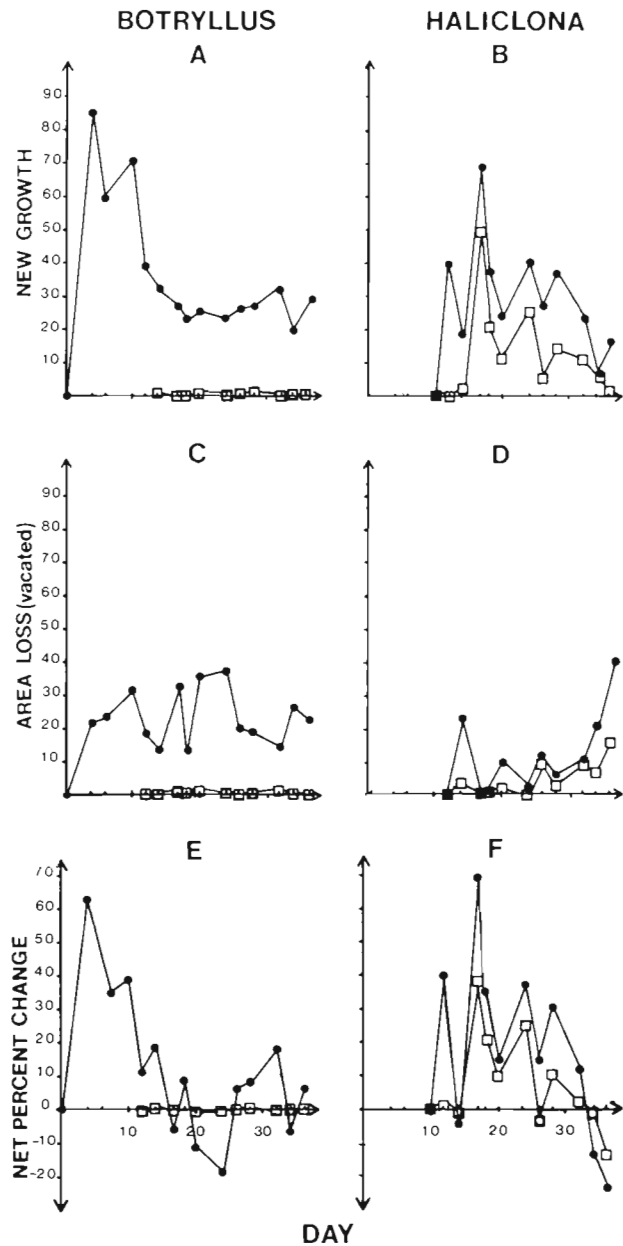


Fig. 3. New area gains and losses (area vacated) of *Haliclona loosanoffi* and *Botryllus schlosseri* on the L20 plate. A & B: percent growth over each time period and overgrowth over the competitor as a percent of colony area of the winner. ● Percent growth (new area gained); □ percent overgrowth. C & D: percent area loss (area vacated) per time period and percent loss due to being overgrown. ● percent loss (area vacated); □ percent area loss due to being overgrown by the competitor. E & F: net percent change in total area (●) and net percent change due to competitive interaction (□)

these plots provide measures of the rates of change of space occupation. The method was very effective in detecting changes in space occupation and in determining the influence of competition thereon (Fig. 3). We detected large differences in the importance of

competitive interactions on growth of the ascidian compared to the sponge. The ascidian growth that was influenced by *H. loosanoffi* was always less than 5 % (Fig. 3 A, C). Thus area changes of the ascidian were not strongly influenced by the sponge. However, the dynamics of *H. loosanoffi* were strongly affected by *B. schlosseri*. An average of 47 % of the growth of the sponge was over the ascidian and 60 % of the area losses could be attributed to a competitive interaction (Fig. 3 B, D). The same patterns were evident in our plots of net area changes *versus* time (Fig. 3 E, F). These differences between sponge and ascidian were likely the result of differences in the size of the organisms (Fig. 2). Approximately 3 % of the perimeter of *B. schlosseri* was in contact with *H. loosanoffi*, whereas about half of the perimeter of the sponge abutted the ascidian. These results indicate that the method successfully measured rates of change in space occupation, and the influence of competitive interactions on these rates.

To determine the effect of colony area and perimeter on area gains and losses, we calculated the correlations of growth per day with loss per day, growth per day and loss per day with area, and growth per day and loss per day with perimeter (Table 1). If growth (new area occupied) were correlated with area loss (area vacated) then on days when considerable growth took place, colonies would also vacate a great deal of space. This would occur if colonies 'crawled' across a surface (e.g. Birkeland et al. 1981, Ryland et al. 1984), or if they grew on one edge while dying back on another as did *Botryllus schlosseri* in our study (Table 1 B). The larger the ascidian colony, the greater the gains and losses of space (Table 1 B). These results correspond to Fig. 3 E, F, showing that *B. schlosseri* had little net area change after its large initial growth, but that it gained and lost area every day. These results indicate that the method was able to detect the effects of colony size on the dynamics of area gains and losses.

We tested the method in determining the sampling frequency necessary to detect all significant area gains and losses by colonies. By actually measuring photographs taken every 2 d, we could calculate what area gains and losses would have been observed had we sampled at 4, 6, 8 or 10 d intervals. We calculated the linear regression of the area changes detectable at infrequent sampling rates *versus* the actual area changes that occurred during the period between the infrequent samples. Thus for the 8 d sampling rate we compared the 8 d area changes to the sum of the area changes between Days 0, 2, 4, 6 and 8 (Table 2). The slope of the regression is a measure of the proportion of the actual change that is detected by infrequent sampling. Longer sampling intervals, having only a few points and one degree of freedom, have slopes that are

difficult to distinguish from 1.0 by statistical means. They are included because in 30 % of the cases the slopes were significantly different from unity at the  $p < 0.05$  level (Table 2). The slopes of the regressions of area change measured from frequent *versus* infrequent sampling in both the sponge and the ascidian declined with longer intervals between samples, indicating that infrequent sampling resulted in significant loss of information (Table 2). The exceptions are cases with few data points (degrees of freedom = 1) where one has low confidence in the estimates of the slopes.

The majority of slopes of the regressions for both sponge and ascidian were significantly different from unity, including every case of total area loss, indicating a significant amount of area change was not detected by longer sampling intervals (Table 2). In the case of *Haliclona loosanoffi*, sampling every 4 d, between 10 and 26 % of new area gained was undetected, 18 % of the area vacated was undetected, and up to 32 % of the area lost to overgrowth was undetected (Table 2). In the case of *Botryllus schlosseri*, sampling every 4 d, between 25 and 35 % of the new area gained was undetected, up to 45 % of the new area gained in overgrowth was undetected, between 43 and 57 % of the area vacated was undetected, and up to 19 % of the area lost to overgrowth was undetected (Table 2). Thus, in most cases, infrequent sampling caused underestimates of area loss and the quality of the estimate worsened as the sampling interval increased. The method of determining the appropriate sampling rate was very effective.

The techniques documented here require moderate computer resources. Digitizing each photograph took an average of ten minutes, with most polygons having 2000 to 3000 points. Analysis of 20 photographs of the complexity shown in Fig. 1 took approximately 1 to 2 h of computing time on a VAX 11/780 with Floating Point Accelerator.

## DISCUSSION

Ecologists interested in growth and interactions among encrusting organisms often need to quantify at least the following about their system: (1) how dynamic is the system; (2) how much of the changes in occupation of space are the results of inter- and intra-specific interactions; (3) what is the appropriate frequency at which to sample their system in order to document changes in occupation of space.

This study was a test of the utility of geometric difference calculations in the analysis of growth and competitive interactions in answering the above questions. We examined the interaction between *Botryllus schlosseri* and *Haliclona loosanoffi* because it was

highly dynamic (e.g. Grosberg 1982) and therefore was likely to provide a thorough test of the method.

The representation of encrusting organisms as polygons provided a powerful tool for such analyses. Calculation of the time series of geometric differences among colony perimeters provided direct documentation of the mobility of colonies (Fig. 1) which grew along some edges and vacated space along other edges. Such patterns have been noted by other authors (e.g. Birkeland et al. 1981, Keough & Butler 1983, Ryland et al. 1984) but it has been very laborious to document movement. Birkeland et al. (1981) recorded the locations of 1 cm diameter colonies of didemnid ascidians as they moved over the surface of a jar. Ryland et al. (1984) traced the outlines of colonies as they changed over intervals of 1 mo (*Lissoclinum voeltzkowi*) and 4 h (*Diplosoma virens*). By hand they superimposed tracings made on consecutive dates and elegantly documented the fluidity of colony boundaries and occupation of space. The geometric calculations presented here allow rapid analyses of this type (Fig. 1), and thus allow one to sample on the basis of the actual growth dynamics of the system.

The geometric calculations provided a very simple means to examine the complex spatial relations of organisms competing for space along their borders (Table 2, Fig. 2). *Botryllus schlosseri* rapidly gained and lost space although interspecific interactions played a minor role in those changes (Fig. 2). *B. schlosseri* has been shown to lose large percentages of its area in a single day in the absence of any obvious interspecific interaction (Grosberg 1982). In contrast, changes in space occupation by *Haliclona loosanoffi* were usually associated with growth or loss in a competitive interaction (Fig. 3 B, D). It would be difficult, without measures of spatial coordinates of colony boundaries, to assess the importance of interspecific interactions in these changes in occupation of space. Since colony area can be easily calculated when the perimeter is known, the influence of colony size on overgrowth ability (Buss 1980) can also be quantified simply using these methods. Differences in response of organisms to one another in the presence and absence of disturbance (Paine 1984) are readily measurable as well.

The sampling frequency necessary to document changes in occupation of space was easily estimable by calculation of the effects of infrequent sampling. The regression method showed that with spatially dynamic organisms like *Botryllus schlosseri*, sampling must be very frequent. Lowering the sampling rate from every 2 d to every 4 d meant that between 20 and 40% of the area gains and losses were undetectable (Table 2, see also Ryland et al. 1984). In slower growing organisms like coralline algae (Paine 1984) or

some tropical bryozoans (Winston & Jackson 1984), sampling rates can be much lower. In general the sampling rate should be such that area changes are just within the limits of resolution of the mapping method (Table 2). The regression method provides a means of determining the appropriate rate.

In many studies of epifaunal encrusting organisms, authors have been limited to analyses of changes in percent cover and diversity or overgrowth measured from single point-in-time samples. The methods presented here provide a means of quantifying not only percent cover and diversity but also the dynamics of colony movement (Fig. 1), the influence of inter- and intraspecific interactions on occupation of space (Table 2), and the rates and outcomes of competitive interactions. The magnitudes and spatial patterns of gains and losses of space are simply and quickly quantified by the use of geometric calculations in association with precise records of the spatial locations of colony boundaries.

## APPENDIX

*Polygon Set calculations:* Algorithm developed by James A. Turner and Harold Borkin, Architectural Research Laboratory, University of Michigan, Ann Arbor.

All original endpoints of line segments in polygons and the intersection points of line segments from polygons are tabulated. New line segments replace original segments when an intersection point lies on an original segment.

In comparing one polygon set to another, 2 types of line segments are defined: (1) line segment outside the other set; (2) line segment inside the other set.

Set operations use the following types of lines to construct the resultant polygon sets:

UNION:  $A \cup B$ . All Type 1 line segments

INTERSECTION:  $A \cap B$ . All Type 2 line segments

DIFFERENCE:  $A - B$ . All Type 1 line segments from Set A; all Type 2 line segments from Set B

DIFFERENCE:  $B - A$ . All Type 1 line segments from Set B; all Type 2 line segments from Set A

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## LITERATURE CITED

- Birkeland, C., Cheng, L., Lewin, R. A. (1981). Motility of didemnid ascidian colonies. *Bull. mar. Sci.* 31: 170–173
- Buss, L. W. (1980). Competitive intransitivity and size-frequency distributions of interacting populations. *Proc. natn. Acad. Sci. USA.* 77: 5355–5359
- Buss, L. W. (1982). Mechanisms of competition between *Onychocella alula* (Hastings) and *Antropora tincta* (Hastings) on an eastern pacific rocky shoreline. In: Larwood, G. P., Nielson, C. (ed.) Recent and fossil bryozoa. Olsen and Olsen, Fredensborg, p. 39–49
- Buss, L. W., Jackson, J. B. C. (1979). Competitive networks: nontransitive competitive relationships in cryptic coral reef environments. *Am. Nat.* 113: 223–234
- Connell, J. H. (1976). Competitive interactions and the species diversity of corals. In: Mackie, G. O. (ed.) Coelenterate ecology and behavior. Plenum Press, New York, p. 51–58
- Connell, J. H., Keough, M. J. (1985). Disturbance and patch dynamics of subtidal marine animals on hard substrata. In: Pickett, S. T. A., White, P. S. (ed.) Natural disturbance: an evolutionary perspective. Academic Press, New York, p. 125–151
- Day, R. W. (1977). The ecology of settling organisms on the coral reef at Heron Island, Queensland. Ph. D. thesis, Univ. of Sydney
- Day, R. W., Osman, R. W. (1981). Predation by *Patiria miniata* (Asteroidea) on bryozoans: prey diversity may depend on the mechanism of succession. *Oecologia (Berl.)* 51: 300–309
- Grosberg, R. K. (1982). Ecological, genetical and developmental factors regulating life history variation within a population of the colonial ascidian *Botryllus schlosseri* (Pallas) savigny. Ph. D. dissertation, Yale Univ.
- Hughes, T. P., Jackson, J. B. C. (1985). Population dynamics and life histories of foliaceous corals. *Ecol. Monogr.* 55: 141–166
- Jackson, J. B. C. (1979). Overgrowth competition between encrusting cheilostome ectoprocts in a Jamaican cryptic reef environment. *J. Anim. Ecol.* 48: 805–823
- Jackson, J. B. C., Buss, L. W. (1975). Allelopathy and spatial competition among coral reef invertebrates. *Proc. natn. Acad. Sci. USA.* 72: 5160–5163
- Karlson, R. H., Jackson, J. B. C. (1981). Competitive networks – a simulation study. *Ecology* 62: 670–678
- Karlson, R. H., Buss, L. W. (1984). Competition, disturbance, and local diversity patterns of substratum-bound clonal organisms – a simulation. *Ecol. Modelling* 23: 243–255
- Kay, A. M., Keough, M. J. (1981). Occupation of patches in the epifaunal communities on pier pilings and the bivalve *Pinna bicolor* at Edithburgh, South Australia. *Oecologia (Berl.)* 48: 123–130
- Keough, M. J., Butler, A. J. (1983). Temporal changes in species number in an assemblage of sessile marine invertebrates. *J. Biogeogr.* 10: 317–330
- Paine, R. T. (1966). Food web complexity and species diversity. *Am. Nat.* 100: 65–75
- Paine, R. T. (1984). Ecological determinism in the competition for space. *Ecology* 65: 1339–1348
- Rubin, J. A. (1982). The degree of intransitivity and its measurement in an assemblage of encrusting cheilostome bryozoa. *J. exp. mar. Biol. Ecol.* 60: 119–128
- Russ, G. R. (1982). Overgrowth in a marine epifaunal community: competitive hierarchies and competitive networks. *Oecologia (Berl.)* 53: 12–19
- Ryland, J. S., Wigley, R. A., Muirhead, A. (1984). Ecology and colonial dynamics of some Pacific reef flat Didemnidae (Asciadiacea). *Zool. J. Linn. Soc.* 80: 261–282
- Sutherland, J. P., Karlson, R. H. (1977). Development and stability of the fouling community at Beaufort, North Carolina. *Ecol. Monogr.* 47: 425–446
- Walters, L. J., Wethey, D. S. (1986). Surface topography influences competitive hierarchies on marine hard substrata: a field experiment. *Biol. Bull. mar. biol. Lab., Woods Hole* (in press)
- Wethey, D. S. (1984). Spatial pattern in barnacle settlement: day to day changes during the settlement season. *J. mar. biol. Ass. U.K.* 64: 687–698
- Winston, J. E., Jackson, J. B. C. (1984). Ecology of cryptic coral reef communities IV. Community development and life histories of encrusting cheilostome bryozoa. *J. exp. mar. Biol. Ecol.* 76: 1–21

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