OVERGROWTH COMPETITION BETWEEN ENCRUSTING CHEILOSTOME ECTOPROCTS IN A JAMAICAN CRYPTIC REEF ENVIRONMENT

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SUMMARY

(1) The outcome of overgrowth interactions and the spatial relationships between interacting colonies were determined for fifteen cheilostome species encrusting the undersurfaces of nine foliaceous corals collected from Rio Bueno, Jamaica.

(2) Ranking of competitive overgrowth abilities of the seven commonest cheilostome species does not form a simple hierarchical sequence but instead forms competitive networks. Outcome of overgrowth interactions between colonies of the same two species was not always the same, and none of the cheilostome species won in all of its overgrowth interactions.

(3) Overgrowth interactions between encrusting cheilostomes are complex. Variations in outcome were significantly correlated with the encounter angle formed by the intersection of the growth direction vectors of interacting colonies. Colony surface condition in the immediate vicinity of overgrowth interaction was also a significant factor for interactions involving the commonest species.

(4) Redirection of growth of a pre-existing growing edge, formation of a new growing edge, and formation of specialized barriers to overgrowth are three growth responses of encrusting cheilostomes that also affect the outcome of overgrowth interactions.

(5) Similar complexity in overgrowth interactions appears to exist between all other major groups of sessile colonial animals and sponges. Under such conditions no species is likely to win all of its competitive interactions and rankings of species’ competitive abilities will rarely, if ever, form simple hierarchical sequences.

INTRODUCTION

Competition between sessile marine organisms living on hard substrata commonly involves overgrowth of part or all of one organism by another (Bryan 1973; Buss 1979; Buss & Jackson 1979; Gordon 1972; Jackson 1977a, 1977b, 1979; Jackson & Buss 1975; Karlson 1978; Osman 1977; Stebbing 1973a, 1973b; Sutherland & Karlson 1977). Overgrowth usually results in the death of the underlying organism, although this is not always the case, especially among sponges (Rützler 1970; Sarà 1970) and large solitary animals (Jackson 1977a; Vance 1978). Overgrowths occur very frequently in encrusting ('fouling') communities, especially when predation and disturbance processes (sensu Dayton 1971) are rare (Buss & Jackson 1979; Jackson 1977b; Karlson 1978; Osman 1977; Stebbing 1973a). In such situations overgrowth ability is an important determinant of the distribution and abundance of different encrusting species.

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Investigation of overgrowth, like other forms of competition, has proceeded with varying success on three different levels. First is the simple demonstration that overgrowth occurs and determination of the frequency and outcome of its occurrence. This is comparable to demonstration of a depression in growth rate or survivorship in experiments with single species and mixed species populations (e.g. Connell 1961; Harper 1977, Chapter 8). In each case we ascertain (by definition) that competition is occurring, but we can only speculate as to what underlying mechanisms might be responsible for the effects we observe. Most studies of competition are limited to this level of understanding (Harper 1977, Chapter 11).

The second level of investigation in the study of competition is the determination of the range of conditions under which competition is more or less likely to occur. For overgrowth this involves observation of the spatial relationships between organisms (i.e. their distribution and orientation on the substratum) as well as prevailing food levels, sea water conditions, etc. Again, such documentation is not a demonstration of mechanism, but it can provide a good indication of what kinds of mechanisms are most likely to be involved.

The third level of investigation is the demonstration of mechanisms actually responsible for the competition effects observed. For overgrowth this must involve demonstration of the factors underlying the ability of one organism to elevate its growing margin up over that of another and to proceed to further overgrow the underlying organism. This must involve differences in growth rates of the two organisms in the region of overgrowth and/or differences in the abilities of the two organisms to manipulate (reposition) their growing margins. We know almost nothing about mechanisms of overgrowth except those involving obvious interference interactions such as digestive dominance and immune responses in scleractinian corals (Hildemann et al. 1977; Lang 1973; Potts 1976).

In this paper I present data on aspects of overgrowth competition between colonies of encrusting cheilostome ectoprocts (bryozoans) living in a Jamaican cryptic reef environment. I first describe some aspects of cheilostome biology essential for understanding overgrowth interactions between these organisms. Next I document the frequency of overgrowth interactions between cheilostome colonies, the predictability of outcome of overgrowth interactions between different pairs of cheilostome species, and the ranking of overgrowth abilities of the more common cheilostome species in the system. Ranking of species’ overgrowth abilities is of some general interest as much current theory of marine benthic community structure is based on the largely untested assumption that such rankings form simple hierarchical (transitive) sequences (Connell 1975, 1976, 1978; Dayton 1971; Paine 1966, 1974; Porter 1972, 1974). I then examine the importance of spatial relationships to the outcome of overgrowth interactions in relation to directions of growth of cheilostome colonies and fouling of cheilostome colony surfaces. Finally I describe two growth mechanisms, frontal budding and elevation of colony margins, which appear to affect the outcome of overgrowth interactions between cheilostomes. The results underline the striking complexity of competitive processes characteristic of the highly diverse cryptic reef community.

**HOW CHEILOSTOMES GROW AND ENCOUNTER EACH OTHER**

Colonies of cheilostomes consist of one or more kinds of physically connected, asexually replicated morphological units (zooids) which individually perform such functions as feeding, reproduction, and support. In encrusting species growth along the substratum
FIG. 1. Common zooid budding pattern in sheet-like encrusting cheilostomes. The growing edge (g.e.), ——, is everywhere coincident with the colony margin along the substratum. The primary zooid or ancestrula (a.) is derived from the metamorphosed larva. Shaded zooids represent a single lineal series.

takes place by intussusceptive budding of new zooids at the colony margin (growing edge) (Banta 1969; Boardman & Cheetham 1973; Silén 1944). Budding commonly results in production of lineal series of zooids beginning proximally (at the point of larval settlement and the origin of the colony) and extending distally to the growing edge (Fig. 1). The orientation of any lineal series is normally at right angles to the tangent of the growing edge. Zooid outlines are also usually elongated in a proximal-distal direction. These two features, orientation of lineal series and zooid elongation, clearly record the direction of growth at any point along the colony margin.

An ontogenetic gradient of zooid morphological development exists along the proximal-distal (older-younger) axis of encrusting, sheet-like cheilostome colonies (Boardman & Cheetham 1973). New zooids superficially appear little more than empty boxes. Older zooids show increasing development of zooid organs, structure of the frontal wall, avicularia, and sexual reproductive structures (ovicells) until a broad zone of similarly mature zooids is reached. Associated with this pattern there may also be zonation of zooid function along the proximal-distal axis. For example, distal zooids may feed more vigorously than more proximal zooids, whereas sexual reproduction as evidenced by the presence of embryos may be limited to somewhat older portions of colonies.

Many sheet-like encrusting cheilostomes grow in all directions along the substratum to form, at least initially, roughly equidimensional colonies. Unless disturbed, the growing edge of such a colony is coincident with its entire margin. Other species produce fan- or ribbon-like encrustations characterized by growth out from limited portions of the colony margin. In either case, the original growth form may be altered by the presence of obstructions and by various disturbance processes. Physical barriers and/or the presence of other sessile organisms may cause local cessation or redirection of growth (Lutaud 1961; Stebbing 1973a). Growth may then begin at any previously inactive point along the colony margin. Predators or physical disturbances (abrasion, sedimentation, etc.) may kill portions of a colony and thereby create new colony margins (Gordon 1972;
Jackson 1977a, 1979). This often results in growth in new directions outwards from the newly formed colony margin. All such responses presumably involve some physiological reorientation of the colony which is reflected in a lag in initiation of new growth (Lutaud 1961).

Contact between cheilostome colonies may occur in two different ways: (i) growing edge to growing edge or (ii) growing edge to non-growing edge. In the first case contact can result from growth by one or both of the colonies involved. If overgrowth occurs, the outcome will depend upon the morphological features, growth characteristics, and other attributes of the species involved. Growing edge to growing edge encounters should be most common among more or less equidimensional colonies.

In the second case contact results from growth of one colony against the non-growing margin of another. If overgrowth occurs, the outcome will depend not only on features enumerated above but also on the ability of the non-growing colony to start growing and/or throw up a ‘defence’ in the encounter zone. Such responses take time. Thus the colony which initiates the interaction (has its growing edge there first) may gain a decided initial advantage. Growing edge to non-growing edge encounters should be most frequent between fan-like, runner-like, or irregularly-shaped encrustations. The growth forms, original growth directions, and past histories of disturbances (predation, physical events, previous overgrowth, etc.) are all factors which affect the irregularity of the colony margin (Jackson 1979).

FREQUENCY AND OUTCOME OF OVERGROWTHS

Methods

One of the most common cryptic habitats on Caribbean reefs is the skeletal undersurface of foliaceous corals like *Agaricia*, *Montastrea*, and *Porites* (Hartman & Goreau 1970; Jackson, Goreau & Hartman 1971). The undersurfaces of these corals support a highly diverse encrusting biota of sponges, ectoprocts, ascidians, algae, etc. Nine foliaceous corals (National Museum of Natural History catalogue numbers USNM 256770-256778) were collected in July 1977 from depths of -11 to -20 m on a vertical reef face just west of Rio Bueno Harbour, Jamaica. Corals were chosen for collection on the basis of obvious abundance of cheilostomes on their undersurfaces in order to maximize the number of cheilostome-cheilostome encounters observed. The corals were maintained in running seawater for microscopic inspection of overgrowths and census of the cryptic community. The corals were then air dried without bleaching.

Census of the cryptic community was by point sampling which provided a rapid and reasonably accurate estimate of the percent cover of primary substratum (the coral undersurface) occupied by different organisms (Jackson 1977b; Sutherland & Karlson 1977). Random points were marked on a transparent acetate sheet which was lain on the coral undersurface. The organisms immediately underlying the points were recorded. The number of points per coral (forty to 100) varied with coral undersurface area (217 to 664 cm²). A total of 548 points were examined microscopically (10×) for all nine corals (total undersurface area 3830 cm²).

Compilation of the frequency and outcome of different cheilostome-cheilostome encounters was made from analysis of dried specimens because small colonies and contacts between colonies are easier to see when dried and not obscured by mucus and sediment. There was no difficulty in telling which portions of colonies were alive when
collected because drying preserves the frontal membranes and opercula of cheilostome zooids and these are present only in living zooids.

Observations of encounters were recorded only in cases where cheilostomes live at the time of collection were in physical contact. Observations were made along the entire length of each colony margin. Each coral underside was scanned under the microscope (10×) and all contacts between cheilostome colonies recorded. Overgrowth was defined as the elevation of the growing edge of one colony over the edge of another to the extent that it covers the orifices of zooids (Stebbing 1973a). It is assumed that once a colony has overgrown another this far, further overgrowth is possible via the same mechanism. This assumption is justifiable, because once a leading edge of a colony is covered by another it can grow no further in this area, while the overgrowing colony usually can continue to do so (Stebbing 1973a). Ties were defined as contacts in which growth had apparently stopped along the margin of contact so that neither colony overgrew the other. Fusion was defined as the merging of two contacting colony margins into a single colony.

An encounter was defined as any continuous line of contact between two colonies for which the outcome of the interaction was the same (i.e. one colony overgrowing the other, or tie interactions with no overgrowth) (Fig. 2(a),(b)). The line may be short (a few mm) or long (up to 5 or 10 cm), but so long as contact was continuous it was recorded as a single encounter. However, if the outcome of an interaction changed along the line of contact between two colonies, each outcome was recorded as a separate encounter (Fig. 2(c)). Discontinuous contacts between the same two colonies were also recorded as separate encounters (Fig. 2(d)).

It should be emphasized that all observations apply only to the situation at Rio Bueno at the time of collection, and thus present a static picture of overgrowth relationships at

![Fig. 2. Procedure for analysis of encounters between cheilostome colonies. Dashed lines represent previously overgrown colony margins; arrows point in direction of overgrowth. Stipple distinguishes colonies. (a) Single encounter, colony 1 overgrowing colony 2; (b) single tie encounter, neither colony overgrowing the other; (c) continuous line of contact recorded as two distinct encounters, one in which colony 1 is overgrowing colony 2, and another encounter in which the outcome is reversed; (d) two distinct lines of contact between the same two colonies recorded as two separate encounters with colony 1 overgrowing colony 2 in both cases.](image-url)
Overgrowth competition between ectoprocts

This is of little consequence to observations regarding conditions which influence overgrowth or mechanisms of overgrowth, but does limit generalization regarding rankings of overgrowth ability which might vary considerably with place or time of year.

Results

Results of the census are summarized in Table 1. Cheilostomes covered 49.9% of the total undersurface area. This is about three times the average cheilostome cover observed in an ongoing long term study of cheilostome population dynamics at these depths at Rio Bueno and simply reflects preferential collecting for cheilostomes. Four cheilostome species (Steginoporella sp. nov., Reptadeonella violacea, Stylopoma spongites, and Parasmittina sp.) comprised 96% of the cheilostome cover. Rank abundances of these four species in Table 1 are the same as observed in the long term study. Nine of the fifteen cheilostome species listed were detected in the census; the remaining six were observed only in detailed examination of colony encounters. Coralline algae and demosponges were the next most abundant organisms. There was only 2.2% unoccupied space.

The number of encounters between cheilostomes and their outcomes are presented in Table 1. Encounters involving overgrowth were overwhelmingly the most common occurrence. Ties were common only in intraspecific encounters. Fusion was observed only in encounters between different regions of the same colony. A total of 221 cheilostome-cheilostome encounters were recorded; 117 (234/2) interspecific encounters and 104 intraspecific encounters. This gives one cheilostome-cheilostome encounter for every 17 cm² of coral undersurface examined. Overgrowth was observed in 115 of the interspecific encounters and eighty-four of the intraspecific encounters. The Kendall rank-order correlation of percent cover of each cheilostome species and the number of encounters each species is involved in is \( r = +0.53 \) (\( P < 0.05 \)). Since the vast majority of encounters involve overgrowth, this correlation suggests that the more space a sessile cheilostome species occupies, the greater the number of overgrowth interactions it must endure.

Seven cheilostome species were involved in more than ten interspecific encounters. All are encrusting, predominantly sheet-like forms (see Jackson 1979 for discussion of the importance of growth form to interactions between sessile organisms inhabiting hard substrata). The contact matrix of the 114 pairwise overgrowth interactions involving these species is shown in Table 2. Values are percentages of interactions in which A over-

### Table 2

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Values in parentheses are intraspecific encounters.
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<td>*Steginoporella magnilabris (Busk)</td>
<td>21.4</td>
<td>60</td>
<td>68</td>
<td>128</td>
<td>35</td>
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<td>*Reptadeonella violacea (Johnson)</td>
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<td>62</td>
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<td>90</td>
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* Species involved in more than ten interspecific encounters.
The number of interactions between species pairs ranged from zero to twenty-three; these are indicated in parentheses.

The same seven species are ranked in Fig. 3 in decreasing order of their wins/losses (W/L) ratios. For any cheilostome species x this ratio is defined as the number of interactions in which species x overgrew all other cheilostome species divided by the number of interactions in which the other cheilostomes overgrew species x. Overall differences in the numbers of wins and losses for these seven species are highly significant (2 x 7 contingency table; $P < 0.001$). Although not enough overgrowths were observed to detect significant W/L differences between all pairs (if indeed they exist), the species are readily separated into three broad categories of competitive overgrowth ability. First are the clear overgrowth dominants *Parasmittina* sp., *Stylopoma spongites*, and *Steginoporella* sp. nov. Each of these is an abundant space occupier (>5% coral undersurface) and all have W/L ratios greater than 1. *Reptadeonella violacea* comprises the second group. Like the above species it is an abundant space occupier with a W/L ratio just above 1. However, *R. violacea* does poorly in overgrowth interactions with the overgrowth dominants (W/L = 0.4) as compared to its performance against lower ranked species (W/L = 3.5). This difference is highly significant (2 x 2 contingency table; $P < 0.001$). Third are the clearly inferior overgrowth competitors *Microporella* sp., *Smittipora levinseni*, and *Cribilina radiata*. These species occupy little space (≤0.5% coral undersurface area) and have W/L ratios well below 1.

All the abundant space occupiers (*Steginoporella* sp. nov., *R. violacea*, *S. spongites*, and *Parasmittina* sp.) have W/L ratios greater than 1. For the fourteen cheilostome species observed in overgrowth interactions, the Kendall rank-order correlation of percent cover and W/L ratios is $\tau = +0.55$ ($P < 0.05$). This suggests that overgrowth ability in cheilostome-cheilostome encounters may have been an important determinant of the relative abundance of the different cheilostome species under these corals.

![Diagram of overgrowth interactions](image)

Fig. 3. Ranking of seven cheilostome species by ratios of wins to losses (W/L) in interspecific cheilostome-cheilostome overgrowth interactions. Wins/losses values given in parentheses. Upward pointing arrows indicate reversals, i.e. interactions in which lower-ranked species (those level with bases of arrows) were observed to have overgrown higher-ranked species (those level with arrow points). The frequency of reversals is indicated by fractions (e.g. 2/4 represents two reversals out of four overgrowth interactions).
None of the seven species in Fig. 3 won in all of its overgrowth interactions. Of the ninety-four pairwise overgrowth interactions between these species there were twenty-five reversals, i.e. cases in which a lower-ranked species was observed to have overgrown a higher-ranked species. Even the highest ranked species were occasionally overgrown. Thus rankings of overgrowth ability of cheilostome species do not form simple hierarchical sequences in this situation.

Another feature evident in Table 2 and Fig. 3 is that the outcome of overgrowth interaction between colonies of the same two species was not always the same. For example, interactions between Steginoporella sp. nov. and R. violacea resulted in fourteen wins for the former and nine wins for the latter species. Often this variation was evident in interactions between different regions of the same two colonies as in the situation illustrated in Fig. 2(c). Variations in outcome also occurred between species pairs including a cheilostome and a species of some other group such as sponges or corals. Data presented in the next section indicate that these variations in outcome in overgrowth interactions are frequently related to two factors: (i) orientation (growth directions) and associated encounter angles between cheilostome colonies and their overgrowth competitors, and (ii) the condition of the cheilostome colony surface in the region of overgrowth.

SPATIAL RELATIONSHIPS BETWEEN COLONIES IN OVERGROWTH INTERACTIONS

Spatial relationships between encrusting cheilostomes include the distribution and orientation of colonies on the substratum surface and the budding patterns of zooids within colonies. In this section I examine two aspects of spatial relationships which appear to influence strongly the outcome of overgrowth interactions between these organisms.

Importance of encounter angles in overgrowth interactions

Previously established spatial relationships largely determine whether contact between colonies results from growth by one or both colonies involved (i.e. growing edge to growing edge or growing edge to non-growing edge encounters). To examine the outcome of these two types of interactions I determined the encounter angle for each of the 115 interspecific cheilostome-cheilostome encounters recorded in Table 1 which involved overgrowth. The encounter angle is defined as the angle between the directions of growth of the overgrown colony and the overgrowing colony. In head-on encounters, for example, growth directions are opposite and the encounter angle is about 180°. When one colony overgrows another from behind their growth directions are similar and the encounter angle is about 0°. In this way three broad categories of overgrowth interactions were defined (Fig. 4): frontal overgrowths (encounter angle 121-180°), flank overgrowths (encounter angle 61-120°), and rear overgrowths (encounter angle 0-60°). Frontal overgrowths involve growing edge to growing edge encounters. Flank overgrowths and rear overgrowths involve growing edge to non-growing edge encounters.

Encounter angles were measured microscopically (10 x) by rotation of the microscope eyepiece containing a crosshair reticle and reading the degrees of rotation from an external scale marked at 10° intervals. Encounter angles were measured at approximately 1 cm intervals along the entire common line of encounter between any two colonies for which the outcome of overgrowth was the same.

The frequency of overgrowths at different encounter angles for the seven cheilostome species involved in more than ten interactions is given in Fig. 5. Often the encounter
Overgrowth competition between ectoprocts

angle changed considerably along the encounter line between two colonies. Thus, for example, a single overgrowth interaction may involve both frontal and flank overgrowth along the same encounter line. For this reason the number of rear, flank, and frontal overgrowth interactions for any species in Fig. 5 may add to more than the total number of overgrowths recorded for that species. Of the 115 interspecific pairwise overgrowth interactions observed, eighty-two (70%) involved frontal overgrowth, sixty-six (56%)
involved flank overgrowth, and twenty-seven (23%) involved rear overgrowth. Although frontal overgrowth interactions were the most frequent, overgrowth at other angles was also common, and thus may be responsible for some of the observed variations in outcome of pairwise overgrowth interactions.

The outcomes of overgrowth at different encounter angles are given in Table 3. Comparison of overgrowth W/L ratios for frontal encounters versus total encounters shows that Parasmittina sp. and Steginoporella sp. nov. fared somewhat better in head-on interactions whereas the remaining five species fared somewhat worse. These differences suggest an encounter angle effect.

Consider Reptadeonella violacea and Steginoporella sp. nov., the two species involved in the most overgrowth interactions. Their W/L ratios for all overgrowth interactions are similar (1.1 v. 1.4) but their W/L ratios in frontal interactions are significantly different (0.8 v. 2.7) (2 × 2 contingency table; P = 0.01). Steginoporella sp. nov. overgrew other species most often in frontal interactions; it was overgrown more often in interactions along its flanks than in frontal interactions. Reptadeonella violacea overgrew other species equally often in frontal and flank interactions; it was most often overgrown in frontal interactions.

Pairwise overgrowth interactions between Steginoporella sp. nov. and R. violacea also show a significant encounter angle effect (2 × 2 contingency table; P = 0.02). Steginoporella sp. nov. overgrew R. violacea eleven times in frontal interactions while

<table>
<thead>
<tr>
<th>Species</th>
<th>Percentage overgrowth interactions</th>
<th>Total overgrowth interactions</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Rear</td>
<td>Flank</td>
</tr>
<tr>
<td>------------------</td>
<td>------</td>
<td>-------</td>
</tr>
<tr>
<td>Parasmittina</td>
<td>won</td>
<td>0(0)</td>
</tr>
<tr>
<td></td>
<td>lost</td>
<td>67(2)</td>
</tr>
<tr>
<td>W/L</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stylopoma</td>
<td>won</td>
<td>31(4)</td>
</tr>
<tr>
<td></td>
<td>lost</td>
<td>40(2)</td>
</tr>
<tr>
<td>W/L</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Steginoporella</td>
<td>won</td>
<td>29(10)</td>
</tr>
<tr>
<td></td>
<td>lost</td>
<td>24(6)</td>
</tr>
<tr>
<td>W/L</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reptadeonella</td>
<td>won</td>
<td>19(6)</td>
</tr>
<tr>
<td></td>
<td>lost</td>
<td>10(3)</td>
</tr>
<tr>
<td>W/L</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Microporella</td>
<td>won</td>
<td>60(3)</td>
</tr>
<tr>
<td></td>
<td>lost</td>
<td>13(1)</td>
</tr>
<tr>
<td>W/L</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Smittipora</td>
<td>won</td>
<td>40(2)</td>
</tr>
<tr>
<td></td>
<td>lost</td>
<td>14(2)</td>
</tr>
<tr>
<td>W/L</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cribrilaria</td>
<td>won</td>
<td>67(2)</td>
</tr>
<tr>
<td></td>
<td>lost</td>
<td>33(6)</td>
</tr>
<tr>
<td>W/L</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Because any overgrowth interaction often involves more than one encounter angle, the numbers of rear, flank, and frontal overgrowth interactions for each species adds to more than the total number of overgrowth interactions scored for that species.
Overgrowth competition between ectoprocts

PLATE 1. Encounters at different angles between Steginoporella sp. nov., Reptadeonella violacea, and Stylopoma spongites. (a) Stylopoma spongites (Styl.) overgrowing fouled Steginoporella sp. nov. (fld. Steg.) from the rear and overgrowing R. violacea (Rept.) from the flank; R. violacea overgrowing fouled Steginoporella sp. nov. from the flank. (b) Unfouled Steginoporella sp. nov. (unfld. Steg.) overgrowing fouled Steginoporella sp. nov. and R. violacea in frontal overgrowth interactions; R. violacea overgrowing fouled Steginoporella sp. nov. from the flank. The unfouled and fouled Steginoporella sp. nov. are not parts of the same colony in this case.

the reverse outcome occurred only once. The two species did equally well in flank and rear overgrowth interactions (ten overgrowths for Steginoporella sp. nov. v. nine for R. violacea).
Comparison of the numbers of wins and losses in frontal overgrowth interactions for the other abundant space occupiers reveals significant differences between only *R. violacea* and *Parasmittina* sp. (2 × 2 contingency table; $P = 0.001$). Other differences probably exist (e.g., between *R. violacea* and *S. spongites*) but there are not enough data. Examples of overgrowth interactions involving *S. spongites*, *Steginoporella* sp. nov., and *R. violacea* at different encounter angles are shown in Plates 1 and 2.
The same kinds of encounter angle relationships were frequently observed, but not quantified, for interactions between Steginoporella sp. nov. and the corals Tubastrea aurea and Madracis decactis, the foraminiferan Gypsina sp., several sponges (including ?Tenaciella sp. and ?Toxemna sp.), and crustose algae. Steginoporella sp. nov. won most of its frontal overgrowth interactions but usually lost in interactions along its flanks or rear with these organisms.

**Importance of colony surface condition in overgrowth interactions**

Of particular interest here are interspecific differences in the condition of the older zooids in cheilostome colonies. Colonies of some species show proximal zones of apparent zooid deterioration or death while similar-sized colonies of other species do not. Zooid deterioration is particularly pronounced in Steginoporella sp. nov. (Plates 1 and 2). Deterioration increases towards more proximal (older) colony regions (S. R. Palumbi and J. B. C. Jackson unpublished data). Comparatively young zooids near the growing edge are bright brick red in colour and unfouled by epizoans. More proximal zooids are dull reddish brown to brown in colour and are often heavily fouled by serpulids, algae, and other organisms. Lophophores are extended less frequently for feeding, and there is a marked increase in the numbers of empty, apparently dead zooids. Zooid deterioration is sometimes evident less than 1 cm from the growing edge but more commonly begins 3 to 10 cm behind it. It is not known whether zooid deterioration is intrinsic (senescence), environmentally induced, or both intrinsic and extrinsic in origin. However, the variable width of the zone of brightly coloured, unfouled zooids at any one time of year strongly suggests some kind of external control. Zooid deterioration was not apparent among any of the other common cheilostome species studied.

Fouled, inactive zooids should be particularly susceptible to overgrowth by other organisms. To evaluate this hypothesis, all overgrowth interactions involving Steginoporella sp. nov. were examined to determine the condition of Steginoporella zooids (unfouled or fouled) along the encounter line between colonies. Results are summarized in Table 4. The number of overgrowth interactions involving fouled colony regions (twenty-two) is roughly half that involving unfouled regions (thirty-nine). Unfouled regions of Steginoporella sp. nov. overgrew other species thirty-four times and were

<table>
<thead>
<tr>
<th>Colony surface condition</th>
<th>Rear</th>
<th>Flank</th>
<th>Frontal</th>
<th>Total overgrowth interactions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unfouled</td>
<td>26(9)</td>
<td>59(20)</td>
<td>76(26)</td>
<td>34</td>
</tr>
<tr>
<td>lost</td>
<td>20(1)</td>
<td>80(4)</td>
<td>20(1)</td>
<td>5</td>
</tr>
<tr>
<td>W/L</td>
<td></td>
<td></td>
<td>26</td>
<td>6-8</td>
</tr>
<tr>
<td>Fouled</td>
<td>50(1)</td>
<td>50(1)</td>
<td>100(2)</td>
<td>2</td>
</tr>
<tr>
<td>won</td>
<td>25(5)</td>
<td>55(11)</td>
<td>45(9)</td>
<td>20</td>
</tr>
<tr>
<td>lost</td>
<td></td>
<td></td>
<td>0-2</td>
<td>0-1</td>
</tr>
</tbody>
</table>

Because any overgrowth interaction may involve more than one encounter angle, the numbers of rear, flank, and frontal overgrowth interactions for each surface condition add to more than the total number of overgrowth interactions scored for that condition.
overgrown five times. Fouled regions of *Steginoporella* sp. nov. colonies overgrew other species twice and were overgrown twenty times. This difference is highly significant ($2 \times 2$ contingency table; $P < 0.001$). For example, unfouled *Steginoporella* sp. nov. won fourteen of their eighteen overgrowth interactions with *R. violacea* ($W/L = 3.5$) whereas fouled *Steginoporella* lost all five of their encounters with this species. The $W/L$ ratio for unfouled *Steginoporella* sp. nov. over *S. spongites* is 4, but for fouled *Steginoporella* is only 0.4. The overall $W/L$ ratio for unfouled *Steginoporella* sp. nov. is 6.8, a value higher than that observed for any other species; for fouled *Steginoporella* sp. nov. it is only 0.1. The same situation is even more dramatically evident in intraspecific overgrowth interactions. Of forty-nine interactions involving unfouled versus fouled colony regions (both intercolony and intracolony interactions) the unfouled colonies or colony regions won every interaction.

**GROWTH RESPONSES TO ENCOUNTERS THAT ALTER SPATIAL RELATIONSHIPS**

The encounter angle between two colonies and their surface conditions are largely determined by events previous to their meeting. Afterwards there are a number of potential growth responses which may be initiated by different cheilostome species. These responses decrease the probability of being overgrown and/or increase the probability of overgrowing another species. As such they are growth mechanisms which change the spatial relationships between colonies to new advantage. Three such growth mechanisms are known so far: redirection of a pre-existing growing edge, formation of a new growing edge, and formation of specialized barriers to overgrowth.

Redirection of a pre-existing growing edge usually involves the raising of the basal wall of the growing edge away from the substratum so that new zooids project outwards into the water rather than along the substratum surface (Jackson & Buss 1975; Stebbing 1973b). In this way the colony may create a barrier to overgrowth and/or may begin to grow up and over its neighbour. Vertical redirection of the growing edge has been previously reported for the cheilostomes *Steginoporella* sp. nov. (called *Steganoporella magnilabris* in Jackson & Buss 1975) and *Stylopoma spongites* and the cyclostome ectoproct *Disporella hispida* (Jackson & Buss 1975; Stebbing 1973b). In the present study, colonies of *Steginoporella* sp. nov., *S. spongites*, and *Parasmittina* sp. were frequently observed with raised growing edges where they were in contact with other sessile organisms.

One common way in which cheilostomes may form a new zone of growth is by frontal budding. Frontal buds may emanate from hypostegal coeloms as in *S. spongites* or as outpocketings of uncalcified parts of frontal walls (Cheetham & Cook 1979). Frontally budded zooids may in turn laterally bud new zooids out over the pre-existing colony surface. The frontal zooid walls of an encrusting, sheet-like cheilostome comprise the outer, exposed colony surface which lies parallel to the substratum. Thus frontal budding results in the elevation of the colony surface by one or more zooid layers further above the surface of the substratum (Jackson & Buss 1975). In this way the cheilostome colony may create a barrier to overgrowth and/or gain the position necessary to grow out over a neighbouring colony, regardless of the original growth directions and encounter angle of the colonies involved. In the present study frontal budding was characteristic of *S. spongites* and *Parasmittina* sp. I have observed colonies of these species more than 1 cm thick; such colonies consist of twenty or more layers of frontally budded zooids.
Formation of specialized barriers to overgrowth includes the production of greatly elongated frontal spines as in *Electra pilosa* (Stebbing 1973a,b) and frontal or terminal stolons (= kenozooids) as in seven species of New Zealand cheilostomes (Gordon 1972). Both types of structures reportedly act to stop or slow down overgrowth by other cheilostomes. None of the species studied in this paper were observed to produce such structures in zones of overgrowth.

In addition to growth responses, behavioural responses (feeding interference, allelopathy) and environmental factors (microtopography, food availability, sedimentation) must also have a profound effect on the outcome of overgrowth interactions, but we have almost no data on their importance.

**DISCUSSION AND CONCLUSIONS**

Data presented above demonstrate that spatial relationships are important determinants of the outcome of overgrowth interactions between encrusting cheilostomes. The existence of comparable growth patterns and functional patterns within other colonial animal groups such as ascidians and many cnidarians (reviewed in Jackson 1979) suggests that spatial relationships may also be important in overgrowth interactions between these organisms.

It is interesting to consider the four most abundant cheilostome species listed in Table 1 in terms of the importance of different factors to their success in overgrowth interactions. All four species have W/L ratios greater than 1 but they appear to achieve their success in quite different ways (Table 5). *Steginoporella* sp. nov. is the most abundant cheilostome species under corals at Rio Bueno, and is among the commonest cheilostomes in many other Caribbean habitats. Much of *Steginoporella*'s success can be attributed to the very high W/L ratio (6-8) of unfouled colony regions. Another important feature is this species' ability to elevate actively growing portions of the colony margin away from the substratum. Such growth isolates much of the colony from overgrowth interactions along the substratum surface and favours survival against otherwise superior overgrowth competitors such as many demosponges (Jackson 1979; Jackson & Buss 1975). Of related importance is the ability of *Steginoporella* sp. nov., like other species in this genus, to grow in a variety of strikingly different growth forms (Cook 1964; J. B. C. Jackson unpublished data).

Zooid deterioration seems to be *Steginoporella*'s biggest problem in maintaining space, not only in terms of increased susceptibility to overgrowth by previously settled organisms, but also to fouling by larvae of superior overgrowth competitors which may eventually overgrow the *Steginoporella* colony (Jackson 1979; Jackson & Palumbi 1979).

<table>
<thead>
<tr>
<th>Species</th>
<th>W/L</th>
<th>Capacity for frontal budding</th>
<th>Ability to reorient growing edge</th>
<th>Resistance to fouling of colony surface</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Parasmittina</em></td>
<td>5.0</td>
<td>+ +</td>
<td>+</td>
<td>+ +</td>
</tr>
<tr>
<td><em>Stylopoma</em></td>
<td>2.6</td>
<td>+ +</td>
<td>+</td>
<td>+ +</td>
</tr>
<tr>
<td><em>Steginoporella</em></td>
<td>1.4</td>
<td>—</td>
<td>+</td>
<td>—</td>
</tr>
<tr>
<td><em>Reptadeonella</em></td>
<td>1.1</td>
<td>± ?</td>
<td>—</td>
<td>+</td>
</tr>
</tbody>
</table>

Table 5. Summary of factors related to the outcome of overgrowth interactions for the four commonest cheilostome species listed in Table 1.
Steginoporella sp. nov. is the only abundant anascan cheilostome found under corals at Rio Bueno, and as such lacks a calcified frontal wall (Ryland 1970). It is also incapable of frontal budding. Instead this species commonly grows in curving, fan-like encrustations. In this way colonies often grow back over themselves, thereby covering older, fouled zooids with younger, unfouled zooids and also raising the colony surface one zooid layer away from the substratum surface. This process is not as effective as frontal budding, however, and I have never seen a coral undersurface entirely overgrown by Steginoporella sp. nov. Highly directional growth and the importance of colony surface condition make spatial relationships extremely important to the outcome of overgrowth interactions involving this species.

Like Steginoporella sp. nov., Parasmittina sp. and Stylopoma spongites exhibit considerable reorientation of their colony margins and growth directions in regions of overgrowth interactions. Nevertheless, they are more restricted to a primarily encrusting habit than is Steginoporella sp. nov. Parasmittina sp. and S. spongites are capable of extensive frontal budding. Their colony surfaces are virtually always unfouled and colony size often relatively large. Occasionally coral undersurfaces are entirely covered by one or the other of these two species. Thus, where they occur, S. spongites and Parasmittina sp. are highly successful. Their lower abundance compared with Steginoporella sp. nov. and Reptadeonella violacea can hardly be attributed to overgrowth abilities and must reflect some other factors. This is especially clear for R. violacea which is the poorest overgrowth competitor of the four commonest species. This species does not show extensive frontal budding and apparently has little ability to reorient its colony margins or growth direction in regions of overgrowth interactions.

The reversible outcome of pairwise overgrowth interactions involving the same two cheilostome species is readily explained by the variety of factors which affect the outcome of these interactions. The same is probably true for demosponges, scleractinian corals, or any other colonial animals which may varyingly employ aggression (Lang 1970, 1973), immune responses (Curtis 1979; Hildemann et al. 1977; Potts 1976), shading or 'over-topping' (Connell 1973; Lang 1970, 1973; Glynn 1976; Porter 1974, 1976; Shinn 1972), and complex excavations and multilayered overgrowths (Goreau & Hartman 1963; MacGeachy & Stearn 1976; Rützler 1970; Sarà 1970), as well as simple overgrowth. Under such circumstances it is extremely unlikely that the outcome of any two-species interaction involving sessile colonial animals will always be the same (e.g. Osman 1977, Table 2). Thus, as predicted previously (Gilpin 1975; Jackson & Buss 1975), no species is likely to win all of its competitive interactions and rankings of species' competitive abilities will rarely, if ever, form simple hierarchical sequences.

ACKNOWLEDGMENTS

T. P. Hughes and E. M. Sides helped collect the corals. A. H. Cheetham, P. L. Cook, and J. E. Winston helped in the identification of the ectoprocts. Analyses of overgrowths and species identifications were performed at the Division of Paleobiology, Smithsonian Institution. L. W. Buss, A. H. Cheetham, R. H. Karlson, T. McClellan, S. R. Palumbi, C. J. Slocum, C. M. Wahle, J. E. Winston, S. A. Woodin, and two reviewers criticized the manuscript and provided many helpful suggestions. S. R. Karlson and J. E. Winston skillfully prepared the figures and plates. This work was supported by NSF Grant OCE 76-23364. To all I am grateful.
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(Received 26 September 1978)