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Inducible aggression and intraspecific competition for space in a marine bryozoan, *Membranipora membranacea*

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Abstract

We experimentally investigated the causes and consequences of stolon production in the marine bryozoan *Membranipora membranacea*. Inducible stolons appear to mediate contests for space among conspecifics by slowing the growth of adjacent competitors. However, because stolons are produced in some but not all competitive interactions, we examined whether environmental factors such as food and hydrodynamic regime regulate their production. Furthermore, because stolons are ephemeral, persisting for only 24 h, we removed stolons to determine whether stolon production affected the outcome of competitive contests. Removing stolons from large colonies reduced their ability to surround a small neighbor, but increased their growth rate. Control colonies, producing their full complement of stolons, grew more slowly than colonies with stolons removed, suggesting that there is a tradeoff between stolon production and growth. The rate of stolon production was higher in colonies grown under lower food conditions. The likelihood that waterborne chemical or hydrodynamic cues induce stolon formation is diminished by our finding that the frequency of stolon production was unaffected by the relative positions of two interacting colonies in unidirectional flow.

In benthic and pelagic aquatic ecosystems, invertebrates such as cladocerans, rotifers, bryozoans, hydrozoans, and corals show dramatic and induced morphological changes in response to biotic cues from either predators or competitors. These inducible, rapid, and often major shifts in morphology are frequently cited as adaptive responses to changing and unpredictable biotic environments (Adler and Harvell 1990; Dodson 1989; Harvell 1990). The best-studied inducible morphologies are the predator-induced defenses of clonal and colonial animals. These include the spines and helmets of Cladocera (Havel 1987; Dodson 1989) and the spines of rotifers (Gilbert 1966) and bryozoans (Harvell 1984). Morphological changes also can be induced by aggressive competitive interactions of clonal and colonial marine invertebrates. These interactions induce structures used to mediate contests for space. Inducible structures used for interspecific competition include nematocyst-filled sweeper tentacles (corals), catch tentacles (anemones) and stolons (hydrozoans) (reviewed by Lang and Chornesky 1990; Buss 1990), and stolons of bryozoans (Stebbing 1973; Osborne 1984). Intraspecific contests for space among clonal and colonial invertebrates also are common, and aggressive structures similar to those deployed

interspecifically can be found (Francis 1973; Buss 1990; Harvell and Padilla 1990).

The underlying rules of intraspecific competitive interactions may be revealed by studying the context dependence of induction. In some cases, such as in competitive contests between colonies of the hydrozoan *Hydractinia echinata*, the propensity to produce hyperplastic stolons is genetically based and is affected by the degree of relatedness between two colonies, as well as by the individual propensity of a colony to produce stolons (Buss 1990; Buss and Grosberg 1990; Yund 1991). The most extreme phenotypes with extensive, nematocyst-filled stolons are produced by colonies that have a genetic predisposition toward production of stolons (Buss and Grosberg 1990; Yund 1991). However, even colonies that do not normally produce stolons may retaliate with stolons when attacked first.

The marine bryozoan *Membranipora membranacea* is a tractable model system in which to examine aggressive intraspecific competition. *Membranipora* colonies are easily grown on artificial substrata such as Lucite and therefore can be readily manipulated and observed. *Membranipora* produces stolons only during intraspecific competitive interactions. Stolons slow the growth of competitors, sometimes allowing larger colonies to completely surround competitors, stopping their growth (Harvell and Padilla 1990). Additionally, stolon induction is context-dependent, providing an excellent experimental system for elucidating the underlying rules governing deployment of aggressive responses.

The rules determining production of stolons in *Membranipora* are quite different than the rules for hydrozoans. The large, circular, encrusting bryozoan colonies live in dense, monospecific assemblages on the blades of various species of laminarian kelps, where competition for

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space is intense during their 8-week summer growing season (Harvell et al. 1990). Interacting colonies on a single kelp blade are unlikely to be related (even distantly) because the larvae have a 4-week dispersal phase that spreads siblings and members of the same population widely (Strathmann 1974). Interactions among colonies range from potentially cooperative interactions among very small colonies ($<0.5 \text{ cm}^2$) mediated by shared electrical signals (Shapiro 1992) to aggressive interactions among larger colonies mediated by stolons. Harvell and Padilla (1990), in a census of two-colony competitive interactions, found that the frequency of stolon production was correlated with both absolute and relative colony size: large colonies produced more stolons than did small colonies, especially when the large colonies were in contact with smaller conspecifics. This size dependence suggests that *Membranipora* colonies modify responses based not only on their own size, but also on the size of a competitor. The mechanisms controlling size selectivity are unknown, but could involve diffusible chemical cues, such as CO_2 or other waste emissions from a competitor. If diffusible cues are used, one would predict a bias in the production of stolons on the downstream side of interacting colonies in unidirectional flow.

Alternatively, the size selectivity in *Membranipora* may be an artifact of other aspects of competition between unequal-size opponents. The most likely of these aspects is habituation, which has been described in other aggressive contests among sessile invertebrates such as clonal anemones and corals (Wellington 1980; Purcell and Kitting 1982; Brace and Santer 1991). If habituation of aggression occurred in *Membranipora*, large equal-size colonies would produce fewer stolons because they would have been in contact for a long time. In contrast, competitive interactions involving large and small colonies would almost always be relatively recent contacts and thus would not yet have habituated. To investigate this and other aspects of the competitive interactions between colonies, we followed the fate of individuals through time. We monitored the growth rate and the number of stolons produced by competing colonies of unequal size for ~ 25 d after their first contact.

Although stolons reduce growth rates of attacked colonies (Harvell and Padilla 1990), the effect stolons have on the final outcome of competitive interactions is unknown. Are the small colonies killed, are they surrounded more quickly, or is their fate unaffected by the stolons? Why are stolons preferentially produced against small colonies? What is the effect of removing stolons from competitive interactions? We used stolon removal experiments monitored over a substantial period of a colony's life to examine the consequences of stolon formation for colony growth rates and space acquisition. Because genetic identity is so important to the induction of stolons in hydrozoans (Buss and Grosberg 1990), we tested whether *Membranipora* colonies would produce stolons when contacting clonemates as well as nonclonemates. Finally, because stolons might be costly to produce, we tested whether the frequency of stolon production was affected by feeding rate.

Methods

Stolon production rates—We conducted experiments and observations to examine stolon production rates and the consequences of stolon production on colonies of *Membranipora* settled naturally onto black Lucite panels for ease of observation. We attached individual 15×15 -cm removable panels (settlement surface down) to PVC plastic racks suspended under breakwater floating docks at the Friday Harbor Laboratories (FHL) in Friday Harbor, Washington. Panels for observation and experimental treatments were haphazardly placed on three different racks. Thus, colonies on the panels were exposed to natural food abundance and water flow. Panels were individually numbered and had one corner clipped to ensure consistent orientation of the panel during observations. We placed racks with panels in the water in late May 1987 and 1988 to collect recently settled individual *Membranipora*. Colonies were thinned to densities such that each colony would come in contact with only one other colony as it grew, each colony would have all other free edges growing unobstructed, and each competitive interaction would involve unequal-size colonies. When colonies were censused, panels were removed from racks and either brought into the lab and maintained in flow-through sea tables or in large containers of seawater on the breakwater. The census included a brief daily or alternate day determination of the number of stolons produced and periodic videotape recording of the colony for area determinations.

Stolon removal experiment—We conducted experiments in which the stolons were removed to assess the consequences of stolons for two competing colonies. We randomly assigned panels to one of three different treatments in 1987: stolon removal, control for damage of stolon removal or sham, and unmanipulated control. The large colonies had an average initial area of 235.4 mm^2 ($\text{SE} = 4.8$), and the small colonies had an average area of 73.3 mm^2 ($\text{SE} = 1.7$). Two of these treatments, the stolon removal and the sham, were repeated in 1988. In 1988, a greater size asymmetry was engineered between the two interacting colonies than in 1987; in 1988 the area of large colonies averaged 910.0 mm^2 ($\text{SE} = 21.9$) and the area of small colonies averaged 34.7 mm^2 ($\text{SE} = 1.0$). We observed two colony competitive interactions from the date the colonies first contacted each other. Stolons were produced only at the edges of a colony immediately in contact with another colony. Thus, each colony had the potential to make stolons at either of the two sides of the region of contact.

The number of stolons made by each colony at each side of the interaction region was recorded daily in 1987 and usually on alternate days in 1988. In the stolon removal treatment, all stolons produced were punctured with a fine insect pin. Puncturing deflated the stolon and did not seem to affect other zooids in the colony. In the sham treatment one zooid near the edge of each side of the contact region in each colony was similarly punctured. The sham treatment controlled for the effects of damaging

zooids near the region of contact but did not affect the stolons themselves. The unmanipulated controls were observed in a similar fashion, but no zooids were punctured or damaged. We videotaped all colonies periodically (every 3–5 d) and measured areas of the colonies using a computerized video digitizing system (W. Haake of Pisces Software).

Feeding and stolon production—We conducted a laboratory experiment with field-collected *Membranipora* colonies to determine whether food levels affected rates of stolon production. We collected pairs of interacting colonies from kelp blades (*Laminaria groenlandica*) taken from the shallow subtidal region (–2 m) at Turn Island near FHL. Pieces of kelp with two touching *Membranipora* colonies were cut with a razor blade from the large kelp blades. We allowed the cut edges of the kelp to heal for 24 h in flowing seawater before the experiment began. Video recordings or tracings on clear plastic were made of the colonies so that areas of colonies could be determined with the video-digitizing system, and we recorded the locations and numbers of all stolons.

We attached the pieces of kelp (two per vessel) to Plexiglas paddles suspended into 4-liter glass vessels filled with filtered (to 1 μm) seawater. The paddles were suspended from a hanging rack attached to a small motor that gently oscillated the rack (Strathmann 1987). The paddles gently stirred the water, keeping the colonies exposed to continuous water motion. Twelve vessels were set in a flow-through sea table to maintain ambient water temperature; the water in each vessel was changed daily, as was the location of the vessel in the sea table. We ran two experiments for five consecutive days each. In both experiments, pairs of colonies were matched for size and haphazardly assigned to one of two treatments. The mean initial size of colonies in each treatment did not differ significantly (t -test, $P > 0.25$). In the first experiment, we added 20 ml of a rapidly growing culture of the unicellular green alga *Dunalliella turtox* to six of the vessels daily after the water change. No algae were added to the other six vessels. In the second experiment, we added 40 ml of *Dunalliella*. We recorded the numbers and locations of all stolons produced each day.

Flow direction and stolon induction—To determine whether cues for the production of stolons were influenced by water flow, either through chemical communication or through hydrodynamic differences in the local flow regime, we conducted an experiment with colonies attached to kelp and placed in a unidirectional flow in a flume. We collected pieces of *Laminaria* with two colony interactions from Turn Island and attached them with cyanoacrylate adhesive to large Plexiglas panels (45 \times 45 cm). The pieces of kelp ($\sim 5 \times 8$ cm) were attached so that their edges were completely adherent to the panel and were smooth; the kelp pieces were attached to the center of each panel to ensure uniform flow across the colonies. Twenty panels were placed in a rack with a 1-cm space between panels. When this rack was placed in a flume, uniform laminar flow was established across each panel.

Colonies were oriented in one of three ways: the smaller colony upstream; the larger colony upstream; the line of contact parallel to the direction of flow. With the line of contact parallel to the direction of flow, only the downstream side of the region of interaction would experience flow from across the colonies.

Self-nonsel self recognition—To determine whether genetic identity recognition was involved in the induction of stolons, we conducted experiments with *Membranipora* colonies on intact blades of *Laminaria*. Three entire blades of kelp were collected from the shallow subtidal of Turn Island and maintained by tying their holdfasts to nylon ropes hanging from the floating dock at FHL. In 1987, individual colonies were marked by a hole punch in the kelp, and all surrounding colonies were cleared from the blade surface without damaging the alga. Individual *Membranipora* colonies were then divided into two unequal portions by removing a swath of each colony about six zooids wide without damaging the kelp surface. The subcolonies were allowed to repair their wounds and create new growing edges. Observations were made once they had re-established contact (12–18 d) to determine whether stolons were induced upon recontact. In 1988, this experiment was repeated and an additional treatment was established. Two different unequal-size colonies—close but not yet touching—were damaged along their growing edge by the same method used in 1987. They were allowed to repair this damage and begin growing again, and were observed to determine whether stolons were made upon contact. This treatment was a control for the effects of colony damage on stolon production rates because the unrelated colonies should produce stolons once they re-established contact. All colonies were uniquely marked with combinations of three colored glass beads sewn to the kelp thallus.

Results

Stolon removal experiments—Individual colonies varied in their production of stolons; some colonies produced stolons virtually every day, whereas other colonies never produced stolons (Fig. 1). However, because colonies were observable for different numbers of days and the stolon production rate was not correlated with the number of observations (small and large pooled, $r^2 = 0.00$; large only, $r^2 = 0.03$; small only, $r^2 = 0.01$) or with the duration of the interaction ($r^2 = 0.00$; Fig. 3), we pooled data across individuals for comparison (Table 1). In all treatments, larger colonies made about twice as many stolons as did smaller colonies, and stolon production was affected by the manipulations (Table 1). In both size classes, stolons were produced most often in the unmanipulated controls and least often in the stolon removal treatment, and these differences were significant ($P < 0.05$; G -test). In addition, larger colonies produced multiple stolons more often (Table 1). Again, the trend among treatments was that the controls produced the most multiple stolons and the removal treatment the least (Table 1).

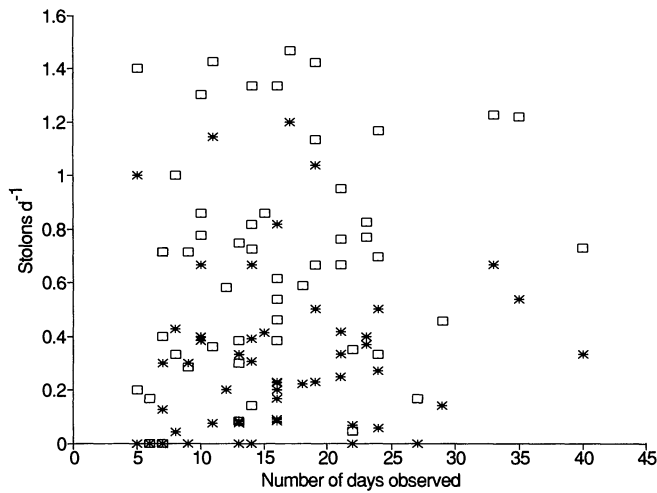


Fig. 1. Among-colony variability in stolon production in the bryozoan *Membranipora membranacea*. Some colonies produced stolons every day and others never produced any. Within small (avg initial area, 73.3 mm²; SE = 1.7) and large (avg initial area, 235.4 mm²; SE = 4.8) size classes, colonies differed in their propensity to produce stolons. Small colonies—*; large colonies—□. This pattern was not correlated with the number of days the colonies were observed. Plotted data are for 1987 only, when colonies were observed on a daily basis; data for 1988 produced the same results.

Stolons can be produced at either end of the region in contact with another colony. Stolon production on one side of the colony was not independent of stolon production on the other side. For each colony, we determined, by daily observations, the frequency at which stolons were made on both sides of the region of contact, on only one side, or not at all. These frequencies were then compared with the frequency one would expect from a binomial probability if stolons were produced independently on the two sides. The two locations of a colony responded more similarly (either both with stolons or both without stolons) than one would expect by chance

Table 1. Frequency of stolons produced in the stolon removal experiment. Frequency of stolons produced by small and large colonies (see Fig. 1 legend) in 1987, and the frequency of single and multiple stolons produced per colony side per day. Frequency was calculated as the number of stolons produced per total possible opportunities for stolon production (*N*). There are four opportunities per colony pair per day because each colony could make at least two stolons.

	Control		Sham		Removal	
	Large	Small	Large	Small	Large	Small
No stolons	0.33	0.63	0.43	0.73	0.71	0.84
Stolons	0.67	0.37	0.57	0.27	0.38	0.16
1 d ⁻¹	0.36	0.27	0.37	0.22	0.26	0.13
2 d ⁻¹	0.27	0.10	0.17	0.04	0.10	0.03
3 d ⁻¹	0.04	0.01	0.02	0.01	0.02	0.00
(<i>N</i>)	(165)	(165)	(294)	(294)	(322)	(322)

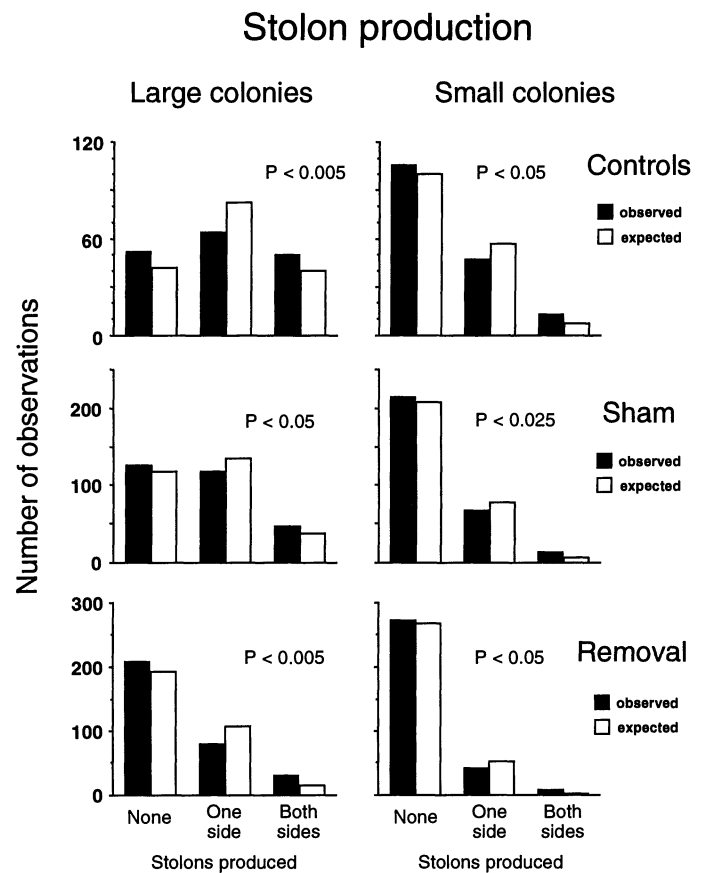


Fig. 2. The nonindependence of stolon production by two sides of a single colony. We determined the frequency of daily observations where individual colonies made stolons on both sides of the region of contact, on only one side, or not at all (observed). These frequencies were then compared with the frequency one would expect from a binomial probability if stolons were produced independently on the two sides (expected). The two locations in a colony responded more similarly (either both with stolons or both without stolons) than one would expect by chance in all treatments for both large and small colonies (*G*-test; *P* values are indicated in each panel).

(*G*-test, *P* < 0.05; Fig. 2). This result was consistent among all treatments for both large and small colonies.

Colony growth rates also differed among the treatments. *Membranipora* colonies have exponential growth measured by the increase in surface area of the colony over time. All growth rates in this study followed an exponential growth trajectory. Linear regressions of ln(colony area) vs. ln(time) had correlation coefficients (*r*²) ranging from 0.89 to 0.999. Therefore, we compared growth rates by comparing the growth exponent of each colony. Growth rates increased with stolon removal, and large colonies grew faster than small colonies (Fig. 3). An ANOVA of these growth data indicated a significant difference among treatments (*P* = 0.035, 2 df) and between large and small colonies (*P* = 0.020, 1 df), but no significant size × treatment interaction (*P* = 0.220, 2 df).

We examined the effects of stolon removal on the ability of larger colonies to completely surround smaller col-

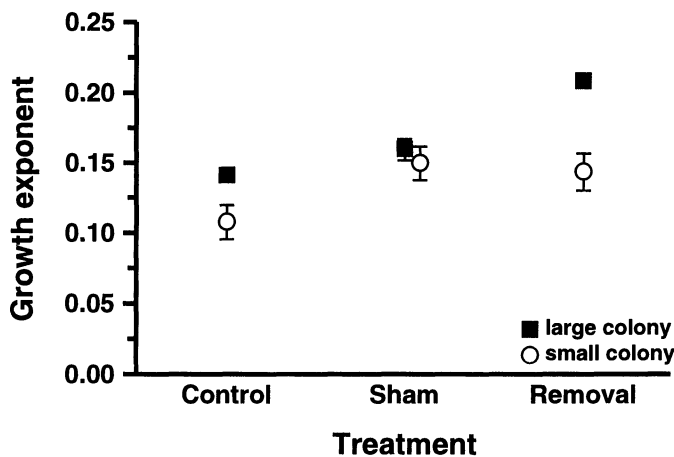


Fig. 3. Colony growth rates in the stolon removal experiment. Differences in growth rate were determined by comparing growth exponents because area increase in colonies over time followed a simple exponential increase: $N = N_0 \exp(rt)$, where N_0 = initial size, r = the rate of increase, and t = time. For both the small and large colonies (see Fig. 1 legend), growth rates increased with stolon removal. Means are plotted with standard error bars.

onies. In 1987, there were too few situations in which the smaller colonies were completely surrounded to compare among treatments. Because stolons were not removed every day in 1988, the stolon removal treatment actually represents a reduction in the number of stolons. In 1988, smaller colonies were completely surrounded in a shorter period of time in the sham treatment (avg, 20.2 d; SE = 3.2, $N = 17$) than in those interactions in the stolon removal treatment (avg, 28.7 d; SE = 3.1, $N = 15$) (t -test, $P < 0.05$).

Feeding and stolon production—At the low food ration (20 ml d⁻¹), the total number of stolons produced by individual colonies between the fed (avg, 14.1; SE = 1.7) and the starved treatments (avg, 16.4; SE = 3.0) did not differ significantly ($P > 0.10$, t -test). However, in the double-ration experiment, the total number of stolons produced by individual colonies was fewer for the fed (avg, 4.3; SE = 2.6) than for the starved treatments (avg, 10.0; SE = 1.4) (t -test, $P < 0.05$).

Flow direction and stolon induction—Stolon production did not differ between upstream and downstream colonies, for either large or small colonies (G -test, $P > 0.10$, $N = 20$). In addition, stolon production did not differ between upstream and downstream sides of two colony interactions perpendicular to the direction of flow (G -test, $P > 0.10$, $N = 20$).

Self-nonsel self recognition—In 1987, none of the 35 colonies examined made stolons against clonemates when they re-established contact at new growing edges. The same result was found with 16 experimental colonies in 1988. However, 18 of the 21 experimentally damaged two-colony interactions made stolons when colonies re-

Table 2. The probability of a colony of *Membranipora membranacea* producing stolons when in contact with clonemates vs. nonclonemates in 1987, 1988, and 1987 and 1988 combined. All differences are significant (G -test, $P < 0.001$).

	With stolons	No stolons
1987		
Clonemates	0	35
1988		
Clonemates	0	16
Nonclonemates	18	3
Total		
Clonemates	0	51
Nonclonemates	18	3

established contact along their new growing edges (Table 2). Stolons were never made between clonemates, but frequently occurred when contact was made with a non-self colony (G -test, $P < 0.001$). In addition, no clonemates were found to fuse when they re-established contact.

Discussion

For the populations of *Membranipora* near Friday Harbor, colony size is frequently limited by competitive interactions. Overgrowth is quite rare, except for fatalities experienced by extremely small colonies (<5 mm; Harvell et al. 1990). Stolons directly influence the outcome of spatial contests between two colonies by acting locally to reduce growth rates of affected regions of colonies (Harvell and Padilla 1990), but our stolon removal experiments show that stolons determine whether a small colony can be completely encircled by a larger one. Without stolons, large colonies rarely completely surround smaller colonies because a colony's growth rate increases with the percentage of its border that is occluded (Harvell and Helling 1993). Thus, as a large colony surrounds a small colony and begins to occlude its borders, the free edge of the small colony advances at an ever-increasing rate. When no stolons are produced, these small colonies can "out-run" large colonies in a race across the substrate. The large colony's successful capture of a small colony is important because the large colony can then occupy all the space the small colony would have eventually acquired. Capture also means that the duel is terminated. For the small colony, capture means the colony will remain forever small and will consequently have low reproductive output. This decrement in the total reproductive area (due to having a smaller size than would have been possible in the absence of this competitive interaction) is partially compensated demographically by the tendency for crowded colonies to reproduce earlier and at a smaller size than do the uncrowded colonies (Harvell and Grosberg 1988; Harvell and Helling 1993).

The experimental removal of stolons not only resulted in a reduction of stolon production, but colonies in the sham treatment produced fewer stolons than colonies in

the control. One assumption of our census technique was that stolons persisted only for a single day before being overgrown so we did not recensus the same stolon. A violation of this assumption could result in an apparently higher production of stolons in the nonremoval treatments simply because there were stolons that might be recounted in those treatments, but not in the removal treatments. However, greater number of stolons in the nonremoval treatments appears to be due to increased production because Harvell and Padilla (1990) estimated a lifespan of 12–24 h for stolons on colonies from these same sites, there was no difference among treatments in the proportion of new vs. existing stolons and there were fewer stolons in the sham than in the control which could be due only to a true difference in stolon production rate.

An increase in colony growth rate was correlated with the reduction in stolon production in our manipulations. Colonies in treatments producing fewer stolons grew at a significantly higher rate than those producing more stolons for both size classes of colonies (Fig. 3). Production of stolons slows the growth of competitors, apparently more so for the larger colony in competitions between colonies of unequal sizes. An average large colony growing at the average rate would have 5 times the surface area after 20 d if stolons were removed. The average smaller colony growing at the average rate would have 2.2 times the surface area after 20 d if stolons were removed. The exact mechanism causing slower growth is unclear. It is important to determine how much growth is slowed by producing stolons (if stolons are energetically costly to produce) or by the aggression from stolons slowing a competitor's growth. Comparison of colonies with intact stolons with colonies that had stolons removed shows that the growth rate (in terms of area increase) of the large colonies was slowed more than the growth of small colonies. Thus, the reduction in growth rate was due to the production of stolons rather than to the effect of the neighbor's stolons because large colonies on average produced more stolons and were aggressively attacked by fewer stolons produced by small colonies. This finding is consistent with the notion that there is a cost to stolon production.

Although individuals varied in their propensity to produce stolons (some individuals never produced them and others produced stolons every day), some general rules for stolon production have emerged. Larger colonies usually produced more stolons than did their smaller competitors, consistent with the results of the single-time census of Harvell and Padilla (1990).

Stolon production by the two regions of a single colony was not independent, and spatially separated zooids responded in unison within a colony. This response could be caused by both parts of the colony independently responding in similar ways to a cue that they received simultaneously, or there could be some internal coordination of stolon production. Apparent coordination and a patterned response among zooids within a *Membranipora* colony also occurs when colonies produce a band of spined zooids in response to nudibranch extract. How-

ever, apparent coordination in spine induction results from independent responses of zooids to a shared cue rather than from a coordinating mechanism among zooids (Harvell 1991).

Both inhibitory and activating factors affect the morphogenesis of stolons in hydrozoans (Müller et al. 1987). In *Hydractinia*, the stolon tip produces an inhibitory factor that prevents stolon formation in its immediate vicinity (Müller and Plickert 1982). Stolon branching is induced by another diffusible factor (Lange and Müller 1991). In scleractinian corals, hydrodynamics can affect the outcome of aggressive interactions; fast flow deflects the aggressive tentacles, making them ineffective if the aggressor is downstream (Genin et al. 1994). If a diffusible cue or hydrodynamic effects were responsible for *Membranipora* stolon induction, we would expect differences in the propensity to produce stolons when smaller or larger colonies were upstream in our flume experiments. In addition, we would expect differences in the probability of stolons being produced on upstream vs. downstream portions of the region of contact between two colonies. However, colony orientation in flow did not affect stolon production, suggesting that contact rather than diffusible cues are operational. In addition, because these stolons are small (the same width and height as regular zooids) and attached to the substrate, they would not greatly alter local flow.

Although stolons seem to be costly to produce and an individual not producing them would have a short-term growth advantage, the cost of stolon production is offset when the stolons are produced in the appropriate contexts. One of the puzzles of the induction and role of stolons is the extreme context dependence of stolon production, particularly with regard to relative colony size. We hypothesize that large colonies produce the most stolons because they are energetically competent because of a large internal area of feeding zooids that can support peripheral stolon production. But this hypothesis does not explain the biased production of stolons against small conspecifics. Two nonexclusive hypotheses could explain the biased incidence of stolons produced against smaller colonies. First, large colonies may selectively produce stolons against small colonies because small colonies are the most favorable opponents to attack; contests are of short duration and can be terminated with capture. Producing stolons against an equal-size opponent would be a lifetime endeavor.

Second, the reduced incidence of stolon production against equal-size colonies could be because colonies become habituated to a neighbor and reduce or stop aggression after a certain amount of time has passed. Thus, many of the equal-size medium-to-large colonies sampled have been in contact for long periods and may have stopped their initial phase of stolon production. A large colony's interactions involving a small colony would always be in an early aggressive phase because small colonies can be surrounded or overgrown within a few weeks. Habituation has been documented in a variety of clonal invertebrate species; especially anemones and corals

(Wellington 1980; Brace and Santer 1991). Purcell and Kitting (1982) examined intraspecific aggression by catch tentacles in the anemone *Metridium senile*. This anemone commonly is found both in groups that are of the same clonal identity and in mixed clonal groups. Purcell and Kitting determined that due to habituation, aggression decreased, allowing mixed clonal aggregations to coexist. However, habituation apparently does not contribute to the tendency for increased stolon production in *M. membranacea* when colonies are asymmetrical, because the number of stolons produced in an interaction does not decline through time (observed for 25 d).

Because stolons are rapidly produced (growth rates of 3–4 mm d⁻¹) and ephemeral (lifetime of 12–24 h; Harvell and Padilla 1990), the timing and frequency of deployment seem to be critical to their success in slowing the growth of conspecifics. In particular, the production of multiple stolons at a single interaction site is critical in stopping the growth of an advancing conspecific. One reason the lifetime of stolons is so short is that an attacked conspecific can eventually overgrow the stolon—usually within a day. However, if multiple stolons are produced, the advancing front of a colony is slowed in the process of overgrowing the first stolon and then halted by contact with the second.

Stolon production is highly conditional and determined by relative and absolute sizes of interacting colonies, food availability, and relatedness of colonies. The effect of resource level on the probability of stolon production was unexpected, particularly because more stolons were produced in the low food treatment. The opposite outcome, an increase in stolon production with increasing food level, would have supported the notion that stolons are energetically costly to produce and that resources for aggression are increased by supplemental feeding. *Membranipora* colonies also produce an inducible defense against predators, and this induced spine response is greater at higher resource levels (Harvell 1991). However, Stemberger (1990) found that rotifers produce larger spines when they are exposed to predator cues under low food conditions. Our result that stolon production increased at low resource levels is difficult to interpret. Because our growth data are consistent with the notion that stolons are costly to produce, the most plausible explanation is that stolons provide an even greater benefit in low-resource environments where the stakes in spatial contests may be higher.

Although previous research has demonstrated the importance of absolute size and genetic incompatibility in determining the outcome of contests for space, our study is the first to clearly demonstrate the importance of relative size in competitive encounters. The explanation for size-specific responses still eludes us, but the potential to rapidly capture small colonies and thus terminate the duel may be responsible for the pattern. Whatever the ultimate cause of the size-specific pattern of stolon production, our stolon removal experiments show that aggressive stolon production by large colonies enables them to more quickly surround and capture small conspecifics, thereby ac-

quiring more space for themselves. Finally, the similarity in probability of stolon production between two sides of an interaction involving a single colony underscores the potential for coordinated activities among zooids, even under conditions favoring a very localized response.

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