

Settlement, Refuges, and Adult Body Form in Colonial Marine Invertebrates: A Field Experiment

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Abstract. We examine the relationship between adult body form (sheet vs. arborescent) and larval settlement in colonial animals. Because thin sheet forms are more susceptible to overgrowth than arborescent forms, we predict that larvae of sheet forms should preferentially settle in refuges from competitors. On both natural and artificial substrata, the larvae of the sheet form (*Membranipora membranacea*) settled more often on high spots, which could serve as refuges from competition. The arborescent forms (*Bugula neritina* and *Distaplia occidentalis*) settled around the bases of bumps more frequently than would be expected by chance. For many arborescent forms, their most vulnerable periods are the days immediately following settlement, when individuals can be consumed easily by predators or dislodged by physical disturbances. Settlement in a crevice (base of a bump) would provide protection from the bulky mouthparts of predators. Moreover, dislodgment would be less likely than if settlement had occurred on flat locations, such as the tops of bumps or the areas between bumps.

Introduction

Striking patterns of spatial distribution are characteristic of many marine invertebrates sessile on algae, rocks, and other hard surfaces. Individuals are often found in aggregations relative to each other (*e.g.*, Knight-Jones, 1951; Crisp, 1961; Wethey, 1984), relative to topographic features of the substrata (*e.g.*, Crisp and Barnes, 1954; Ryland, 1959; Crisp, 1961; Wisely, 1960; Hayward and Harvey, 1974; Keough and Downes, 1982; Wethey, 1986; LeTourneux and Bourget, 1988), or relative to microflora (*e.g.*, Crisp and Ryland, 1960; Brancato and Woollacott, 1982; Strathmann *et al.*, 1981). These patterns may arise

at the time of larval settlement or develop later as a result of differential mortality. The distribution of individuals at the time of larval settlement has a strong influence on their future success. Individuals that settle near dominant competitors are more likely to die quickly, as are those that settle within the range of predators or where disturbance events frequently occur.

There are a number of potential escapes from sources of biotic mortality, including simple avoidance of settlement near enemies (*e.g.*, Grosberg, 1981; Young and Chia, 1981) and recruitment to spatial refuges (*e.g.*, Connell, 1961; Dayton, 1971; Paine, 1974; Wethey, 1983; Walters and Wethey, 1986). Organisms located in spatial refuges increase their chances of survival against competitors, predators, and disturbance events. Size can also be protective to colonies once they have grown to certain dimensions unaffected by competitors; this is the size refuge. Potential morphological escapes may also exist. Among colonial organisms attached to hard substrata, one can distinguish a number of morphological types, including sheet and tree forms (Jackson, 1979). The outcomes of competitive interactions can be strongly influenced by the morphologies of the competitors. Tree forms are relatively isolated from the substratum-associated competitors (Jackson, 1979; Grosberg, 1981), whereas sheet forms encrust the substratum and may suffer competitive interactions along their edges. Thin sheets tend to lose to thicker forms (Buss, 1980; Seed and O'Connor, 1981; Russ, 1982; Sebens, 1985, 1986; Walters and Wethey, 1986) unless they have a height advantage in the zone of contact (Walters and Wethey, 1986). Therefore, one would predict that animals with thin, sheet-like growth forms should preferentially settle on or near locations where they have a height advantage (Walters and Wethey, 1986).

Although tree forms are less likely to be overgrown by competitors, they can be more visible to predators and

are more susceptible to total colony mortality than sheet forms. On irregular substrata, a potential settlement refuge location would be found around the bases of bumps. Here, certain predators may not be able to reach newly settled individuals. Here they are also protected from more disturbance events than they would be if they were located on a flat surface or on the top of a bump.

We examined the patterns of larval settlement in three species of encrusting colonial animals with different growth forms. We asked whether the settlement patterns were consistent with our prediction that species with thin sheet morphologies should choose spatial refuges from competitors, whereas species with tree morphologies should choose refuge locations that would reduce the risk of predation and disturbance. The encrusting cheilostome bryozoan *Membranipora membranacea* was our example of a thin sheet morphology, and the arborescent bryozoan *Bugula neritina* and the pedunculate ascidian *Distaplia occidentalis* were our examples of tree morphologies. We examined two kinds of substrata. The kelp *Laminaria saccharina* is a substratum commonly colonized by all three species. Settlement plates cast from bumps on Lego toy building blocks and pits created from bubble plastic served as model topographies of the same spatial scale as those found on *Laminaria*. Our analysis was carried out in two phases: (1) we examined the extent to which settlement on our model substrata mimicked that on natural surfaces; and (2) we examined in detail the spatial pattern of settlement on the model substrata.

Materials and Methods

Study organisms

The bryozoans *Membranipora membranacea* and *Bugula neritina* have small, ciliated larvae (*Membranipora*: 750 μm ; *Bugula*: 200 μm , from Reed, 1987) that have limited swimming abilities in the ocean (Chia *et al.*, 1984). However, these larvae can choose their settlement locations. When competent, they move closely over the substrata and test it (Woollacott and Zimmer, 1978, for *Bugula*; Atkins, 1955, for *Membranipora*). During this phase, *Bugula* larvae form temporary attachments using adhesives that are sufficiently strong to prevent the individual from being mechanically dislodged (Loeb and Walker, 1977). *Bugula* can quickly dissolve the adhesive or change its viscosity to detach from, or reject the surface (Reed and Woollacott, 1982).

In the plankton, *Distaplia occidentalis* larvae are much larger than those of the other two species, measuring up to 3.2 mm in length (Cloney and Torrence, 1984). Most encounter a number of surface locations before metamorphosing on one of them (R. A. Cloney, pers. comm.). Torrence and Cloney (1988) suggest that sensory neurons in the adhesive papillae may be common in ascidians. In

the laboratory, adhesion in *Distaplia* occurs within 30 s at 15°C (Cloney, 1978). Tail resorption reduces the size of the newly settled individual to approximately 650 μm within 7 min (Cloney, 1978).

For the purposes of this study, it was important to distinguish between newly settled and metamorphosed individuals. Newly metamorphosed *Membranipora* colonies have only the twin ancestrula skeleton fully formed, and *Bugula* has only the first zooid skeleton completed. *Distaplia* colonies were considered new individuals if they occupied less than 1 mm².

Experimental procedure

To study larval settlement on natural substrata, we examined the alga *Laminaria saccharina*. Plants were collected on the floating docks at the Friday Harbor Laboratories, San Juan Island, Washington state (48° 32' 42" N; 123° 0' 39" W) and on the floating public docks at Fisherman's Bay on Lopez Island, Washington state (48° 30' 30" N; 122° 54' 51" W). Entire blades were either placed in running seawater tables and a census taken within 48 h, or frozen immediately for a later census. Random pieces of the alga (20 × 20 cm) were cut from the central portion of large (1.0–2.0 m in length) *Laminaria* fronds. All new settlers were recorded on each algal square. As the topographies of the blades are quite variable, we could not distinguish a pit from a bump. Instead, each topographical feature on the blade was defined as a continuous slope extending from a lowest to a highest point (Fig. 1). The lowest point on one side of an algal blade is the highest point on the reverse side. The diameter (base) and the height of each topographic feature were recorded with vernier calipers. The slopes ranged in length from 1 to 20 mm. The location of each animal was determined by cre-

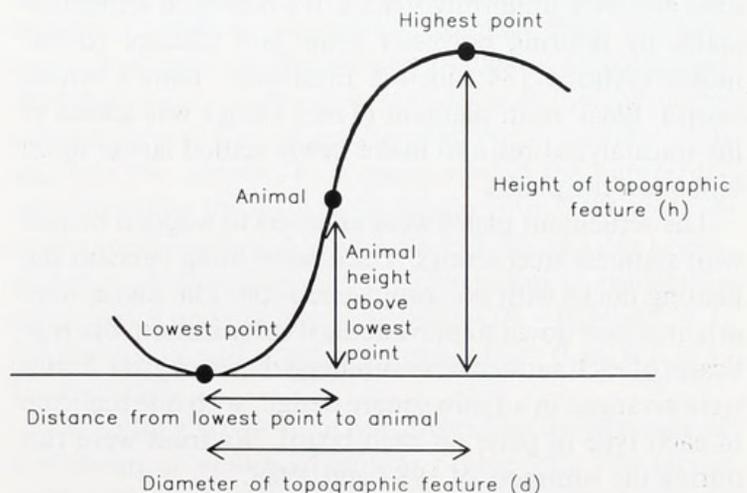


Figure 1. Each colony was mapped in relation to the nearest topographic high and low point. The dimensions of the topographic feature were measured.

ating a right triangle with the animal location and the lowest point as two of the points (Fig. 1). The distance from the lowest point to the animal and the animal height above the lowest point were measured (Fig. 1).

Using the diameter (d) and height (h) of each topographic feature, we calculated:

(1) the radius of curvature (rc) of the topographic feature:

$$rc = \frac{h^2 + (d/2)^2}{2*(1 + d)*(d/(2*h))}$$

(2) the vertical position (vp) of the animal, which we use to determine the location (top, side or base) of the organism on the topographic feature:

$$vp = (\text{animal height}/h).$$

Wilcoxon rank sum tests were used to determine if there were differences in locations occupied by larvae of the three common species. We examined the effects of size and shape of topographic features (height, diameter, and radius of curvature) as well as larval position (animal height and vertical position). When differences were found, pairwise Wilcoxon rank sum tests were run to determine which species were significantly different. Data from the Friday Harbor Laboratories and Lopez Island were pooled after Wilcoxon rank sum tests showed that there were no differences between the two sites.

To model the kinds and size scales of topographic features found on natural substrata, such as the alga *Laminaria saccharina*, we constructed three types of plastic plates 8.9 cm in diameter: (1) small Lego (Lego Systems Inc.) building block bumps (cylindrical, 2 mm high, 5 mm diameter) simulated small algal bumps; (2) large Lego building block bumps (cylindrical, 5 mm high, 9 mm diameter) simulated large algal bumps; and (3) bubble plastic pits (hemispherical, 2 mm deep, 5 mm diameter) simulated small algal pits. These materials were used because their topographic features were of the appropriate spatial scale and were uniformly spaced. We produced settlement plates by pouring polyester resin into silicone rubber molds (Sylgard 184 Silicone Elastomer, Dow Corning Corp.). Black resin pigment (Titan Corp.) was added to the uncatalyzed resin to make newly settled larvae more visible on the plates.

The settlement plates were attached to wooden boards with stainless steel screws. These were hung beneath the floating docks with polypropylene rope. The plates were oriented face down to prevent algal colonization. Six replicates of each surface were submerged in each trial. Plates were arranged in a Latin square design, with one replicate of each type of plate on each board. Six trials were run during the summers of 1987 and 1989.

Photographs were taken every two days at the Friday Harbor Laboratories and once or twice a week at Lopez Island during 1987. Additional data were collected by di-

rect observation at Lopez Island in 1989. Flash-lit photographs were taken underwater using Kodak Technical Pan 2415 film and a Nikonos 5 camera equipped with a 5:1 extension tube and focal framer. Negatives were observed under a dissecting microscope equipped with an ocular micrometer to determine the specific locations of newly settled individuals. We distinguished among four kinds of locations on the plates with bumps: (1) top of bump; (2) side of bump; (3) touching the base of the bump; and (4) on the flat surface not touching the base of the bump. On the pitted surface, we distinguished among three kinds of locations: (1) in the pit; (2) touching the edge of the pit, and (3) on the flat surface not touching the pit. Individual larvae were scored as touching a topographic feature if they were within 250 μm of the feature. This distance represents approximately one body length of the settled larvae (200 to 750 μm in length).

To determine whether larvae settled preferentially in relation to topographic features, we compared our observations to a random distribution. For example, if larvae settled randomly, then the proportion of larvae settling in pits should be equal to the proportion of space accounted for by pits. In this way we calculated the number of larvae expected to settle in each of our classes of locations (on or in pits or bumps, touching pits or bumps, away from pits or bumps). Paired simultaneous t -tests were used to compare the observed *versus* expected number of individuals in each location on a settlement plate. The simultaneous t -tests were weighted because the estimates of proportions of larvae were all based on samples of different sizes. The estimate p of a proportion has a gaussian distribution with a variance $p(1 - p)/N$, where N is the sample size (Snedecor and Cochran, 1967: p. 208). We weighted our estimates by the reciprocal of this variance because we have higher confidence in estimates with the lowest variance. Plates with less than two individuals were not included. We used the Bonferroni inequality to make the tests simultaneous (Miller, 1966). For example, when we compared three settlement locations, to maintain an overall error rate of 0.05, we used an error rate of $0.05/3 = 0.016$ in each individual comparison.

To determine whether settlement preference changed as space became occupied, we examined the relationship between the proportion of larvae settling in the feature and the proportion of unoccupied space accounted for by that feature. On all dates we calculated the space available for settlement by subtracting from the total the area occupied by settled individuals. We assumed that all newly metamorphosed larvae occupied 1 mm^2 . We compared settlement in samples with more than the average amount of free space, to settlement in samples with less than the average amount of free space.

Stoloniferous hydrozoan (primarily *Obelia dichotoma* and *Obelia geniculata*) and entoproct (*Barentsia benedeni*) colonies were present on all of the plates within 10 days, and at least a few stolons rapidly covered the entire surface of most plates. To determine whether the stolons affected settlement of *Bugula*, *Distaplia*, and *Membranipora*, the tops of the Lego bumps were divided into ten pie-shaped wedges. Similarly, the bases of the Lego bumps were divided into ten equal sections. If settlement was random with respect to stolons, then the ratio of wedges where stolons and larvae co-occur, to wedges with larvae, should equal the ratio of wedges with stolons to total wedges. Paired simultaneous *t*-tests were used to determine whether the observed and expected ratios were equal.

Very few individuals of other species settled on our experimental plates. Approximately 75% of the plates of each type had no other species settling on them. The remaining 25% had an average of two individuals of other species on them. These other species included: the bryozoans *Tegella armifera* and *Schizoporella unicornis*, the ascidian *Diplosoma macdonaldi*, the barnacle *Balanus crenatus*, the serpulid polychaete worm *Pseudochitonopoma occidentalis*, and spirorbid polychaetes.

Results

Natural alga substrata

Bugula neritina, *Distaplia occidentalis*, and *Membranipora membranacea* settled in locations with similar diameters and radii of curvature (Table I). *Bugula* and *Distaplia* settled in significantly lower elevations relative to topographic features than did *Membranipora* (Table I: Vertical Position). *Bugula* settled on topographic features that were significantly taller than those on which the other two species settled (Table I).

Settlement plate experiments

On the Lego settlement plates, settlement was non-random for all species (Table II). *Distaplia* and *Bugula* were found most often around the bases of bumps (Table II). These locations covered less than 5% of the total surface area of the settlement plates, yet more than 50% of the larvae of *Distaplia* and *Bugula* settled there.

Both arborescent forms, *Distaplia* and *Bugula*, were found significantly less often than expected on flat surfaces of the large and small Legos and the flat surfaces of plates with small pits (Table II). *Distaplia* settled more than expected by chance in the pits. In contrast, *Bugula* significantly avoided pits (Table II). The sheet form, *Membranipora*, was found more than expected on the tops of bumps and on the flat surfaces away from the topographic features in the large Lego treatment, but less than expected around the bases of bumps (Table II). On the pitted surfaces,

Table I

Settlement locations of Membranipora membranacea, Bugula neritina and Distaplia occidentalis on the alga Laminaria saccharina

Species	N	Mean	Group
Height of Topographic Feature			
<i>Bugula</i>	64	9.22	A
<i>Distaplia</i>	95	7.81	B
<i>Membranipora</i>	147	7.80	B
Diameter of Topographic Feature			
<i>Bugula</i>	64	26.30	A
<i>Distaplia</i>	95	28.13	A
<i>Membranipora</i>	147	27.12	A
Radius of Curvature of the Topographic Feature			
<i>Bugula</i>	64	213.62	A
<i>Distaplia</i>	95	446.45	A
<i>Membranipora</i>	147	453.29	A
Animal Height Above Lowest Point			
<i>Bugula</i>	64	1.80	A
<i>Distaplia</i>	95	1.44	A
<i>Membranipora</i>	147	5.32	B
Vertical Position of the Animal			
<i>Bugula</i>	64	0.23	A
<i>Distaplia</i>	95	0.18	A
<i>Membranipora</i>	147	0.71	B

N = the number of individuals, Mean = the mean in millimeters, and Group = the results of Wilcoxon rank sum tests. Different letters refer to significant differences (*P* < 0.05). For explanation of the measured values, see Figure 1 and the text.

Membranipora settled significantly less than expected in the pits and more than expected around the edges of the pits. *Bugula* and *Distaplia* settled preferentially around the bases of bumps, while *Membranipora* appeared to avoid this location. To estimate whether there was pre-emption of space by *Bugula* and *Distaplia*, we compared *Membranipora* settlement in samples with more than the average percent free space to settlement in samples with less than the average. Free space around the bumps decreased during the settlement season from 2.0% to 1.5% on the small Legos and from 4.3% to 3.6% on large Legos. *Membranipora* settlement was independent of availability of free space on both large Lego plates (*F* = 0.24; d.f. = 1, 23; *P* = 0.63), and small Lego plates (*F* = 0.16; d.f. = 1, 19; *P* = 0.69).

The settling larvae were not affected by the presence of hydrozoan or entoproct stolons (Table III). The larvae neither preferentially settled in locations where stolons were present nor did they significantly avoid these locations.

Table II

Test of randomness of settlement locations; the results of simultaneous paired *t*-tests comparing the expected versus the observed number of settlers

Species	Location	N	Difference	S.E.	Sign.
Large Lego					
<i>Bugula</i>	Top	16	-2.14	0.33	Less
	Base	16	5.28	0.64	More
	Flat	16	-2.60	0.96	Less
<i>Distaplia</i>	Top	25	-2.60	0.36	Less
	Base	25	11.05	1.33	More
	Flat	25	-1.18	0.46	Less
<i>Membranipora</i>	Top	16	5.47	1.16	More
	Base	16	-0.65	0.13	Less
	Flat	16	3.92	0.57	More
Small Lego					
<i>Bugula</i>	Top	16	-2.75	0.43	Less
	Base	16	7.01	1.30	More
	Flat	16	-2.57	0.77	Less
<i>Distaplia</i>	Top	25	-4.05	0.49	Less
	Base	25	15.78	1.99	More
	Flat	25	-5.67	0.90	Less
<i>Membranipora</i>	Top	15	1.21	0.88	n.s.
	Base	15	-0.20	0.08	n.s.
	Flat	15	1.26	0.84	n.s.
Small Pits					
<i>Bugula</i>	Pit	11	-1.86	0.60	Less
	Edge	11	3.22	0.96	More
	Flat	11	-1.51	0.43	Less
<i>Distaplia</i>	Pit	19	3.99	0.82	More
	Edge	19	1.38	0.29	More
	Flat	19	-4.57	0.85	Less
<i>Membranipora</i>	Pit	9	-3.23	0.78	Less
	Edge	9	1.64	0.52	More
	Flat	9	2.15	0.95	n.s.

N = the number of plates on which at least two larvae settled; Difference = the mean for *N* plates of the observed - expected values; S.E. = the standard error of the Difference; and Sign. = the direction of the significance value with n.s. = not significant ($P > 0.05$). A Bonferonni comparisonwise error rate of 0.016 was used to keep the experimentwise error rate = 0.05.

Discussion

In this study we examined the relationship between larval settlement pattern and adult growth form in colonial epifauna on hard substrata. We asked whether larvae of species with thin sheet morphologies chose different settlement locations from those of larvae of species with arborescent morphologies. We argued that species with thin sheet growth forms should be more susceptible to overgrowth by competitors than species with tree morphologies. Because topographic high spots may serve as spatial

refuges from competitors (Walters and Wethey 1986), we expected species with thin sheet morphologies to settle preferentially on topographic high spots.

In the present study, the thin sheet species, *Membranipora membranacea*, preferentially settled on the highest available locations on topographically complex surfaces (tops of bumps and flat areas between pits: Table II). This is consistent with our predictions, because the tops of bumps and the flat areas on a pitted surface are both locations where a colony has a height advantage over competitors, and thus has a potential refuge from competition. This result indicates that physical cues may allow larvae to escape from competitors, much as biogenic cues (*e.g.*, Grosberg, 1981; Young and Chia, 1981) allow larvae to avoid recruitment near enemies.

We argued that species with arborescent growth forms should be relatively immune to competitors, but that they might suffer damage from mobile predators like fish. In North Carolina, for example, filefish feed voraciously on newly settled colonies of *Bugula stolonifera* growing on flat surfaces (L.J.W., pers. obs.). Thus, tree forms might be expected to settle in cracks and crevices. In the present study, the arborescent forms, *Distaplia occidentalis* and *Bugula neritina*, settled preferentially around the bases of topographic irregularities (Table II). This result is consistent with our predictions, because the bases of bumps on our experimental plates are the locations most like crevices.

Similar spatial partitioning occurred on the alga *Laminaria saccharina* (Table I). Arborescent *Distaplia* and *Bugula* were found low on the slopes of the alga, while the thin sheet *Membranipora* was found significantly higher (Table I: Animal Height). The algal low spots,

Table III

Test of response of larvae to hydroid and entoproct stolons

Species	Location	N	Diff.	S.E.	p Value	Sign.
<i>Bugula</i>	Top	1	0.00	N.A.	N.A.	N.A.
<i>Bugula</i>	Base	22	-0.53	0.50	0.3293	n.s.
<i>Distaplia</i>	Top	4	2.50	2.50	0.3910	n.s.
<i>Distaplia</i>	Base	43	-1.10	3.11	0.7243	n.s.
<i>Membranipora</i>	Top	50	3.25	2.82	0.2553	n.s.
<i>Membranipora</i>	Base	10	-2.14	8.86	0.8144	n.s.

If settlement is random with respect to stolons, then the ratio of wedges with stolons and larvae, to wedges with larvae, should be equal to the ratio of wedges with stolons to total wedges. N = the number of individuals; Diff. = the mean of the difference: [(wedges with stolons)/(total wedges)] - [(wedges with larvae + stolons)/(wedges with larvae)]; S.E. = the standard error of the Difference; and Sign. = the sign of the significance value if $\alpha < 0.05$. A negative difference denotes bumps that had more larvae settling than it had stolons, and N.A. = not applicable.

where *Bugula* and *Distaplia* settled, are functionally equivalent to the bases of Lego bumps and the pits in the artificial settlement surfaces (Table II). Similarly, the high positions on algal slopes where *Membranipora* settled are functionally equivalent to the elevated locations where they settled on the settlement plates (Table II). However, topography does not fully control settlement pattern, because neither previously settled individuals, nor the stolon mats of hydrozoans and entoprocts, affected settlement by the larvae (Table III), even though the presence of any organisms on the substratum alters the local microtopography.

An alternative mechanism that could account for the settlement patterns is passive transport of larvae by hydrodynamic forces. Because of their limited swimming abilities (Chia *et al.*, 1981), larvae are often passively transported in boundary layer flows (*e.g.*, Butman, 1987). One can model passive larval transport as analogous to sediment transport (*e.g.*, Middleton and Southward, 1984). The patterns of transport are influenced by the turbulent motion of the water and by the topography of the substratum. When the surface topography protrudes beyond the 'viscous sublayer' into the turbulent overlying water, turbulent eddies can cause erosion. The roughness Reynolds number, Re^* , is a measure of the degree to which roughness elements protrude above the viscous sublayer:

$$Re^* = u^*L\rho/\mu$$

where u^* is the shear velocity of the fluid flow regime, L is the height of the roughness element, ρ is the density of seawater, and μ is the dynamic viscosity of seawater.

In a wave-influenced environment, u^* is approximately 10% of the maximum water velocity (Denny, 1988; Denny and Shibata, 1989; Svenden, 1987). We estimate u^* to be in the range of 1.6 to 2.4 cm/s, yielding Re^* values of 30–50 for the small Legos and 75–120 for the large Legos. If the roughness Reynolds number is less than 5, the bumps lie within the viscous sublayer. Thus, in all cases, the bumps on our settlement plates are in a potentially erosional regime. Larvae differ from sediment particles in their ability to adhere to surfaces. In flume experiments with our settlement plates, sediment never accumulated on the tops of the Lego bumps, presumably because the erosional forces are very high in these locations. Therefore, if the pattern were passive, larvae would not have accumulated on the tops of bumps. However, the tops of the bumps are the locations where *Membranipora* larvae did accumulate. Thus, we believe that the passive model cannot explain our patterns.

Competitive interactions were infrequent on these settlement plates, because recruitment rates were low and space did not become limiting during our experiments. The only common encounters were between the entoproct

and hydrozoan stolons and the three species, with the later arrival always growing over the previously established colony. Neither colony appeared to be affected by these interactions. Although space was not filled on our settlement plates during the time course of this study, little bare space existed on the docks from which the plates were suspended. Because so little free space existed on the persistent hard substrata, we believe that competition could act as a selective agent on larval behavior.

The results of these studies are consistent with our prediction that adult body form should be correlated with larval settlement pattern. The arborescent forms (*Bugula* and *Distaplia*) settled preferentially in the small amount of space touching the bases of the bumps, potentially hidden from predators and disturbance events. The thin sheet form (*Membranipora*) settled most frequently on the highest available locations on topographically complex surfaces. Thus *Membranipora*, the adult growth form of which is most susceptible to overgrowth, had larvae that settled in potential refuges from competitors. Adult competitive ability and susceptibility to predation and disturbance may be an important influence on selection for larval settlement behavior.

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