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Settlement and post-settlement processes limit Calliarthron on subtidal walls

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SETTLEMENT AND POST-SETTLEMENT PROCESSES LIMIT

***CALLIARTHRON* ON SUBTIDAL WALLS**

A Thesis

Presented to

The Faculty of the Department of Biology

San Jose State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Nisse Aloma Goldberg

August 2001

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ABSTRACT

SETTLEMENT AND POST-SETTLEMENT PROCESSES LIMIT *CALLIARTHRON* ON SUBTIDAL WALLS

by Nisse Aloma Goldberg

Cover of geniculate coralline algae is significantly greater on subtidal platforms than on vertical walls in a central California cove. *Calliarthron* settlement and growth were compared on horizontal and vertical substrates attached to platforms and walls. Spores were present along reef walls, as indicated by post-settlement recruitment on horizontal substrates attached to reef walls. Post-settlement densities were significantly lower on vertical substrates attached to walls than on horizontal substrates attached to platforms. Growth rates of basal crusts and frond densities were significantly greater on horizontal substrates attached to platforms than on vertical substrates attached to walls. Light measurements and manipulations of barnacle settlement suggest that reduced light levels reaching wall habitats and overgrowth by sessile organisms reduce *Calliarthron* growth on subtidal walls. These results indicate that the low abundance of *Calliarthron* on subtidal walls is a function of poor post-settlement recruitment and slower growth rates.

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Introduction

Macroalgal cover is consistently greater on subtidal horizontal substrates such as reef platforms and boulders, and cover of sessile invertebrates is greater on subtidal walls (rocky substrate with average ninety degree orientation from horizontal) in a variety of benthic habitats. The dominance and diversity of colonial sessile invertebrates on vertical walls can be caused by availability of larvae, competition, lack of bare space, sedimentation, and scour (McLean, 1972; Foster, 1975a; Jackson, 1977; Sebens, 1986; Vance, 1988; Chadwick, 1991; Burdette, 1992; Konar and Foster, 1992; Chapman et al., 1995; Bruno and Witman, 1996; Witman and Graham, 1998; Baynes, 1999). Only Baynes (1999; discussed below) has examined why macroalgae are not abundant on subtidal walls.

I investigated why geniculate coralline algae, in particular *Calliarthron*, is rare on subtidal walls but dominates reef platforms in central California *Macrocystis pyrifera* C. Agardh kelp forests along exposed coasts (McLean, 1962; Harrold et al., 1988). For example, *Calliarthron* percent cover on rocky reef platforms can reach one hundred percent but is typically less than twenty percent on vertical surfaces (Reed and Foster, 1984; Konar and Foster, 1992). *Calliarthron cheilosporioides* Manza and *C. tuberculosum* (Postel and Ruprecht) Dawson, henceforth grouped as *Calliarthron* because they may be the same species (Foster, pers. comm.), show similar distribution patterns on reef platforms and walls in *M. pyrifera* forests (Konar and Foster, 1992). Other common geniculate coralline algae found in central California kelp forests are *Bossiella schmittii* (Manza) Johansen and *Corallina officinalis* Linnaeus (Konar and

Foster, 1992). *Bossiella schmittii* is the dominant geniculate coralline alga on rocky outcroppings of subtidal walls and is second in abundance to *Calliarthron* on reef platforms (Konar and Foster, 1992; Konar, 1993). *Corallina officinalis* is relatively rare on horizontal substrates (less than one percent cover; Konar and Foster, 1992).

Calliarthron is a perennial understory alga with a basal crust and upright fronds, can persist in low-light conditions, is the most abundant coralline settler on horizontally-oriented surfaces, and has little seasonal variation in cover (Johansen and Austin, 1970; Reed and Foster, 1984; Konar and Foster, 1992). Calcified thalli can provide protection from grazers and scour (Leukart, 1994). The stiff, intertwined fronds of geniculate coralline algae can form complex three-dimensional structures (i.e. mats) that harbor a high diversity of invertebrates (Dearn 1987; Kenner, 1987). Populations are maintained via recruitment (spores are dispersed year-round) and frond fragmentation (Reed and Foster, 1984; Konar and Foster, 1993).

The causes for the low cover of *Calliarthron* on vertical walls are not known but may be associated with spore dispersal and settlement. In general, non-motile spores are released into the surge zone and settle passively into microbial films within the boundary layer (Amsler et al., 1992). Propagules oscillate downward along a wall surface and settle on uneven substrates (Graham and Sebens, 1996); eddies form when water flows over uneven substrates and such small-scale turbulence may determine where a spore finally settles (Foster, 1975b; Fletcher and Callow, 1992). Algal spores attach to the substrate by a mucilage sheath (Boney, 1981). Upon contact with a microscope slide (and presumably rock surfaces), the mucilage sheath covering a *Calliarthron* spore adheres to the substratum and forms a hard wall (Johansen, 1969). The strength of

adhesion to the substrate increases over time: reduced water motion increases the chance of successful spore attachment (Fletcher and Callow, 1992). Although few researchers have investigated competition between algal spores and sessile-invertebrate larvae, observations indicate that sessile-invertebrate dispersal and attachment mechanisms along walls are more successful (Foster, 1972; Baynes, 1999).

Macroalgae may be poor competitors for primary space against faster-growing colonial animals in the low light environment on walls (Jackson, 1977). At ambient light levels on horizontally-oriented settlement plates, filamentous and fleshy algae grow faster than crustose coralline algae and sessile invertebrates (Baynes, 1999). When the plates are shaded, sessile invertebrate and crustose coralline algal cover becomes similar to that on adjacent walls, suggesting that irradiance levels affect, in part, assemblage composition. Baynes (1999) found irradiance reaching the subtidal walls was one-fourth that reaching reef platforms. The fish *Hypsypops rubicundus* (Girard) lays eggs on cultivated algal nests commonly located on vertical walls (Foster, 1972). The origin and maintenance of these nests suggest macroalgae may be excluded from walls by competition with sessile invertebrates. The turf-forming algae establish by recruitment (Foster, pers. comm.) and are maintained by male fish that clear nests of debris, non-filamentous macroalgae, and animals during the breeding season (Foster, 1972).

Algal and sessile invertebrate distributions are affected by water circulation at small scales (on the order of centimeters) and large scales (on the order of meters). Foster (1975b) found greater diversity of algae along edges of artificial substrates than on flat upper surfaces. He speculated that water flow separates when coming in contact with a vertical surface, resulting in eddies that may concentrate spores; laminar flow without

eddies characterizes water flow over flat surfaces. Substrates with surface relief may have greater algal diversity than smooth substrates. For example, Konar (1993) observed geniculate coralline algae growing on rocky outcroppings on subtidal walls, but not on the vertical surface of the walls. On a larger scale, the distribution of sessile invertebrates along the sides of a sunken ship was related to differences in water flow- cover was greater along the sides of the bow and stern of a sunken ship (areas of greater water motion) than along the amidship sides (Baynes and Szmant, 1989). Water motion reduces sediment deposition and increases exchange of nutrients and waste products at small and large scales (Foster, 1975b; Baynes and Szmant, 1989). Findings by Foster (1975b) and Baynes and Szmant (1989) suggest that water motion may affect distributions of algae on subtidal walls. These studies did not test for differences in algal cover or water motion between horizontal and vertical surfaces.

Light also affects the distribution and growth of geniculate coralline algae in kelp forests (Konar and Foster, 1992). In the kelp forest at Stillwater Cove, central California, geniculate coralline algae had greater cover and growth rates at 10 m versus 20 m depth, indicating that light may be limiting with increased depth (Konar and Foster 1992). Calcification rates in coralline algae are influenced by photosynthesis and external carbonate ion concentrations: growth is reduced when light is limiting (LaVelle, 1979; Borowitzka, 1981). Leukart (1994) measured growth rates of encrusting coralline algae at various depths and seasons in sublittoral Helgoland. In summer when irradiance was greatest, coralline algae grew at all measured depths (2, 4, 6, and 8 m). During periods of low light (November through January), they stopped growing at the 6- and 8-m stations. Leukart (1994) suggests that coralline algae do not need low light regimes for growth but

are found in deeper water where competition and grazing may be reduced. Geniculate coralline algae grow faster when the surface canopy cover has thinned (winter months; Johansen and Austin, 1970; Reed and Foster, 1984; Konar and Foster, 1992).

Transplanted *Calliarthron tuberculosum* fronds grew more slowly on subtidal walls (0.88 mm in one month) than on reef platforms (2.08 mm in one month) at depths ranging from 12 to 15 m (Lamerdin, *unpublished data*). Irradiance reaching the platform was nine times greater than irradiance reaching the wall. Although Lamerdin did not measure growth of recruits (basal crusts less than 5 mm diameter), his results suggest that low light levels limit the growth of *Calliarthron* fronds on walls.

To better understand the patterns of *Calliarthron* distributions in Stillwater Cove, I established whether *Calliarthron* frond densities were greater on horizontal than on vertical surfaces in Stillwater Cove. To determine the causes of these distributional patterns, I assessed *Calliarthron* post-settlement recruitment on horizontal and vertical surfaces attached to platforms and walls, compared *Calliarthron* densities and growth rates on horizontal and vertical surfaces attached to platforms and walls, compared percent surface irradiance and water motion between walls and platforms, and determined whether overgrowth by sessile invertebrates affected *Calliarthron* growth on wall habitats.

Materials and Methods

Distribution patterns

To determine if *Calliarthron* frond densities were greater on horizontal substrates than on vertical substrates in Stillwater Cove, California, USA (36°34'N, 121°56'W; detailed site description in Reed and Foster, 1984), I measured frond densities in a randomly-placed 10 X 8 cm quadrat on platforms (horizontal surfaces with areas greater than 2 X 2 m), walls (vertical surfaces with areas greater than 2 X 2 m), rises (vertical surfaces with areas approximately 12 X 14 cm on reef platforms), and ledges (horizontal surfaces with areas approximately 12 X 14 cm on walls). Platforms, walls, rises, and ledges were chosen haphazardly with 23 replicates of each substrate type. Frond densities per quadrat were compared among treatments with a one-way analysis of variance and Bonferroni post-hoc tests.

Settlement experiment

The hypothesis that *Calliarthron* spore abundance was greater on reef platforms than on walls was tested assuming post-settlement recruitment (coralline basal crusts) densities were a measure of spore availability. Hruby and Norton (1979) observed a direct relationship between the species composition of algal propagules in the surface waters near the shore and the species composition of algal settlers on glass slides attached to boulders in the intertidal: species most abundant in the surface waters were also the most abundant settlers. Two 12 X 14 cm settlement plates (sanded PVC sheet) were welded together along one edge: one in the horizontal position and the other in the vertical position to form an “L-shaped” plate-pair. Settlement on the horizontal plates

attached to walls would address whether spores were available along walls. Settlement on the horizontal plates attached to the reef platforms functioned as a control for spore availability on platforms where *Calliarthron* was known to release spores (*Calliarthron* can settle on artificial substrates on reef platforms, Johansen and Austin, 1970). If there were crusts on the horizontal plates, settlement on vertical plates attached to the wall and platform would address whether spores could settle on vertically-oriented substrates where spores are known to be available. Settlement plates provided uniform (albeit artificial), easily manipulated substrates and their use avoided confounding factors due to microhabitat differences on natural substrate (Kaehler and Williams, 1997). Post-settlement recruitment on the plates and cleared natural substrate was compared to examine whether the PVC plates were a suitable settlement surface. Settlement plates were left in the field until identifications of coralline recruits could be made.

Settlement plate-pairs were deployed on 20 March 2000 to two reefs within Stillwater Cove. Each reef consisted of a northeast-facing wall that was greater than 2 m tall and 2 m wide, and a horizontal platform. The wall at Reef One had less surface relief than the wall at Reef Two. Stainless steel bolts were epoxied (Splash Zone Z Spar®) into 3-cm deep holes drilled in the rock and eight plate-pairs were bolted to each vertical wall and to each adjacent platform. Irregularities in the natural substrate determined where holes were drilled. Plate-pairs were positioned on the wall and platform approximately 0.5 m to 1.0 m from the top edge of the wall, and were at least 14 cm apart from each other. Three areas (144 cm²) on each wall and platform were cleared with hammer and chisel. Barnacles, hydroids, unidentified juvenile brown, and red algae were periodically brushed from the plates and clearings because I wanted to eliminate potential

interspecific competition for space. Grazer densities on plates were recorded five times during the experiment. Because grazer densities were low (<1 gastropod or sea star per 8 plates) and crusts (< 0.25 mm diameter) were growing where grazer tracks were observed, I assumed that grazing of spores was relatively minor compared to algal settlement rates (see Leonard, 1994).

Post-settlement recruitment densities (density of visible crusts) on the horizontal plates, vertical plates, and clearings were measured on 17 May 2000. The experiment was not terminated earlier because dense diatom films grew over coralline crusts, making counting difficult. Photographs of the central surface of each plate (area = 6.0 X 3.4 cm) were taken *in situ* with a Nikonos II® underwater camera, Oceanic 2001® strobe, and Nikonos® close-up kit with 80 mm lens. Photoquadrats were projected on a screen. Crusts greater than 0.1 mm in diameter were counted in randomly-chosen 1-cm² areas that had minimal diatom cover until mean crust densities stabilized. Settlement on plates and on natural substrate was compared. Settlement on platform-vertical and wall-horizontal treatments was not tested statistically because these were not the main treatments of interest. A two-way analysis of variance was used to test for differences between crust densities on horizontal plates attached to platforms (fixed) and crust densities on vertical plates attached to walls (fixed) at the two reefs (random). Because crusts on two plates per treatment were completely obscured by diatom growth, six plates per treatment were used for statistical analyses.

Growth experiment

To test whether *Calliarthron* basal crust growth rates, basal crust cover, and frond densities were greater on horizontal plates attached to reef platforms than on vertical plates attached to reef walls, settlement plate-pairs were first seeded with similar densities of *Calliarthron* post-settlement recruits and then attached to reef platforms and walls. I assumed that recruits were *Calliarthron* that came from the same population with similar initial survivorship and the differences in growth and in final densities could be attributed to treatment effects. *Calliarthron* growth on horizontal plates attached to reef walls and platforms was compared to growth on vertical plates attached to reef walls and platforms to evaluate whether growth was affected by plate orientation, by main substrate orientation (platform and wall), or by both factors. I continued to monitor the geniculate coralline recruits from the settlement experiment after 17 May using the same sampling protocol as for the growth experiment. Because recruits growing in the growth experiment had similar recruitment conditions but different growth conditions and recruits growing in the settlement experiment had different recruitment and growth conditions, results from the growth and settlement experiments were analyzed separately.

The growth experiment was done in three phases: deployment of artificial substrates (sanded PVC plates) within a *Calliarthron* mat to seed plates with *Calliarthron* recruits, transfer of plate-pairs to Reefs One and Two (the same reefs used for the settlement experiment), and monitoring of *Calliarthron* growth. Each plate-pair consisted of two plates (each 12 X 14 cm) joined by a hinge that allowed the plates to lay flat or in an "L-shaped" position- one plate in the horizontal position and the other plate in the vertical position. Three settlement plate-pairs were attached to a PVC bar, ranging from zero to one centimeter above the substrate. On 22 March 2000, fifteen racks were

attached to a platform that was covered with *Calliarthron* mats and was located between Reefs One and Two. Plates were left undisturbed until average *Calliarthron* cover per treatment was three to six percent and typical crust diameter was approximately one millimeter. Before attaching racks to Reefs One and Two, each plate-pair was configured into the "L-shape" and haphazardly re-assigned to a rack. Six racks were placed on each reef on 18 June 2000. Three racks were attached to the platform one meter from the platform edge and one meter apart from the nearest rack. Three more racks were attached one meter down from the platform edge on the adjacent wall face and one meter apart from each other. Grazers and colonial invertebrates were removed periodically with a soft toothbrush.

Percent cover of crusts and crust growth per plate were measured on the horizontal plates attached to the platform (P-h), vertical plates attached to the platform (P-v), horizontal plates attached to the wall (W-h), and vertical plates attached to the wall (W-v). An *in situ* photograph of the central surface (6 X 3.4 cm) of each plate was taken (for growth experiment: on 23 June, 22 July, 26 August, 20 September, 21 October, and 13 December; for settlement experiment: on 17 May, 23 June, 22 July, 26 August, 20 September, 28 October, and 8 December) as previously described, and projected onto a sheet of paper covered with 100 evenly-spaced dots. Because photoquadrats were projected independently of paper placement, biases associated with dot placement were assumed to be minimal (Littler and Littler, 1985). Final percent cover of *Calliarthron* crusts was recorded as the number of dots that touched crusts from photoquadrats taken on 13 December for the growth experiment and on 8 December for the settlement experiment. The diameters of the five largest crusts per plate were measured from the

first set of photographs. Thereafter, those crusts were measured monthly. Due to the difficulty in discerning individuals, crusts may have been individuals or the fusion (two or more crusts sharing a common edge) of more than one individual. Measurements of crust diameters on a plate were terminated when crusts were no longer surrounded by bare space.

Calliarthron frond growth was compared qualitatively among the four treatments (P-h, P-v, W-h, and W-v). The five tallest fronds per plate were measured monthly *in situ* with a ruler (for growth experiment: on 12 August, 16 September, 18 October, 15 November, and 8 December; for settlement experiment: on 19 August, 16 September, 11 October, 15 November, and 18 December). Measurements were taken on 8 February for the settlement experiment but were not included in analyses due to an incomplete data set (several replicates were lost or damaged). I assumed that the tallest fronds represented individuals from the cohort that had settled between 22 March and 18 June. To estimate frond growth per month on each plate, the difference in mean frond height measured on 18 December from the mean frond height measured the first month ($n = 5$ individuals per plate) was divided by the number of months that fronds were observed. Mean frond growth rates per treatment were calculated as frond growth rate per plate divided by the number of plates that fronds were observed in each treatment.

Final frond density and final average frond height per plate per treatment were determined on 3 December 2000 for the growth and settlement experiments. Fronds taller than 0.25 mm were counted over the entire surface of the settlement plate because frond densities in the center of the plate were not significantly different from densities counted within 1 cm from the plate edge (paired t-test per treatment, $P > 0.05$). Mean

frond height per plate was defined as the average height of ten randomly-chosen individuals within a 7.5 X 7.5 cm area in the center of each plate on 18 December. Average frond height was set to zero if there were less than ten fronds on the plate.

Differences in the means among treatments of *Calliarthron* crust growth (growth experiment- the difference in diameters measured on 23 June and 21 October; settlement experiment- the difference in diameters measured on 17 June and 20 September) per treatment, final percent cover, and final frond densities per plate per treatment were tested statistically. Cover data were arc-sine transformed and crust growth and final frond density data were square-root transformed to satisfy the assumption of equal variances. A mixed-model multifactorial analysis of variance was used to test for differences among treatments. Main factors were site (random; Reefs One and Two), main substrate orientation (fixed factor; platform and wall), and rack (random and nested within the interaction term: site and main substrate orientation; 3 replicate racks per main substrate orientation). Plates were the lowest level of replication. Variances were pooled if no significance ($P > 0.25$) was detected among interactions (Underwood, 1997; Edwards, 1998), thereby increasing degrees of freedom and power to test the main effects of substrate orientation and plate orientation. Tukey post-hoc tests were used to compare P-h and W-v treatments when main factors substrate orientation and plate orientation were significantly different. If the main factors were not significant ($P > 0.05$) then power analysis was performed as outlined in Zar (1984).

Water motion and downwelling irradiance

Clod cards (gypsum balls; Doty, 1971) were used to compare water motion measured on the reef platform and on the adjacent wall. Differences in gypsum weight-loss provide a reasonable measure of water flow and scour (Eckman et al., 1989). A mixture of 750 g plaster of paris, 500 ml water, and 15 ml latex paint, was poured into molds (tennis balls cut in half), dried at 150° C for 12 hours, and sanded to equal weight (± 0.3 g). Clods were glued to PVC plates (7 X 4 cm) with PVC glue, weighed, and attached to bolts interspersed among the plate-pairs on platforms (n = 2) and on walls (n = 2) at the two reefs. On 26 April, 6, 13, and 20 May, and 10 June, clod cards were deployed to the settlement experiment sites. Another series of clod cards were deployed to the growth experiment sites on 28 June, 15 July, 9 and 27 September, and 27 October. Dissolution rates of clods left in undisturbed sea water over the same period as those left in the field were measured. After one week, clod cards were retrieved, dried, re-weighed, and a new set of clod cards deployed. Relative water motion was defined as the diffusion index factor (DF) described by Doty (1971). A Mann-Whitney test was used to test for differences between platform and wall DF values. Main factors were reef (two replicates), and main orientation (platform and wall), and experiment (settlement and growth experiments at the same two reef replicates). Because there was no significant difference between the two experiments ($P = 0.213$) and between the two reefs within each experiment ($P > 0.570$), the reef and experiment factors were pooled.

Irradiance that reached crusts growing in the horizontal and vertical planes of Reef Two platform and wall was measured at midmorning on 29 April, 8 July, 5 August, 2 September, 7 October, 4 November, 8 December 2000, and 3 January 2001 at 8.5 and 9.1 m depths. Atmospheric conditions were either sunny and cloudless or overcast.

Irradiance ($\mu\text{mol Einsteins m}^{-2} \text{s}^{-1}$) was measured with a cosine photon collector attached to a Li-Cor®- model 1400- data logger. The collector was held in the horizontal and vertical plane on the wall and platform next to a settlement plate for two minutes (average irradiance was recorded every 15 seconds). Two measurements were taken per position and a mean irradiance per plane was calculated. Irradiance was measured in the horizontal plane at 11.5 m (where *Calliarthron* was growing on a reef platform) to determine whether light reaching the vertical plates on the wall and platform was less than the light reaching 11.5 m depth. Irradiance values were standardized as percent subsurface irradiance.

Downwelling irradiance was measured just beneath the surface and at depth, and percent subsurface irradiance was calculated using Beer's Law ($E_{(d)} = E_{(0)} e^{-kz}$ in which $E_{(d)}$ = downwelling irradiance at depth z , $E_{(0)}$ = surface downwelling irradiance, k = attenuation coefficient, and z = depth in meters; Kirk, 1994). When the kelp canopy covered the surface, I measured irradiance outside the kelp forest in order to calculate the attenuation coefficient. This value most likely underestimates the attenuation coefficient within the kelp forest, as there is generally greater light and less particulate organic matter in the water column outside of kelp forests (Eckman et al., 1989; pers. ob.). Depth (1.5, 8.5, 9.1, and 11.5 m) was plotted versus the natural log of the downwelling irradiance, and the attenuation coefficient was calculated as the slope of the line. Subsurface irradiance was calculated with Beer's Law, using downwelling irradiance measured at 1.5 m. Percent subsurface irradiance at each position was defined as the ratio of irradiance to surface irradiance. When the kelp forest had thinned substantially and the attenuation coefficients inside and outside the kelp forests were the same (4

November, 8 December, and 3 January), percent subsurface irradiance was calculated as the ratio of measured irradiance just beneath the surface to measured irradiance at each reef position. A paired t-test was used to test for significant differences between light reaching the platform in the horizontal plane and light reaching the wall in the vertical plane. Data were arc-sine transformed to satisfy the assumption of equal variances. To investigate whether *Calliarthron* growing on P-v and W-v was light-limited, depths were calculated where irradiance values measured at P-v and W-v were equal to irradiance reaching a horizontal surface in the horizontal plane.

Overgrowth by sessile organisms

To investigate the effects of barnacle overgrowth on *Calliarthron* frond growth, I removed barnacle recruits from 4 of the 8 plate-pairs at the settlement experiment on 19 August. Barnacle recruits had covered 50 to 100 percent of the vertical and horizontal plates attached to Reefs One and Two walls in August. Frond densities per plate were measured on 18 December. No fronds were found on vertical plates attached to Reef One wall. Densities were compared between the horizontal and vertical plates on Reef Two wall with a two-way analysis of variance (factors: barnacle treatment (fixed) and plate orientation (fixed)). Data were square-root transformed to satisfy the assumption of equal variances. The diameters of bryozoan colonies growing on settlement plates were measured at Reef Two wall of the settlement experiment to compare growth rates of bryozoan colonies and geniculate coralline crusts.

Results

Distribution patterns

Frond densities were significantly greater on reef platforms than on walls and rises, which were not significantly different in Stillwater Cove (result of analysis of variance test among treatments: $P < 0.001$; results from post hoc tests: platforms versus walls and platforms versus rises: $P < 0.010$; walls versus rises $P = 0.616$; Fig. 1). Live fragments of *Calliarthron* fronds were found attached to ledges in addition to fronds growing from crust holdfasts; no attached frond fragments were found on rises, walls, or platforms.

Settlement experiment

Calliarthron settled on plates attached to vertical walls at both reefs (Table 1). Crust densities on W-h plates were comparable to crust densities on P-h plates (Table 1). Crust densities were significantly greater on P-h plates than on W-v plates ($P = 0.049$; Table 1 and 2). Post-settlement recruitment at Reefs One and Two was not significantly different (Table 2). Densities on wall clearings and on W-v plates were similar, but densities on platform clearings were less than on P-h plates (Table 1). Densities on clearings may have been underestimated due to the difficulty in distinguishing crusts from rose-tinted rock.

Calliarthron growth

Calliarthron percent cover was greater on P-h plates than on W-v plates in the growth experiment ($P < 0.001$; Table 3 for full and reduced analysis of variance models, and Fig. 2a). Cover was significantly greater at Reef Two than at Reef One, was not

significantly greater on the platform than on the wall (power less than 40%), and was significantly greater on the horizontal plates than on the vertical plates (Table 3). Cover of crusts may have been overestimated due to growth of recruits settling during the experiment. Despite variability in basal crust growth among replicate racks between June and October, trends suggest that growth was greater on the P-h plates than on W-v plates, growth was greater on platforms than on walls, and growth was greater on horizontal plates than on vertical plates (Appendix Table 1 and Fig. 1). The W-h plates were often covered with diatoms and fine sediment.

Coralline crust cover and growth in the settlement experiment showed similar trends as in the growth experiment although the results from the settlement experiment were a combination of settlement and growth conditions: cover and growth were greater on P-h plates than on W-v plates (Fig. 3a and Appendix Table 2 and 3). Cover was reduced at Reef One with no significant difference between platforms and walls ($P = 0.848$). At Reef Two, cover was significantly greater on the platform than on the wall ($P = 0.001$). At both reefs, horizontal plates had greater *Calliarthron* cover than on vertical plates ($P < 0.001$). Cover on the platform clearings was lower than on P-h plates; cover on the vertical clearings was similar to cover on the W-v plates (Fig. 3a). Coralline crust growth was greater at Reef Two, greater on the platform, and greater on the horizontal plates between June and September (Appendix Table 3 for full and reduced model). Crust growth on the platform clearings was similar to growth on P-h plates. Growth on the wall clearings was similar to growth on the W-v plates (Table 4). The W-h plates were often covered with fine sediment and diatoms.

Final frond densities, frond growth rates, and frond heights were greatest on the P-h plates and least on the W-v plates at both sites of the growth experiment (Table 4, Fig. 2b). At Reef One in December, fronds were growing on all the P-h plates, on one of the P-v plates, on one of the W-h plates, and on none of the W-v plates (Fig. 2b). At Reef Two, frond densities on the P-h plates were significantly greater than on W-v plates ($P = 0.041$). Frond densities were not significantly greater on the platform than on the wall (power less than 40%, Table 5). Frond densities were significantly greater on the horizontal plates than on the vertical plates (Table 5). At Reef Two in December, fronds were observed on all replicates of P-h and W-h treatments and one-third of the P-v and W-v plates. Frond growth was underestimated due to the increased number of plates with emergent fronds, which lowered the mean and increased variability.

Final frond densities, frond growth rates, and frond heights in the settlement experiment showed similar trends as in the growth experiment (Table 4, Fig. 3b). Few fronds appeared on the H-v plates, the P-v plates, or on wall clearings at Reef One by December (Fig. 3b). At Reef Two, frond densities on the P-h plates were significantly greater than on the W-v plates ($P < 0.001$). As in the growth experiment, frond densities were not significantly greater on the platform than on the wall but were significantly greater on the horizontal plates than on the vertical plates (Appendix Table 4). Fronds appeared on the platform clearings in November and on the wall clearings in December, and densities were low (Fig. 3b). Frond growth was greatest on W-h plates at Reef One and on P-h plates and platform clearings at Reef Two (Table 4). No growth was measured on the vertical plates and clearings because fronds were not observed until the last sampling date (Fig. 3b). Frond height was greatest on the P-h plates and W-h plates

at Reefs One and Two. Frond height was generally lower on the clearing treatments than on the plates (Table 4).

Physical parameters

Relative water motion was significantly greater along the platforms than along the walls at Reefs One and Two ($U = 90$, $P = 0.003$). During the settlement experiment (April through June), mean clod card DF value ($\pm$ S.E.) was 4.9 ± 2.0 on Reef One platform, 5.5 ± 0.4 on Reef Two platform, 2.6 ± 0.2 on Reef One wall, and 2.9 ± 0.4 on Reef Two wall. During the growth experiment (June through October), mean clod DF value ($\pm$ S.E.) was 4.8 ± 0.9 on Reef One platform, 4.9 ± 0.9 on Reef Two platform, 2.9 ± 0.9 on Reef One wall, and 3.9 ± 1.0 on Reef Two wall.

Percent subsurface irradiance in the horizontal plane on the reef platform was significantly greater than in the vertical plane next to the wall at Reef Two ($t_{0.05,6} = 8.06$, $P < 0.001$). Attenuation coefficients ranged from 0.13 to 0.29. Plankton blooms, thick surface kelp canopies, and particulate organic matter reduced water visibility in the kelp forest during summer and early fall. During May through September, the surface kelp canopy was thicker (more than 3 fronds thick) over Reef One than over Reef Two. Percent subsurface irradiance reaching the platform and wall in the vertical plane was generally half the percent subsurface irradiance reaching the platform or wall in the horizontal plane (Fig. 4). Irradiance measured from the platform in the vertical plane was theoretically equal to the irradiance in the horizontal plane at an average depth of 16.1 m. Irradiance measured from the wall in the vertical plane was equal to irradiance reaching a

platform in the horizontal plane at 19.3 m average depth. Calculated depths changed as a function of the surface irradiance and attenuation coefficient.

Grazing and overgrowth by sessile organisms

Invertebrate densities on the plates and clearings were low regardless of treatment type (1 to 3 grazers per 8 plates of the same treatment). Grazers included limpets, gastropods, and sea stars. Tracks through the diatom film were observed on the settlement plates, but crusts were not noticeably affected. Limpets *Collisella* sp. and *Acmaea mitra* (Rathke) and the sea star *Asterina miniata* (Brandt) were common. Only *Acmaea mitra* and the chiton *Tonicella* sp. were observed to graze on coralline crusts. Grazing appeared to cease once fronds emerged. Grazers were removed twice a week during the duration of the experiments.

Final frond densities were greater on plates with no barnacles growing over basal crusts from September through December at Reef Two wall ($F_{1,4} = 6.17$, $P = 0.029$). Frond densities were greater on the horizontal plates attached to the wall ($F_{1,4} = 130.42$, $P < 0.001$). Mean frond density ($\pm$ S.E.) on the horizontal plates with barnacle settlement was 146.5 ± 4.3 fronds per plate, and mean frond density ($\pm$ S.E.) on the horizontal plates without barnacle settlement was 241.0 ± 7.9 fronds per plate. Mean frond density ($\pm$ S.E.) on the vertical plates with barnacle settlement was 1.0 ± 2.0 fronds per plate, and mean frond density ($\pm$ S.E.) on the vertical plates without barnacle settlement was 13.5 ± 7.9 fronds per plate. Mean growth of bryozoan colonies ($\pm$ S.E.) from 28 October to 8

December on the vertical plates attached to Reef Two wall was 2.0 ± 0.4 mm per month, almost four times the growth of *Calliarthron* crusts during the settlement experiment.

Discussion

Contrary to expectations, spores (as measured by crust densities on artificial substrates) were more abundant along walls than along platforms regardless of physical differences between reefs in Stillwater Cove (Table 1). Propagules, perhaps buoyed by their mucilage sheaths, apparently moved across the platform, and oscillated downward along the wall to settle on available substrate (i.e. horizontal plates). The generally slower water flow along the wall presumably allowed the spores time to settle and attach (Fletcher and Callow 1992). As observed by Neushul et al. (1976), the artificial and natural substrates had similar species composition (i.e. this study: *Calliarthron*, sessile invertebrates, and encrusting algae) but abundances varied (less *Calliarthron* settlement on platform clearings than on settlement plates). Reed and Foster (1984) observed slower geniculate-coralline recruitment rates on cleared substrates and speculated that toxic leachates may affect recruitment. Alternatively, substrate cleared by chisel may be friable: flaking of the substrate would prevent successful spore attachment. Crust densities on artificial substrates may have been an overestimation of settlement success or post-settlement survival and growth.

Coralline spores did settle on vertical surfaces (plates and cleared substrates) on reef platforms and walls but in low densities (Table 1). The effects of settlement mortality or grazing of *Calliarthron* spores, despite low grazer densities and frequent removal of grazers by divers, may have been greater on the vertical surfaces than on the horizontal surfaces. Leonard (1994) suggested that grazing would prevent algal recruitment in low light environments if the number of potential recruits was small and algal growth rates were slow as may be the case on vertical substrates. Alternatively,

spores may have been physically unable to attach to the vertical plates. *Laminaria hyperborea* (Gunnerus) Foslíe spores released in stagnant water settled in significantly greater densities on horizontal than vertical surfaces (Fredericksen et al., 1995).

Fredericksen et al. (1995) suggested that spores first settle passively to a horizontal surface and then use their motility for microsite selection. Non-motile spores such as those of *Calliarthron* may have had very limited time to attach to a vertical substrate before being affected by gravitational forces. Although the effects of relief on vertical walls were not studied, settlement on horizontal surfaces attached to subtidal walls and the substantial frond densities observed on subtidal ledges (Figs. 1-3) indicated that, as found by Foster (1975b) on horizontal plates, the more rugose the wall, the greater the potential for spore settlement.

Growth of geniculate coralline algae was variable among sites and season as observed by Konar and Foster (1992). Basal crust growth rates of geniculate coralline algae were lower at Stillwater Cove than at the nearby cove Point Lobos (Johansen and Austin, 1970) which is characterized by less turbid water (Spalding, pers. comm.). Despite similar settlement at the two reefs, *Calliarthron* growth was reduced at Reef One. The wall assemblage at Reef One consisted primarily of encrusting coralline algae and barnacles, and at Reef Two, bryozoans, fleshy red algae, sponges, and tunicates grew on the wall (pers. ob.). A thicker surface kelp canopy, different water circulation around the reef, or little surface relief along the wall may have affected *Calliarthron* growth at Reef One. Differences in growth between summer and fall were observed, though not tested (Figs. 2 and 3). During June through September, Reefs One and Two were characterized by a thick surface kelp canopy, water turbid with phytoplankton blooms and particulate

organic matter, reduced water motion, and imperceptible basal crust growth and frond production (Figs. 2-4). Encrusting corallines persisted during winter months in Helgoland and began to grow when ambient light levels increased (Leukart, 1994). In this study, crusts persisted during summer months and began to grow in September when surface canopy was thinning (Figs. 2 and 3). Johansen and Austin (1970) reported greater frond growth in winter months at 11 m than in summer months at 5 and 8 m, indicating that shallower depths do not necessarily result in faster growth throughout the year. Heine (1983) attributed the minimum productivity of two understory algae during summer months to nutrient-poor waters and low light regimes.

Lower light levels and possibly reduced water motion may inhibit basal crust growth along vertical walls. Growth rates of basal crusts growing on horizontal surfaces attached to the platform at both reefs (with an average growth rate of 0.74 mm/mo at 8.5 m) were comparable to growth rates ranging from 0.5 to 0.6 mm/mo at 10 m measured by Konar and Foster (1992). Growth rates of basal crusts growing on vertical plates attached to reef walls (with an average growth rate of 0.18 mm/mo at 9 m and at a calculated depth of 19 m if irradiance was measured in the horizontal plane) were lower than the measured growth rate of 0.3 mm/mo on horizontal surfaces at 20 m depth, suggesting that the orientation of the reef (horizontal platform or vertical wall) may have similar effects on *Calliarthron* growth as increased depth (Konar and Foster, 1992). Regardless of recruitment conditions, growth was significantly lower on the vertical plates than on the horizontal plates, with greatest differences between *Calliarthron* growth on the vertical plates attached to the walls and on the horizontal plates attached to the platforms. Trends suggest that *Calliarthron* growth was affected by a combination of

physical factors, including light and potentially water motion, associated with plate and reef orientation.

Coralline crusts may not out-compete colonial sessile invertebrates for space but they can survive overgrowth (Sebens, 1986), indicating a method by which coralline settlers on subtidal walls can persist. Growth rates of bryozoan colonies on the vertical plates were almost four times the growth rates of basal crusts, suggesting that coralline crusts were not effective competitors for space. Coralline crusts can survive overgrowth by sessile invertebrates if the organisms are removed periodically (Sebens, 1986). For example, after detaching barnacles from vertical plates attached to reef walls, the once-hidden crusts were pigmented with apparent meristems (pers. ob.). Barnacles growing on *Calliarthron* contributed to reduced frond densities on vertical plates attached to walls. However, fronds that were able to extend between barnacle recruits continued to grow. Attached frond fragments observed on wall ledges suggest a dispersal mechanism by which *Calliarthron* can avoid overgrowth on wall habitats.

Physical conditions on vertical substrates were unfavorable for production of fronds. Harlin and Lindbergh (1977) studied algal recruitment on artificial substrates of varying small-scale roughness in the intertidal. The geniculate coralline alga *C. officinalis* settled on all treatments but only grew fronds on roughened substrates, suggesting that environmental 'cues' may determine whether the alga produces fronds. Encrusting coralline cover increases with depth (Konar and Foster, 1992). Either geniculate coralline algae are rare at depths greater than 20 m or they persist as crusts. A seasonally thick surface canopy compounded by lower light levels reaching subtidal

walls (Fig. 4) may have had the same effect on frond production as increased depth or canopy shading (Johansen and Austin, 1970; Konar and Foster, 1992).

Calliarthron fronds can grow on vertically-oriented substrates, albeit slowly and in low densities (Table 4, Figs. 2b, and 3b). Frond growth rates measured on vertical plates (0.47 mm/mo at 9.1 m) were ten times greater than rates measured at 20 m by Konar and Foster (1992). Fronds that extend outward from a wall are able to intercept downwelling irradiance, are in the surge zone where nutrient exchange is greater, and are less susceptible to grazing. Most upright macrophytes, in addition to geniculate coralline algae, found growing on subtidal walls in Stillwater Cove extend more than 1 cm from the wall (e.g. the seasonally abundant *Fryella gardneri* (Setchell) Kylin, *Fauchealaciniata* Taylor, *Callophyllis flabellulata* Harvey, *Rhodoptilum plumosum* (Harvey and Bailey) Kylin, and *Rhodymenia californica* Kylin; pers. ob.).

In conclusion, the low cover of *Calliarthron* on subtidal walls in Stillwater Cove was not due to spore availability but to limited post-settlement recruitment and, secondarily, to slow growth. Although crust density was used as a proxy for spore availability, post-settlement recruitment was overwhelmingly greater on horizontal plates than on vertical plates. Presumably this low settlement was at least partly responsible for low adult cover on walls. The combination of low light, overgrowth by other organisms, and reduced water motion contributed to slower basal crust growth on vertical substrates. Fronds can grow on vertical substrates, despite the longer time interval between settlement and frond production and lower frond densities on vertical substrates relative to horizontal substrates. However, this slow growth may result in reduced survivorship relative to platforms, and thus also contribute to their low abundance on subtidal walls.

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Table 1.

Settlement densities on horizontal and vertical plates attached to platforms and walls. Mean crust density per cm² ($\pm$ S.E.) per treatment per plate orientation (n=6 plates per plate treatment and n=3 per clearing treatment). 1= Reef One and 2= Reef Two.

	Plate Orientation			
	Horizontal		Vertical	
Platform treatment	Plate	Clearing	Plate	Clearing
	1. 10.0 $\pm$ 1.7	1. 3.3 $\pm$ 1.6	1. 3.0 $\pm$ 0.8	N/A
	2. 9.8 $\pm$ 1.7	2. 4.0 $\pm$ 1.4	2. 1.2 $\pm$ 0.4	
Wall treatment	1. 16.8 $\pm$ 2.0	N/A	1. 2.2 $\pm$ 0.8	1. <1
	2. 24.8 $\pm$ 1.3		2. 1.8 $\pm$ 0.6	2. 2.5 $\pm$ 0.5

Table 2.

Analysis of variance of the effects of reef and plate orientation on *Calliarthron* settlement density estimates at the two reefs. n = 6 plates per orientation.

Source of variation	df	Mean square	F-statistic	P-value
Reef	1	0.000	0.000	1.000
Orientation treatment	1	450.667	168.979	0.049
Reef x orientation treatment	1	2.667	0.682	0.682
Error	20	15.400		

Table 3.

Analysis of variance of the effects of reef orientation (platform and wall), plate orientation (horizontal and vertical), and rack replicates on *Calliarthron* cover at the two reefs of the growth experiment. n = 3 plates per rack, 3 racks per reef orientation. (a) Full model. (b) Reduced model.

(a)

Source of variation	df	Mean square	F-statistic	P-value
Reef (R)	1	0.554	12.048	0.008
Reef orientation (RO)	1	0.141	6.693	0.235
Plate orientation (PO)	1	0.622	62.218	0.080
R x RO	1	0.021	0.464	0.515
R x PO	1	0.010	0.362	0.564
RO x PO	1	0.028	0.862	0.524
R x RO x PO	1	0.032	1.111	0.323
Rack(R x RO)	8	0.046	1.371	0.233
Rack(R x RO) x PO	8	0.029	0.865	0.552
Error	48	0.034		

(b)

Source of variation	df	Mean square	F-statistic	P-value
Reef (R)	1	0.554	12.048	0.008
Reef orientation (RO)	1	0.141	3.055	0.119
Plate orientation (PO)	1	0.622	19.195	0.000
RO x PO	1	0.028	0.851	0.360
Rack(R x RO)	8	0.046	1.424	0.206
Error	59	0.032		

Table 4.

Growth rates of *Calliarthron* basal crusts and fronds, and final frond height (mean $\pm$ S.E.) measured on horizontal and vertical plates attached to reef platforms and walls. N/A= not applicable

Treatment	Growth experiment			Settlement experiment		
	Crust growth (mm) per plate per month, n=9 plates	Frond growth (mm) per plate per month, n plates	Final frond height (mm) per plate, n=8 plates	Crust growth (mm) per plate per month, n=4 or n quadrats	Frond growth (mm) per plate per month, n plates	Final frond height (mm) per plate, n plates
Horizontal plate on Reef One platform	0.59 $\pm$ 0.29	0.80 $\pm$ 0.35, n=5	1.45 $\pm$ 0.91	0.52 $\pm$ 0.33	0.31 $\pm$ 0.48, n=5	2.58 $\pm$ 1.29, n=7
Clearing on Reef One platform	N/A	N/A	N/A	0.50 $\pm$ 0.29, n=2 quadrats	No data	0.67 $\pm$ 0.94, n=3 quadrats
Vertical plate on Reef One platform	0.11 $\pm$ 0.46	0	0.074 $\pm$ 0.77	0.15 $\pm$ 0.19	0	0
Horizontal plate on Reef One wall	0.24 $\pm$ 0.32	0.15, n=1	0.12 $\pm$ 0.73	0.33 $\pm$ 0.24	1.20 $\pm$ 0.13, n=2	1.83 $\pm$ 1.00, n=4
Vertical plate on Reef One wall	0.09 $\pm$ 0.34	0	0	0.12 $\pm$ 0.21	0	0
Clearing on Reef One wall	N/A	N/A	N/A	0, n=3 quadrats	0, n=3 quadrats	0, n=3 quadrats
Horizontal plate on Reef Two platform	1.21 $\pm$ 0.32	1.70 $\pm$ 0.69, n=9	2.31 $\pm$ 0.69	0.63 $\pm$ 0.016	1.64 $\pm$ 0.66, n=8	4.04 $\pm$ 0.72, n=7
Clearing on Reef Two platform	N/A	N/A	N/A	0.52 $\pm$ 0.22, n=3 quadrats	1.54 $\pm$ 0.59, n=3 quadrats	3.83 $\pm$ 0.29, n=3 quadrats
Vertical plate on Reef Two platform	0.67 $\pm$ 0.23	0.75 $\pm$ 0.58, n=4	0.31 $\pm$ 1.04	0.22 $\pm$ 0.09	0	0.69 $\pm$ 1.46, n=7
Horizontal plate on Reef Two wall	0.52 $\pm$ 0.25	0.81 $\pm$ 0.70, n=7	1.87 $\pm$ 1.04	0.47 $\pm$ 0.09	0.84 $\pm$ 0.52, n=8	5.67 $\pm$ 0.60, n=3
Vertical plate on Reef Two wall	0.25 $\pm$ 0.29	0.47 $\pm$ 0.60, n=3	0	0.24 $\pm$ 0.20	0	1.27 $\pm$ 1.07, n=3
Clearing on Reef Two wall	N/A	N/A	N/A	0.08 $\pm$ 0.36, n=3 quadrats	0	0.77 $\pm$ 0.78, n=3 quadrats

*Only plates with more than 5 fronds were used to calculate frond growth per plate per month. Only plates with more than 10 fronds were used to calculate final frond height.

Table 5.

Analysis of variance of the effects of reef orientation (platform and wall) and plate orientation (horizontal and vertical) on *Calliarthron* frond density at Reef Two of the growth experiment. n = 3 plates per rack, 3 racks per reef orientation.

Source of variation	df	Mean square	F-statistic	P-value
Reef orientation (RO)	1	46.925	2.905	0.101
Plate orientation (PO)	1	479.778	21.895	0.009
RO x PO	1	12.625	0.576	0.490
Rack (RO)	4	23.171	1.435	0.253
Rack (RO) x PO	4	21.913	1.357	0.278
Error	24	16.152

Fig. 1. *Calliarthron* frond densities on platforms, rises, ledges, and walls in Stillwater Cove, California (see text for definitions). $n = 23$ per substrate type.

Fig. 2. Crust growth, crust percent cover, frond growth, and frond density per plate (12 X 14 cm) per treatment at Reefs One and Two of the growth experiment. (a) Crust diameter per plate per treatment per month (n = 9 per treatment). Boxed values ± S.E. indicate final percent cover per plate per treatment, measured on 13 December 2000. (b) Frond height per plate per treatment per month (sample size per month noted by numbers above bars). Boxed values ± S.E. indicate final frond densities per plate per treatment measured on 8 December 2000 (n = 9; plates with zero frond densities were included). Abbreviations include: P-h: horizontal plane on the platform; P-v: vertical plane on the platform; W-h: horizontal plane on the wall; W-v: vertical plane on the wall.

Fig. 3. Crust growth, crust percent cover, frond growth, and frond density per plate (12 X 14 cm) per treatment at Reefs One and Two of the settlement experiment. (a) Crust diameter per plate per treatment per month ($n = 8$ for platform treatment, $n = 4$ for wall treatment, and $n = 3$ for clearings). Boxed values $\pm$ S.E. indicate final percent cover per plate per treatment, measured on 8 December 2000 ($n = 8$ for platform treatment, $n = 4$ for wall treatment, and $n = 3$ for clearings). (b) Frond height per plate per treatment per month (sample size per month noted by numbers above bars). Boxed values $\pm$ S.E. indicate final frond densities per plate per treatment measured on 8 December 2000 ($n = 8$ for platform treatment, $n = 4$ for wall treatment, and $n = 3$ for clearings; plates with zero frond densities were included). Abbreviations include: P-h: horizontal plane on the platform; P-v: vertical plane on the platform; W-h: horizontal plane on the wall; W-v: vertical plane on the wall.

Fig. 4. Percent subsurface irradiance measured in the horizontal plane at three depths (8.5, 9.1, and 11.6 m) and vertical plane at two depths (8.5 and 9.1 m). Abbreviation: P-h: horizontal plane on the platform; P-v: vertical plane on the platform; W-h: horizontal plane on the wall; and W-v: vertical plane on the wall.

Appendix Table 1.

Analysis of variance of the effects of reef orientation (platform and wall), plate orientation (horizontal and vertical), and rack replicates on *Calliarthron* basal crust growth (from 23 June to 21 October) at the two reefs of the growth experiment. n = 3 plates per rack, 3 racks per reef orientation.

Source of variation	df	Mean square	F-statistic	P-value
Reef (R)	1	6.988	22.324	0.001
Reef orientation (RO)	1	4.505	6.491	0.238
Plate orientation (PO)	1	5.561	99.306	0.064
R x RO	1	0.694	2.218	0.175
R x PO	1	0.056	0.401	0.544
RO x PO	1	0.495	3.056	0.331
R x RO x PO	1	0.162	1.154	0.314
Rack(R x RO)	8	0.313	4.939	< 0.001
Rack(R x RO) x PO	8	0.140	2.213	0.043
Error	48	0.063		

Appendix Table 2.

Analysis of variance of the effects of reef orientation (platform and wall) and plate orientation (horizontal and vertical) on *Calliarthron* cover at the two reefs of the settlement experiment. n = 4 plates per plate orientation.

Source of variation	df	Mean square	F-statistic	P-value
Reef (R)	1	0.491	24.802	< 0.001
Reef orientation (RO)	1	0.133	0.479	0.614
Plate orientation (PO)	1	2.509	22.208	0.133
R x RO	1	0.278	14.016	0.001
R x PO	1	0.113	5.683	0.025
RO x PO	1	0.107	2.322	0.370
R x RO x PO	1	0.046	2.344	0.139
Error	24	0.020		

Appendix Table 3.

Analysis of variance of the effects of reef orientation (platform and wall) and plate orientation (horizontal and vertical) on *Calliarthron* basal crust growth (from 21 June to 20 September) at the two reefs of the settlement experiment. n = 4 plates per plate orientation. (a) Full model. (b) Reduced model.

(a)

Source of variation	df	Mean square	F-statistic	P-value
Reef (R)	1	0.239	8.538	0.007
Reef orientation (RO)	1	0.113	9.446	0.200
Plate orientation (PO)	1	1.615	57.819	< 0.001
R x RO	1	0.012	0.426	0.520
R x PO	1	0.000	0.000	0.997
RO x PO	1	79.623	79.623	0.071
R x RO x PO	1	0.001	0.036	0.851
Error	24	0.028		

(b)

Source of variation	df	Mean square	F-statistic	P-value
Reef (R)	1	0.239	9.424	0.005
Reef orientation (RO)	1	0.113	4.779	0.044
Plate orientation (PO)	1	1.615	63.818	< 0.001
RO x PO	1	0.079	3.132	0.088
Error	27	0.025		

Appendix Table 4.

Analysis of variance of the effects of reef orientation (platform and wall) and plate orientation (horizontal and vertical) on *Calliarthron* frond density at Reef Two of the settlement experiment. n = 4 plates per reef orientation.

Source of variation	df	Mean square	F-statistic	P-value
Reef orientation (RO)	1	0.0329	0.032	0.860
Plate orientation (PO)	1	826.808	81.312	< 0.001
RO x PO	1	7.309	0.719	0.413
Error	12	10.168

Appendix Figure 1. Basal crust growth per rack (R) replicate of the growth experiment at the two reefs. Note different scales. (a) Growth on platform. (b) Growth on walls.