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Title

Human and Natural Causes of Variation of Forage Species on Nearshore Rocky Reefs

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A central goal of community ecology is to understand spatial and temporal variation in species assemblages. In central California, nearshore rocky reefs fluctuate between forested states of giant kelp, and "barren" states with minimal foliose algae and high densities of sea urchins. Many have sought to explain the mechanisms behind such phase shifts (Harrold and Reed 1985, Scheibling and Hennigar 1997), driven in part by the belief that forested reefs are more productive than barrens in terms of commercially valuable fish and invertebrates (Schiel and Foster 1986). However, the benthic communities on urchin barren reefs can vary dramatically and little attention has been given to understanding the ecological processes creating these patterns. Such variation among barren types is important to study because it may influence fish biomass as well as the speed at which barrens transition to a forested state. My research focused on how an associated defense involving the colonial sea anemone, *Corynactis californica*, facilitates an algal community on otherwise barren reefs and how human activities that alter sediment loading to the coastal ocean might influence the spatial distribution of this anemone.

Sea urchin barrens are often dominated by encrusting coralline algae and have urchin densities as high as 80/m². One of the few places where foliose algae exist on these reefs is on rocky outcrops, which are inaccessible to urchin grazers. Algal refuges on barrens may be particularly important to reef associated fish, as they provide important habitat for their invertebrate prey. Results from my research suggested that colonies of *Corynactis* can provide refuges for algae and small invertebrates. This associational defense, afforded to organisms growing in close proximity to *Corynactis*, is a result of its powerful nematocysts, or stinging cells, with which they use to capture zooplankton. In field surveys where *Corynactis* covered approximately 30% of reef surface area, I found that sea urchins were rarely in contact with *Corynactis* tentacles (Figure 1). Upon contacting *Corynactis* in the laboratory, both purple and red urchins (*Strongylocentrotus spp.*) responded by retracting their tubefeet (Figure 2). Tubefeet are important for locomotion, particularly for the shorter spined purple urchins. These studies revealed that both of these abundant, barren-forming sea urchin species are averse to contact with *Corynactis*.

Previous studies have found that *Corynactis* colonies impede movement in other benthic invertebrates, namely *Pisaster* sea stars, and in doing so create a refuge for their bivalve prey (Patton *et al.* 1991). My research found a similar pattern to exist for grazing sea urchins. In laboratory trials, a barrier with 30% *Corynactis* cover deterred starved purple urchins from accessing kelp on the other side, thus defending an existing “patch” of algae (Figure 3). In order to test whether *Corynactis* could facilitate the establishment of algae in barren habitats, I manipulated the density of *Corynactis* on scallop half-shells and transplanted them to an urchin barren at Coal Oil Point Reef in the Santa Barbara Channel. Transplanted shells were either bare or entirely covered with *Corynactis*, except for a 2.25 in² section scraped from the center of the

shell. Strong differences in the assemblage of colonizing biota between shells with and without a “barrier” of *Corynactis* were apparent after only two months. Filamentous algae developed on the scraped section of *Corynactis*-covered shells, whereas the shells lacking *Corynactis* remained unchanged (Figure 4). This pattern persisted on the shells with a high coverage of *Corynactis*, with foliose red algae gradually replacing filamentous red algae within 12 months.

Most studies of associational defenses focus on the protection that one individual provides to organisms growing in its immediate vicinity. This model may not apply to *Corynactis*, which is tiny relative to other benthic organisms and can vary from 0 to 100% cover over small spatial scales. I tested whether the protection afforded by *Corynactis* to algae and invertebrates was dependent on the extent of its coverage by transplanting half shells of mussels that varied in the percentage of their shell that was covered by *Corynactis*. The shells were collected from offshore oil platforms in the Santa Barbara Channel, *Corynactis* cover was manipulated in the laboratory, and shells were transplanted to an urchin barren on Carpinteria Reef. Between 0 and 85% of the surface area of the mussel shells were covered with *Corynactis*. The extent to which the remaining bare space changed was strongly influenced by the distribution of *Corynactis*. The bare space on transplanted shells having less than 15% *Corynactis* cover remained unchanged for 9 months, and eventually developed patches of encrusting coralline algae after 13 months. There was a strong positive correlation between *Corynactis* cover and the amount of bare space colonized by either algae or tube dwelling amphipods on shells having greater than 15% cover of *Corynactis* (Figure 5). The results from this experiment suggest that there is a critical mass of *Corynactis* necessary to facilitate recruitment of turf-forming organisms and the strength of this defense increases with increasing *Corynactis* cover.

Associated defenses are generally not one-way interactions. Often the defended species is a strong competitor, but vulnerability to herbivory, predation, or environmental stress confines it to areas in close proximity to species which mitigate these negative effects. The vulnerable species may compete for resources with the protector and, in the absence of negative effects, outcompete its beneficent neighbor. Not only do algae and anemones compete for attachment space on rocky reefs, but previous findings (Coyer *et al.* 1993) suggest that algae may interfere with anemone feeding. When blades of algae abrade the tentacles of cup corals, the polyps retract their tentacles and suspend feeding. This pattern is consistent with my results from an algal removal experiment on Naples Reef in the Santa Barbara Channel. I removed algae every 3 weeks from 1 m^2 plots starting in May 2003. After 4 months, both density and cover of *Corynactis* were higher in plots where algae were removed (Figure 6, 7).

These experiments indicate that the strength and direction of the *Corynactis*-algae interaction depends on consumer pressure. Under low grazer densities, algae may be expected to outcompete *Corynactis* for attachment space and overgrow existing individuals. As grazer densities increase, algae are cropped to within the narrow confines of *Corynactis* patches. Financial and logistical support from the Santa Barbara Coastal Long Term Ecological Research Program (SBC LTER) has enabled me to further explore this hypothesis by using transplanted mussel shell outplants that vary in *Corynactis* cover. At multiple sites in the Santa Barbara Channel I am tracking the communities that colonize these shells and I am measuring grazing intensity. Preliminary results suggest that there is a direct relationship between grazing intensity and the dynamics of this associated defense.

The spatial distribution of *Corynactis*-algal turf patches depends heavily on factors that influence demographic rates in *Corynactis*. Once *Corynactis* larvae settle and become

established on a reef, the rate at which colonies form and expand depends on factors such as predation, food supply, and competition. Muntz *et al.* (1972) found that a *Corynactis* congener was absent from areas exposed to siltation. In the Santa Barbara Channel, my own surveys and those of the SBC LTER found *Corynactis* to be rare on reefs in close proximity to shore. To test if the absence of *Corynactis* could be explained by turbidity and/or exposure to silt, I added a range of silt concentrations to *Corynactis* colonies in the laboratory. Over the four month experiment, *Corynactis* divided less and became smaller in high silt treatments (Figure 8, 9). I suspected the mechanism behind these patterns had to do with silt interfering with anemone feeding, but the results of this part of the study were inconclusive. While turbid waters may be created via resuspension events, these results suggest proximity to shore and exposure to the constituents of terrestrial runoff may influence the distribution of this under-appreciated animal. I hope this CEQI-sponsored research will help to broaden the current kelp forest-urchin barren paradigm and heighten awareness as to how land use practices may influence community dynamics on nearshore rocky reefs.

References

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Presentations generated by the project

Poster, Silt as a Marine Contaminant: It's Effect on Demographic Rates in the Colonial Sea Anemone, *Corynactis Californica*, and Important Indirect Effects on the Benthic Community, 17th Annual Research Symposium, UC Toxic Substances Research and Teaching Program, 2004

Poster, The Effect of Siltation on the Colonial Sea Anemone, *Corynactis californica*, 16th Annual Research Symposium, UC Toxic Substances Research and Teaching Program, 2003

Poster, Human and Natural Causes of Variation in Benthic Community Composition on Nearshore Rocky Reefs, 15th Annual Research Symposium, UC Toxic Substances Research and Teaching Program, 2002

Poster, Human and Natural Causes of Variation in Fish Forage Species on Nearshore Rocky Reefs, 14th Annual Research Symposium, UC Toxic Substances Research and Teaching Program, 2001

Poster, Mechanisms Controlling Oligochaete Populations at a Natural Hydrocarbon Seep, 13th Annual Research Symposium, UC Toxic Substances Research and Teaching Program, 2000

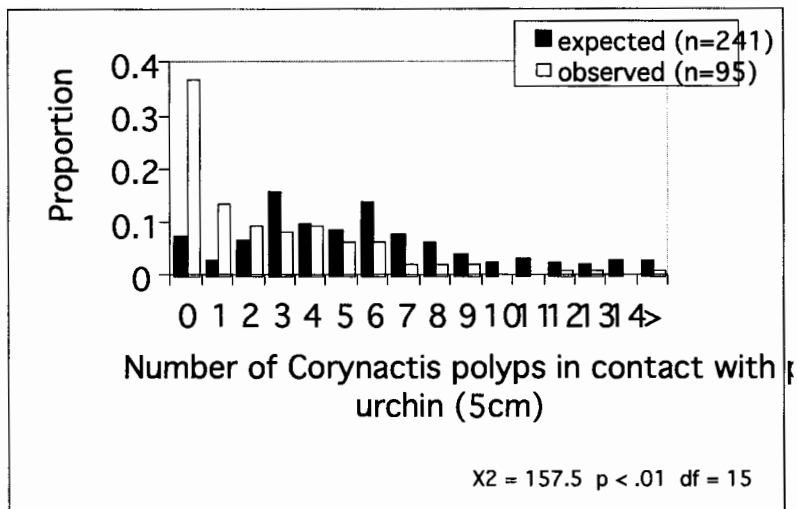


Figure 1: Number of *Corynactis* individuals in contact with 5 cm urchin, compared to number expected if randomly distributed over same area. χ^2 test of Homogeneity $\chi^2=157.5, p < 0.01$

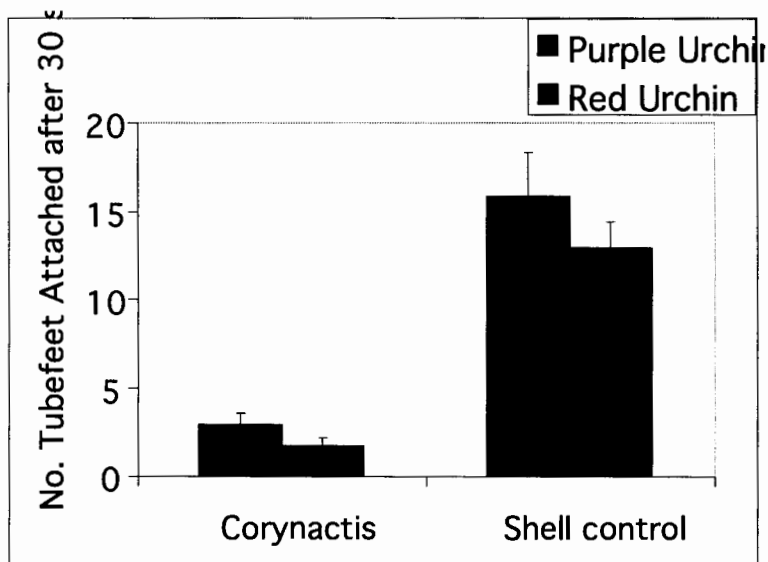


Figure 2: Number of tubefeet in contact with substrate, 30 seconds after being placed on the substrate. Student's t-test $p < 0.001$ for both purple and red urchins.

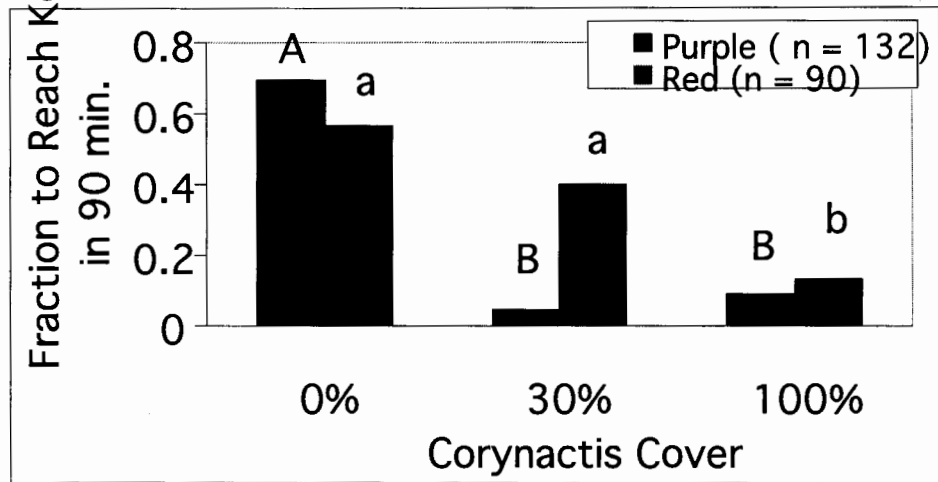


Figure 3: Fraction of starved sea urchins to cross a barrier with 0, 30, and 100% cover of *Corynactis* and reach kelp on the other side in a 90 minute period. Pairwise χ^2 square test. Capital letters distinguish significant differences among purple urchin treatments, lower case letters distinguish significant differences among red urchins.

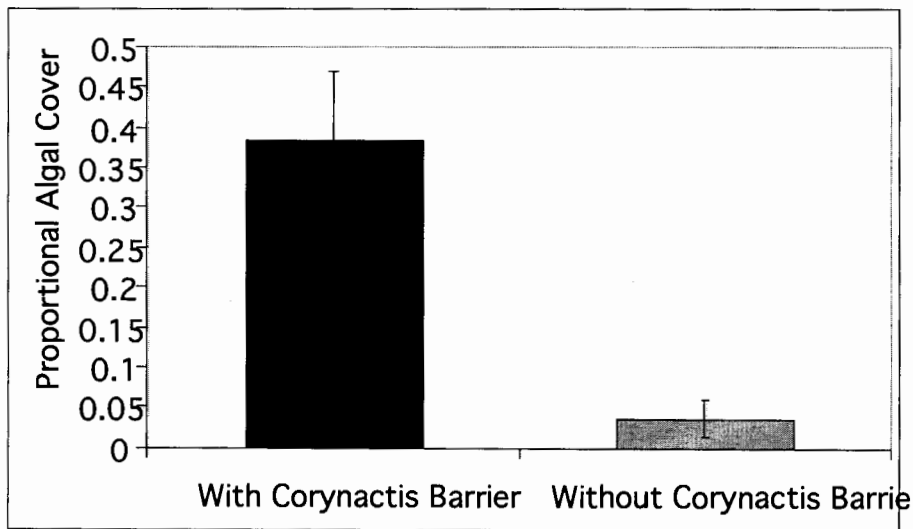


Figure 4: Algal cover on outplants with and without a barrier of *Corynactis*. Student's t-test: $p < 0.001$

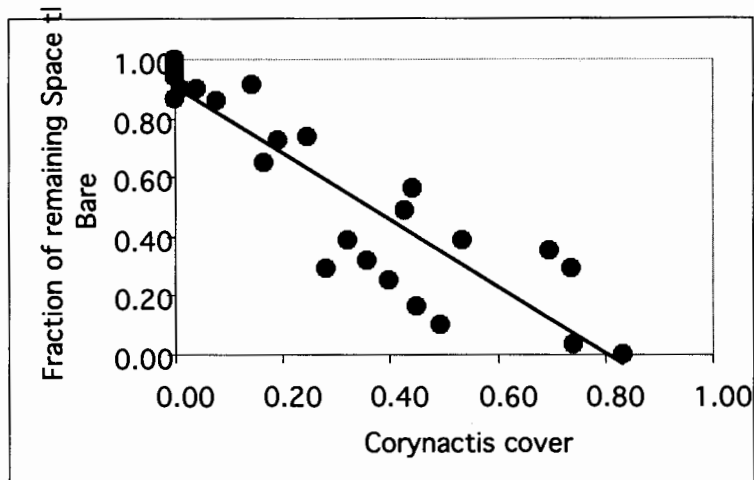


Figure 5: Fraction of remaining space on outplants that is bare with respect to *Corynactis* cover. ($r^2 = 0.81$ $p < 0.01$)

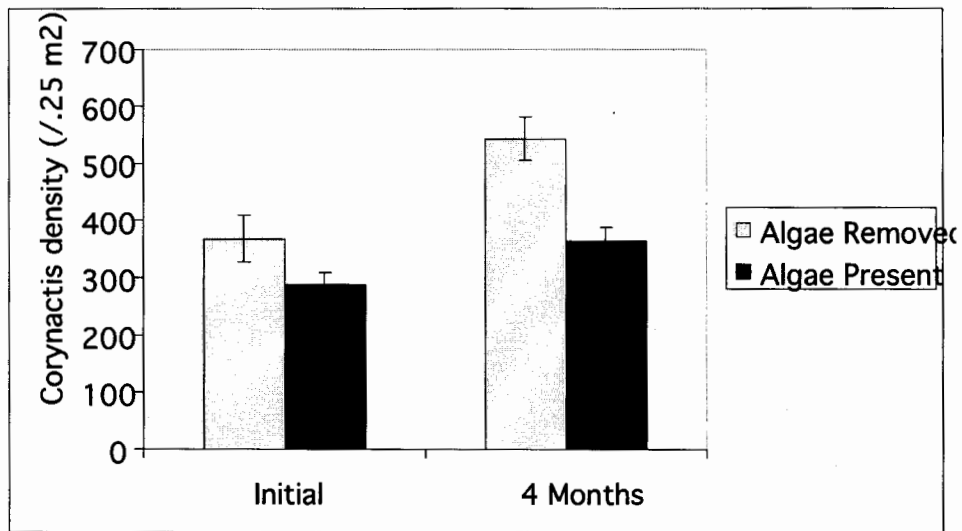


Figure 6: *Corynactis* density in 0.25 m^2 plots where algae were removed and present. *Corynactis* were censused at the beginning of the experiment and after 4 months. Students t-test (on proportional change in density): $p = 0.03$

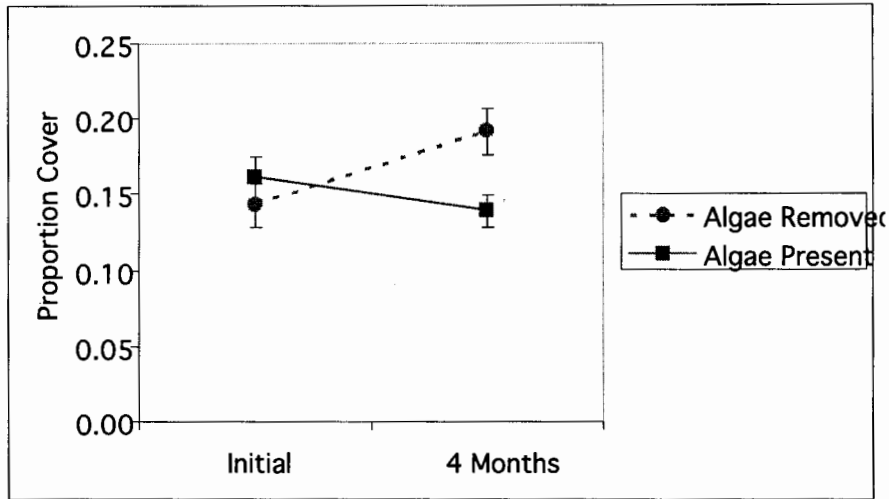


Figure 7: *Corynactis* proportional cover in 1 m² plots where algae were removed and present. Cover was measured at the beginning of the experiment and after 4 months. Student's t-test (on absolute change in *Corynactis* cover): $p < 0.01$

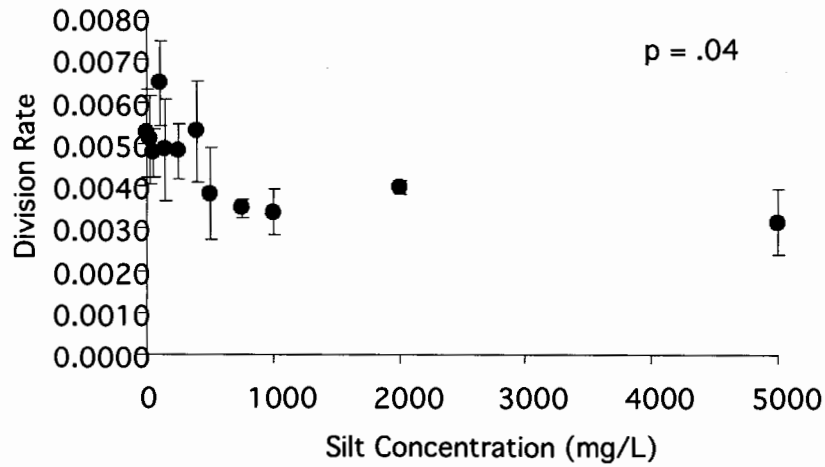


Figure 8: Average *Corynactis* division rate along a gradient of silt concentration (ANCOVA $p = 0.02$)

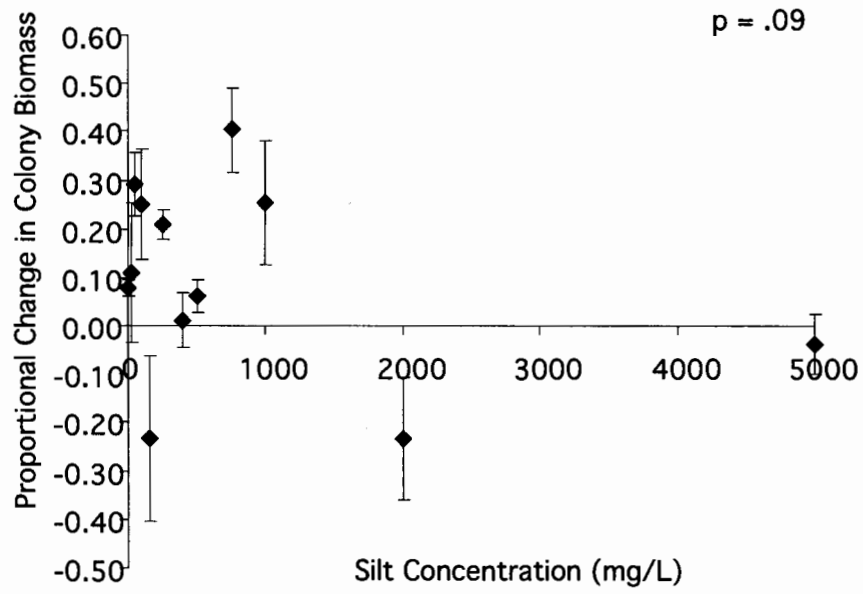


Figure 9: Proportional change in *Corynactis* biomass along a gradient of silt concentration (ANCOVA $p = 0.09$)