Multiple successional sequences have been observed following disturbance in communities on marine hard substrata. Observations of the turf-forming alga, Iridaea cornucopiae Post. & Rupr. (Gigartinaceae), suggest that I. cornucopiae may assume its dominance by its ability to vegetatively pre-empt space. High limpet densities in the natural community, suggest that I. cornucopiae may be a grazer-resistant and, perhaps, grazer-dependent alga. Succession would be expected to take different trajectories if conditions affecting vegetative recovery or levels of herbivory were varied.

Observational and experimental studies indicate that established beds of I. cornucopiae resist both invasion by ephemeral algae (in the presence of limpet grazers) and physical disturbances. The community can rapidly adjust, by vegetative regeneration of dominant perennial algae, to disturbances which remove only the canopy. Recovery from disturbances which remove perennating structures, however,
is slow.

Effects of herbivores and season of initial disturbance on primary succession were experimentally investigated, using copper paint barriers for limpet exclosures. Effects of copper paint on subsequent colonization were quantified for the first time. Most groups of organisms were not affected by the presence of the paint. Densities of barnacles and limpets were reduced, while abundances of some early successional algae were enhanced (possibly due to reduced limpet densities).

Removal of limpets resulted in qualitatively different early successional pathways. In the presence of limpets, the successional pathway was characterized by high levels of free space and persistence of perennial algae. In the absence of limpets, the early successional assemblages were dominated by ephemeral algae.

Season of initial disturbance affected successional trajectories mainly because of seasonal patterns in the establishment of perennial algae. Different species of ephemeral algae were able to recruit in both seasons of disturbance tested (fall and spring), but perennial algal establishment was highly seasonal. The removal of ephemeral species by grazers may be a necessary condition for early establishment of perennial algae, but it clearly is not sufficient. Space made available by grazers during physiologically stressful periods may be effectively unavailable for colonization by perennial algae.

by

Annette M. Olson

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EARLY SUCCESSION IN BEDS OF THE RED ALGA, 
IRIDAEA CORNUCOPIAE POST. & RUPR. (GIGARTINACEAE):
ALTERNATE PATHWAYS

INTRODUCTION

When a disturbance frees space and space-related resources in a community, organisms quickly begin to occupy the space and to use the liberated resources. Certain species tend to dominate space soon after disturbance, while other species tend to replace them, predominating later. This temporal sequence of occupants is termed "ecological succession."

Despite a vast theoretical and empirical literature on succession, American ecologists remain divided on the best way to describe and explain successional sequences. In critical reviews, McIntosh (1980, 1981) and Finegan (1984) describe the controversy as a conflict between holistic (e.g., Clements 1916; Clements and Weaver 1924; Margalef 1963a, 1963b; Whittaker 1975) and reductionistic (e.g., Gleason 1927, Egler 1954, Drury and Nisbet 1973, Pickett 1976, Connell and Slatyer 1977) perspectives in ecology.

Proponents of these perspectives differ in the relative importance they attribute to deterministic versus stochastic processes in structuring communities. Holists tend to emphasize relatively predictable relationships among colonizing species, such as facilitation (Clements 1916) and competition (Clements and Weaver 1924, Clements
et al. 1929). In this scheme, successional sequences are relatively simple, resulting in a stable "climax" community structure (e.g., Whittaker 1975). Reductionists, on the other hand, place more importance on the chance events and external conditions impinging on colonizing species, including local disturbance (Pickett 1976, Connell and Slatyer 1977), propagule availability (Gleason 1927; Egler 1954; Drury and Nisbet 1973; Connell and Slatyer 1977; Cattelino et al. 1979; Noble and Slatyer 1980; Horn 1981a, 1981b), and herbivory (Connell and Slatyer 1977). In reductionist models, successional pathways may be complex and a stable climax community does not necessarily exist.

A growing number of essentially reductionist succession models incorporate both deterministic and stochastic factors in complex models of succession (e.g., Cattelino et al. 1979; Noble and Slatyer 1980; MacMahon 1980, 1981; Horn 1981a, 1981b). In these models, the set of deterministic factors considered important in succession is extended to include species life histories (Gleason 1927; Egler 1954; Drury and Nisbet 1973; Pickett 1976; Horn 1974, 1975, 1981a, 1981b; Cattelino et al. 1979; Noble and Slatyer 1980; Botkin 1981) and additional interspecific relationships, such as tolerance and inhibition (Drury and Nisbet 1973; Connell and Slatyer 1977; Horn 1981a, 1981b). Relatively linear successional sequences result from the life histories of, or the interactions among, colonists.
Stochastic processes (e.g., variability in season or intensity of initial disturbance, propagule availability, and herbivory) serve as contingencies that divert or interrupt deterministic sequences. Consequently, alternate sequences, or pathways, may exist by which succession proceeds under different sets of initial and/or ongoing conditions. Diagrams of successional pathways thus resemble flow-charts (Cattelino et al. 1979; Noble and Slatyer 1980; Harcombe et al. 1980 [figure in Draper and Hamilton 1984]; MacMahon 1980, 1981; Parminter 1983 [figure in Draper and Hamilton 1984]), with linear sequences and decision boxes representing deterministic and stochastic factors, respectively.

The degree of community stability should also influence successional pathways. If a community resists a particular type or intensity of disturbance (Margalef 1969, Sutherland 1981, Connell and Sousa 1983, Pimm 1984), the community remains unchanged and, by definition, succession does not occur. If a particular type or magnitude of disturbance produces a change in the community, however, succession results. In holistic models, succession would deterministically lead toward the climax community structure. Because multiple pathways may exist in reductionist models, however, the question arises whether succession would lead to the pre-disturbance community structure (i.e., adjust, Margalef 1969; recover, Sutherland 1981), or whether a new community structure would emerge
(i.e., permanent alteration, Sutherland 1981; instability, Connell and Sousa 1983).

A model of succession in a community should specify the conditions which result in "switches" between alternate successional pathways. The first "switch"-point in a succession model would occur at the intensity of disturbance necessary to produce a change in the community initiating succession (a Type II disturbance, Sutherland, 1981). A subsequent contingency would occur if a disturbance produced a change from which the community could not recover, resulting in a new community structure (a Type III disturbance, Sutherland 1981). The specific locations of these switch-points on a disturbance intensity gradient would depend on the means available to the dominant residents for persisting through a disturbance (Cattelino et al. 1979, Noble and Slatyer 1980). For example, at low disturbance intensities, both vegetative and reproductive structures of dominant species in a community may be unaffected, conferring resistance stability on the community. At intermediate intensities, disturbance may destroy reproductive capacity, but the vegetative structures of the dominant species may persist, allowing them to pre-empt space following the disturbance, enhancing recovery, or adjustment stability. However, at high intensities, disturbance may destroy both vegetative and reproductive tissue.

Colonization following intense disturbance would be by
recruitment from propagules. Depending on other contingencies, such as herbivory and season of initial disturbance, various community structures may emerge. Herbivores may alter successional pathways by preventing competitive exclusion among colonists (e.g., Connell 1971, 1975; Lubchenco and Menge 1978, Lubchenco 1978). Season of initial disturbance may affect propagule availability, stress tolerance, and other factors that influence establishment and growth of colonists (e.g., Sousa 1979, Sousa et al. 1981, Turner 1983, Jara and Moreno 1984).

Empirical studies confirm that succession in many terrestrial and marine communities need not be restricted to a single linear sequence. In studies of primary succession following glacial retreat, Matthews (1979a, 1979b) found diverging successional pathways leading to alternate states. Studies of secondary succession in forests also suggest that succession follows multiple pathways (Arno and Simmerman 1982; Horn 1981a, 1981b; Franklin and Hemstrom 1981). Alternate successional trajectories have also been documented in marine fouling communities (e.g., Sutherland 1974, 1981) and in rocky intertidal systems (e.g., Lubchenco 1978, 1980, 1982; Lubchenco and Menge 1978; Sousa 1979, 1980, 1984; Paine and Levin 1981; Turner 1983, 1985). Further, alternate pathways may either converge on a singular "climax" community (e.g., secondary forest succession, Horn 1974, 1975, Christensen and Peet 1981, 1984; mussel beds, Paine

Historically, most studies of succession have been conducted in terrestrial forest systems, where the longevity of the dominant organisms (even in early stages of succession) often prohibits direct observation of successional sequences (see review in Austin 1977). In the few long-term studies of succession in permanent plots, factors affecting succession after the initial disturbance are usually not experimentally manipulated (e.g., Dyrness 1973, Austin 1977, Swaine and Greig-Smith 1979, Christensen and Peet 1981, Pickett 1982). In rocky intertidal systems, however, both the temporal and spatial scale of the communities are often amenable to experimental manipulations (e.g., Lubchenco and Menge 1978; Lubchenco 1978, 1980, 1982; Sousa 1979, 1980; Turner 1983, 1985). Successional sequences can be directly observed and mechanisms can be experimentally investigated.

I experimentally investigated specific conditions that result in alternate trajectories during early succession in a long-term study of successional pathways in beds of the high intertidal alga, *Iridaea cornucopiae* Post. & Rupr.
Beds of *I. cornucopiae* can locally dominate the intertidal zone above mussel beds (Waaland 1977, Kozloff 1983), particularly on north-facing slopes (pers. obs.), on exposed, rocky shores of the northeast Pacific Ocean. Its extensive encrusting holdfast suggests that *I. cornucopiae* may assume its dominance and confer stability on the community by vegetatively pre-empting space. High limpet densities, averaging around 1000 m\(^{-2}\) in the natural community (Olson, unpublished data), suggest that *I. cornucopiae* is a grazer-resistant and, perhaps, grazer-dependent alga. Although little is known of the ecology of *I. cornucopiae* beds, their dynamics may be similar to those of other rocky intertidal systems similarly dominated by red algae in the family Gigartinaeae (Foster 1982; Jara and Moreno 1984; Lubchenco 1978, 1980, 1982; Lubchenco and Menge 1978; Sousa 1979, 1980; Sousa, et al., 1981). In these communities, factors switching succession among alternate pathways include (1) persistence and recovery of the dominant perennial algae by vegetative means, (2) alteration of competitive relationships by herbivory (including biotic disturbances caused by herbivores), and (3) variation of these effects with season of initial disturbance.

Succession in *I. cornucopiae* beds would thus be expected to switch between alternate pathways if conditions affecting vegetative recovery and levels of herbivory were
varied. I tested these expectations by monitoring unmanipulated plots and by conducting canopy and holdfast removal and limpet exclusion experiments in two seasons. I attempted to answer the following questions:

1. How consistent are the patterns of species composition and relative abundance in established beds of *Iridaea cornucopiae* over time and space.

2. How does the community respond to physical disturbances that remove the canopy, but leave the basal structures intact? In particular, does the perennial crustose holdfast of *I. cornucopiae* allow it to recover from canopy removal?

3. Does differential herbivory switch succession between alternate pathways?

4. Do disturbances in different seasons result in alternate pathways of succession?
STUDY SITE

This study was conducted on a basaltic headland at the south side of the mouth of Whale Cove, 23 km north of Newport on the central Oregon coast (Figure 1). The study site is located on a north-facing bench, cut by wave action into low cliffs. The basaltic substratum, a breccia (Snavely and MacLeod 1971), has a relatively smooth, fine-grained surface from which project harder fragments of irregular shapes and sizes. Deep vertical and oblique fracture lines form crevices which divide the rock surface.

At the seaward edge of the bench, patches of Postelsia palmaeformis Rupr.--a kelp restricted to wave-exposed sites (Ricketts et al. 1968)--indicate a high wave-energy environment. Mussel beds (Mytilus californianus Conrad) occupy the relatively flat surface of the bench. The study community, dominated by the turf-forming red alga, Iridaea cornucopiae, occurs at the back of the bench in a broad band on sloping surfaces above the mussel beds. Cliffs to the south rise approximately 10 m above the bench, shading the study site for portions of the day throughout the year.
Figure 1. Location of study area.
METHODS

Study Design

The objectives of the study were, first, to describe the species composition and abundances in the natural community over time and, second, to experimentally investigate three factors—physical disturbance, herbivory, and season of initiation—affecting successional pathways in the community. However, time and personnel limitations precluded implementation of a full factorial design, including all three factors and appropriate controls (Figure 2). Thus, a more limited experimental design was adopted (Figure 2, unshaded areas), which addressed two separate questions: First, at "natural" levels of herbivory, how does the community respond to disturbance? and, second, what is the effect of different levels of herbivory on early successional trajectories? The effects of season of initiation were investigated in both sub-studies.

*Iridaea cornucopiae* and herbivore abundances varied along a wave-exposure gradient (Olson, unpublished data). I controlled for effects of wave-exposure and other micro-site variability, by using a randomized block design which clustered plots together in replicate blocks. Blocks were subjectively located along a 30 m horizontal transect in the *I. cornucopiae* beds at the site. Criteria for establishing a block were that the area should (1) have
Figure 2. Study design. A full factorial design to investigate the effects of four factors--level of disturbance, season of disturbance, presence/absence of limpets, and presence/absence of exclosures--on succession. The actual treatments implemented are indicated by the unshaded areas. F = Fall (September - October 1982); S = Spring (May 1983).
relatively high, uniform canopy cover (≥50%) of *Iridaea cornucopiae*, (2) be approximately 2.5 m wide and 1.5 m high to allow for spacing of experimental plots (Figure 3), and (3) lack any major heterogeneities (e.g., large crevices or holes). The lower edge of all blocks lay at approximately 3 - 4 m above mean low low water (MLLW).

Within each of six replicate blocks, nine plots were laid out as in Figure 3A. Plot locations were limited by the *I. cornucopiae* cover and substratum homogeneity criteria listed above, with the exception that it was not always possible to avoid placing a plot over one of the harder rock fragments that project from the bedrock.

The three-row plot layout in Figure 3A was selected for three reasons. First, it was not possible to locate all plots within a block at a single tidal height, because the total area of the *Iridaea cornucopiae* beds at the site was limited in extent. Second, treatments involving limpet barriers of copper-based paint could affect surrounding areas by leaching of copper, particularly at low tide when water drains from the algae and seeps down the rock surface. Staggering the plots created a buffer area around each plot to minimize potential confounding effects of copper paint toxicity from neighboring plots. Third, staggering the plots provided space to kneel while maintaining the treatments and monitoring the results. In some blocks, a heterogeneous substratum altered the plot spacing somewhat, but care was taken to ensure that a block
Figure 3. Plot layout and design. A. Idealized layout of plots within a block to minimize between-plot interference (see text) and provide access for monitoring. B. Design of plots and treatments. 1. Canopy removal and non-paint control treatments. 2. Paint control treatment. 3. Limpet exclosure treatment.
was not more than 3.0 m wide and that plots were spaced at least 40 cm apart, vertically. Z-spar marine epoxy putty permanently marked plot locations prior to assignment of treatments.

**Treatments**

The study design yielded nine treatments (Table 1). First, permanent "control" plots were established in each block (treatment 1, Table 1) to provide a description of the natural community, to follow natural variation over time, and to serve as an unmanipulated reference point. Nothing was manipulated in these plots.

Second, I experimentally removed the algal canopy (treatments 2 and 6, Table 1; Figure 3B-1) to determine the response of the community to moderate disturbance. The canopy removal simulated naturally occurring disturbances, such as log-bashing (Dayton 1971), that remove or damage upright algal structures, leaving basal perennating structures intact. I initiated this treatment in fall 1982 and again in spring 1983 (Table 1) to assess the effect of season of disturbance on recovery.

A paint-scraper or putty knife was used to remove the algal canopy. Upright algae (>=5 mm) that remained after scraping were removed with a forceps. In addition, because it was impossible to avoid killing some limpets and barnacles during scraping, all limpets were removed and all barnacles were killed and the wall plates of their tests
<table>
<thead>
<tr>
<th>Treatment</th>
<th>Date of Initiation</th>
<th>Treatment Summary</th>
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</thead>
<tbody>
<tr>
<td>1. Unmanipulated</td>
<td>2 OCT 82</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>2. Fall-Canopy Removal</td>
<td>15 SEP 82</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>-</td>
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<tr>
<td>3. Fall-Non-paint Control</td>
<td>3-4 OCT 82</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>4. Fall-Paint Control</td>
<td>3-4 OCT 82</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
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<tr>
<td>5. Fall-Limpet Exclosure</td>
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<td>-</td>
<td>+</td>
<td>-</td>
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<tr>
<td>6. Spring-Canopy Removal</td>
<td>12-14 MAY 83</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>7. Spring-Non-paint Control</td>
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<td>-</td>
<td>+</td>
<td>+</td>
<td>-</td>
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<tr>
<td>8. Spring-Paint Control</td>
<td>12-15 MAY 83</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>9. Spring-Limpet Exclosure</td>
<td>12-15 MAY 83</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>+</td>
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\( ^a + = \text{yes}, - = \text{no} \)

\( ^b + = \text{present}, - = \text{absent} \)
were removed. Edges of the scraped plots were chiseled bare to inhibit lateral vegetative encroachment of algae. After the canopy removal treatment, algal crusts and holdfasts remained, but upright algal fronds, barnacles, and limpets were initially absent. Subsequently, limpet invasion, barnacle and algal recruitment, and vegetative algal recovery were permitted, but lateral vegetative encroachment by algae was prevented by periodic wire-brushing of plot borders.

Third, limpet exclosure and control treatments were established in experimentally denuded plots (treatments 3-5 and 7-9, Table 1) to test the effects of herbivory on primary successional pathways. The denuding treatment simulated natural disturbances, such as exfoliation of the rock surface or severe scouring by wave-borne debris, that would initiate primary succession by exposing bare rock surfaces. I initiated these treatments in fall 1982 and again in spring 1983 (Table 1) to assess the effect of season of disturbance on successional patterns.

Denuded plots were first scraped with a paint-scraper, then burned with a propane torch for at least 15 minutes, brushed with a wire brush, and painted with lye-based oven cleaner paste (J. Cubit, pers. comm. cited in Padilla 1981). The paste was washed away by subsequent high tide(s). The burn-brush-and-lye procedure was repeated until all visible plant and animal remains (with the exception of bleached coralline algal crusts and some
calcareous bases, or "scars", of barnacle tests) were removed from the rock. The denuding treatment resulted in essentially bare rock, with algal crusts and holdfasts—as well as upright algae, barnacles, and limpets—initially absent.

Limpets were excluded by a 5 cm wide continuous stripe of copper-based anti-fouling paint around plots (treatments 5 and 9, Table 1; Figure 3B-3; e.g., Cubit 1975, 1984; Lubchenco and Cubit 1980; Paine 1981). These "exclosures" maintained limpet densities near zero, because limpets are inhibited from crossing copper paint barriers. Comparisons between non-paint control plots (without paint and with limpets; treatments 3 and 7, Table 1; Figure 3B-1) and paint control plots (with paint and with limpets; treatments 4 and 8, Table 1; Figure 3B-2) tested the effect of the copper paint on successional events. Comparisons between the control and exclosure plots tested the effect of limpet grazing on successional pathways.

These treatments were periodically maintained by (1) cleaning diatoms and other algae off the paint stripes (2) annually repainting the paint stripes, (3) wire brushing the unpainted borders in the non-paint and paint control treatments to prevent lateral encroachment, and (4) manually removing limpets from exclosures (Table 2).

Results were monitored only in the 20 cm x 20 cm "sample space" located in the lower portion of each 30 cm x 40 cm plot (Figure 3B). Each plot had a border
Table 2. Maintenance of limpet exclosures. Number of limpets removed from each replicate exclosure during each maintenance period. A blank indicates that the exclosure did not exist during the period; a dash, that the exclosure was not checked due to hazardous wave conditions.

<table>
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<tr>
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</tr>
<tr>
<td>1/84</td>
<td>6</td>
<td>0</td>
</tr>
</tbody>
</table>

a 1 6-9 mm chiton removed
b 1 Onchidella borealis removed
15 cm wide across the upper edge and 5 cm wide on the other three sides. In treatments using copper paint, a 10 cm buffer area separated the sample space from the paint stripe across the top of the plot (Figure 3B-2, -3).

**Monitoring**

Abundances of organisms were periodically monitored in each plot to assess the effects of the various treatments. Algal taxonomy followed Abbott and Hollenberg (1976); invertebrate taxonomy followed Morris et al. (1980). Percent cover for algae, bare rock, and barnacles, was estimated using a method adapted from Menge and Lubchenco (1981, also see Menge 1976, Lubchenco and Menge 1978). On a vinyl quadrat, 50 -1 mm diameter holes were positioned in a stratified random design. The species of algae or animal appearing under a hole was assigned a cover of 2%. Species present in the plot, but not falling under a hole were recorded as "traces" and assigned a cover of 0.2%.

I quantified the three-dimensional structure of the community as follows: Organisms directly attached to the substratum under a hole were recorded as occupying "primary space". Including bare rock, occupation of primary space totalled 100%. An upright algal frond or filament under a hole was recorded as occurring in the canopy in "secondary space" (or in "tertiary space" if it over-lay another alga also occupying the canopy under a hole). Canopy space could sum to more, or to less, than 100%. Finally, if an
organism was not attached to the substratum under a hole, but to another organism, it was recorded as occurring in "quaternary space".

Density \( \text{(number of individuals} \times 100^{-1} \text{cm}^{-2}) \) was estimated for herbivores, barnacles, and other invertebrates. I constructed a 20 x 20 cm quadrat frame of PVC pipe. The quadrat could be positioned over a plot by nails placed through holes in the corners of the frame and into corresponding holes in the Z-spar plot markers. The frame was divided into 16 squares, each 5 x 5 cm, with nylon mono-filament line. Four of the squares were randomly selected, in a Latin square pattern, as sub-samples totalling 100 cm\(^2\). Numbers of individual invertebrates were counted in each of the four sub-samples. The same four sub-samples were used throughout the study period.

Permanent plots were monitored three times during the study period. Pre-treatment percent cover data were taken for both fall- and spring-initiated canopy removal and non-paint control plots. Pre-treatment density data were taken only for spring canopy removal and non-paint control plots. In paint-control and exclusion plots, pre-treatment data were not taken in either season. Experimental plots were monitored monthly or as weather permitted for 16 mo following fall initiation of treatments (8 mo following spring initiation). Monitoring of barnacle density data did not begin until June 1983.
Data Analysis

Missing Data

Replacement data were estimated by interpolation for four plots that were not monitored on one date each, due to inclement weather or inadvertent omission. Species present in the missing samples of each replicate were known in some cases. In other cases, species were assumed to be present in the missing sample, if they were present in the previous and subsequent monitoring periods. Data for each species from the two previous and two subsequent monitoring dates were plotted on graphs. Species' cover or total density was interpolated from the graphs.

A second type of missing data occurred because small individuals of *Iridaea cornucopiae* and the upright gametophytes of *Gigartina* spp. were not always distinguishable in the field and were recorded as "red blade, Gigartinaceae." The ratio of *Iridaea* to *Gigartina* cover was determined at the first subsequent monitoring date when the two taxa were distinguishable. This ratio was used to estimate the cover of each taxon as a fraction of the "red blade" cover.

Data Summaries

To simplify data presentation and analysis, four parameters of community structure—available space and barnacle, algal, and herbivore abundances—were further
subdivided into 17 categories (Appendix I). A majority of the species observed during monitoring were included in one of the 17 categories. However, a few taxa (e.g., nemerteans, insect larvae, cushion-like blue green algae) were excluded from further analysis, because they were low in abundance and did not readily fit in one of the categories.

Data for each of the categories were transformed for generation of summary statistics. For percent cover data the arcsine square root transformation (ARCSIN $\sqrt{Y/100}$) was used. For density data the square root transformation ($\sqrt{Y+0.5}$) was used. Summary statistics (mean and standard error of the mean) were calculated for each category on each monitoring date. Inferential statistics were not employed, because the questions posed in this study were qualitative. Results are presented as transformed mean cover or density (+ S.E.), with the ordinates back-transformed.
COMMUNITY DESCRIPTION

Beds of *Iridaea cornucopiae* form a dense, rather uniform turf above the level of the mussel beds on wave-exposed rocky shores. Close inspection reveals much complexity. In unmanipulated plots, *Iridaea cornucopiae* dominated the canopy and primary space (Figure 4A, B), although average canopy cover declined from 64 to 50 % during this study. The upright gametophytes of *Gigartina papillata* (C. Ag.) J. Ag. and *G. agardhii* Setch. & Gardn., the next most abundant perennial algae, together occupied 1 to 2 % of primary space in the community. (*Gigartina papillata* and *G. agardhii* are heteromorphic species [West 1972]. Primary cover data represent only the discoid holdfasts of the upright, gametophytic phase. The crustose tetrasporophyte, indistinguishable under most field conditions from other fleshy red crusts, is included among the data on crustose algae in Figure 5C). Average canopy cover for *Gigartina* spp. also declined from 9 % to 2 % during the study period. While the holdfasts of other perennial algae declined from 5 to 2 % on the average, their canopy increased from 3 to 8 %. This increase is primarily due to an increase in mean canopy cover of *Endocladia muricata* (Post. & Rupr.) J. Ag. from <1 to 3 % (Olson, unpublished data).

Despite the domination of space by perennial algae, abundant free space was available for algal and
Figure 4. Abundance of perennial algae in unmanipulated plots. Mean ± standard error of transformed data are plotted in degrees (see Methods). Ordinates are back-transformed to cover (%). n = 6. * = relative abundances of I. cornucopiae and the upright gametophytes of Gigartina spp. include estimated data for one replicate on each of these dates (see Methods, Missing Data). A. Canopy cover. B. Occupation of primary space. Gigartina spp. are heteromorphic. In this and subsequent graphs, data for the genus are for the upright gametophyte. Data on the crustose tetrasporophyte are included among the crustose algae. Note difference in scales of the ordinates in axes A and B.
Figure 4.

- IRIDAEA CORNUCOPIAE
- GIGARTINA SPP
- OTHER PERENNIAL ALGAE

A

COVER (%)

B

COVER (%)

SAMPLING DATE

9/82 6/83* 1/84*
invertebrate colonization, ranging from 37 to 42% mean cover during the 16 mo study period (Figure 5A). The nature of the available space changed over time, however. On the average, bare rock became more abundant (increasing from 11 to 26% cover, Figure 5A), while live barnacle cover decreased (from 21 to 13%, Figure 5B). It is not known whether the increase in bare rock was directly attributable to decreased barnacle cover or to other factors. Average barnacle density also decreased from 89.3 to $52.4 \times 100^{-1} \text{cm}^{-2}$ between the 6/83 and 1/84 sampling of unmanipulated plots.

The average cover of microalgal film, crustose algae, and holdfasts of perennial algae remained relatively constant through time (Figure 5C). Microalgal film was essentially absent from the unmanipulated community. Crustose perennial algae increased in average abundance from 11 to 29% cover, while the holdfasts of upright perennial algae decreased from 47 to 25% mean cover. The decrease in mean cover of the crustose holdfast of *I. cornucopiae* from 36 to 19% (Figure 4B) accounted for most of the increase in cover of crustose algae and the decrease in cover of perennial holdfasts shown in Figure 5C.

While perennial algae dominated the canopy, ephemeral algae were rare in the natural community, occupying less than one percent of the total canopy in an average plot (Figure 5D).

Gastropod herbivore densities (Figure 6) vary greatly
Figure 5. Abundance of free space, barnacles and algal growth forms in unmanipulated plots. Mean ± standard error of transformed data are plotted and ordinates back-transformed to cover (%) or density. n = 6, unless noted. ND = no data. A. Free space. "Total free space" includes tests of living and dead barnacles, barnacle scars, and dead coralline algal crusts, as well as bare rock (also plotted separately). B. Barnacle abundance. C. Occupation of primary space by algal growth forms. Crustose algae in this and subsequent graphs include the crustose tetrasporophyte of Gigartina spp. and the crustose base of I. cornucopiae when fronds are absent. Primary cover data for upright ephemeral algae are omitted in this and subsequent graphs due to inaccuracies in field data recording. D. Canopy of algal growth forms.
Figure 5.

A. Cover (%) for different species across sampling dates.

B. Density (x100 cm^-2) for different species across sampling dates.

C. Cover (%) for different sampling dates.

D. Cover (%) for different sampling dates.
Figure 6. Abundance of gastropod herbivores in unmanipulated plots. Mean ± standard error of transformed density data are plotted. Ordinate is back-transformed. n = 6. ND = no data.
with season, time of day, and tidal cycle (T. Turner, pers. comm., pers. obs.). In unmanipulated Irisidaea cornucopiae beds, limpet densities averaged from 4.4 to 11.5 x 100^{-1}cm^{-2}, with the greatest densities occurring during late spring and summer months. Littorina scutulata Gould and L. sitkana Philippi species were more variable—densities averaged from 3.9 to 22.5 x 100^{-1}cm^{-2}. Because littorines move through Irisidaea beds in dense, spatially small aggregations, their distribution is patchy and unpredictable.

In summary, the unmanipulated community had several features: Abundant free space (comprised mainly of bare rock and barnacles) was available for algal and invertebrate colonization. Both primary and canopy space were dominated by Irisidaea cornucopiae, while other upright perennial algae were uncommon and ephemeral algae were rare or absent. Densities of gastropod herbivores were high, but variable. In addition, cover of upright algae and barnacles decreased, while bare rock, algal crusts, and Endocladia muricata increased during the 16 mo study period. This trend may be due to the loss of algal canopy and death of barnacles and limpets during unusual freezing weather (associated with extreme low tides at night) immediately prior to the final monitoring.
EXPERIMENTAL RESULTS

Canopy Removal

Prior to canopy removal, cover of algae in primary space and in the canopy was comparable in experimental plots to that in unmanipulated plots. Microalgal film was absent, crustose algae occupied 10 to 20% of primary space, and upright perennial algae dominated both primary space and the canopy. Upright ephemeral algae were rare or absent (Figure 7).

When the canopy was removed in the fall, the canopy of I. cornucopiae and Gigartina spp. (Figure 7B) rapidly recovered by vegetative regeneration from their persistent basal crusts (Figure 7A). Other perennial algae similarly recovered from basal structures, including crusts (e.g., Analipus japonicus (Harv.) Wynne), prostrate axes (e.g., Endocladia muricata), or filaments (e.g., Polysiphonia hendryi Gardn.). Additionally, the relative abundance of ephemeral (microalgal film and upright ephemerals) and perennial algae did not change (Figure 7A, B). Further, relative abundances among perennial algae (crusts, I. cornucopiae, Gigartina spp., and other perennials) were not altered by canopy removal (Figure 7A, B).

In contrast, when the canopy was removed in the spring, crustose algae and the basal structures of upright perennial algae did not persist (Figure 7C). The combined
Figure 7. Recovery of algae following canopy removal. Mean ± standard error of transformed data are plotted and ordinates back-transformed to cover (%). Error bars are not shown when they are smaller than the symbol. n = 6. * = relative abundances of I. cornucopiae and Gigartina spp. include estimated data for some replicates on these dates. + = interpolated data included for crustose algae, I. cornucopiae, Gigartina spp., and other perennial algae for two replicates on this date. A. Fall--occupation of primary space. B. Fall--canopy. C. Spring--occupation of primary space. D. Spring--canopy. Note differences in scale of ordinate between graphs of primary space (A, C) and canopy (B, D).
Figure 7.

**PRIMARY SPACE**

**CANOPY**

- MICROALGAL FILM
- CRUSTOSE ALGAE
- UPRIGHT ALGAE
- EPHEMERALS
- PERENNIALS
- IRIDAEA CORNUCOPIAE
- GIGARTINA SPP
- OTHERS

OPEN = PRIMARY SPACE
CLOSED = CANOPY

INITIATION OF TREATMENTS

**TIME SINCE DISTURBANCE (MO)**
primary cover of crustose and upright perennial algae was reduced from 53 to 12 %, on the average. This drastic decrease in primary cover occurred when daytime extreme low tides following canopy removal coincided with sunny weather. Algal crusts (including the crustose holdfasts of Iridaea cornucopiae and Gigartina spp.) became bleached, detached from the rock, and disappeared during subsequent high tides. They were washed away or eaten by limpets which appeared to be attracted to the necrotic tissue. The rapid death and detachment of crusts was particularly remarkable, because crusts and holdfasts had not easily detached from the rock during prolonged burning with a propane torch and repeated application of oven-cleaner. Accompanying the reduction in occupation of primary space, the relative abundance of the crustose and the upright growth forms was reversed. Crusts were more abundant than upright algae throughout the remainder of the study period.

Nevertheless, I. cornucopiae remained relatively more abundant than other perennials (chiefly due to vegetative regrowth from fragments of its basal crust surviving in cracks), while Gigartina spp. and other perennial algae remained at very low cover (<1%) (Figure 7C, D).
Herbivore Manipulation

The exclosure treatment proved effective in maintaining reduced limpet densities: In both fall- and spring-initiated exclosures, average limpet densities were maintained at fewer than $0.9 \times 100^{-1} \text{cm}^{-2}$ (Figure 8C, F). (Limpets found in exclosures during monitoring or maintenance were destroyed or removed, Table 2). In contrast, limpet densities in non-paint and paint controls were much greater in fall- ($22.2$ and $11.9 \times 100^{-1} \text{cm}^{-2}$, respectively, Figure 8A, B) and in spring-initiated treatments ($11.5$ and $5.1 \times 100^{-1} \text{cm}^{-2}$, respectively, Figure 8E, F).

Limpet exclosures had an unanticipated, variable effect on littorine densities. In the first 9 mo, littorines tended to be less abundant in fall exclosures ($0$ to $0.6 \times 100^{-1} \text{cm}^{-2}$ average density) than in non-paint ($2.0$ to $2.6 \times 100^{-1} \text{cm}^{-2}$) and paint controls ($0.3$ to $1.8 \times 100^{-1} \text{cm}^{-2}$). In September 1983 (12 mo), however, densities of littorines increased markedly in all fall- and spring-initiated treatments, reaching average densities in exclosures comparable to those in paint controls (Figure 8A-F).

In general, exclosures had fewer limpets and littorines than non-paint and paint control plots. In controls, average limpet abundances were less in spring- than in fall-initiated control treatments and were slightly
Figure 8. Effect of herbivore manipulation on abundance of gastropod herbivores. Mean ± standard error of transformed density are plotted and ordinates are back-transformed. Error bars are not shown when they are smaller than the symbol. n = 6. A. Fall-initiated non-paint control (-P = paint absent, +L = limpets present). B. Fall-initiated paint control (+P = paint present, +L = limpets present). C. Fall-initiated limpet exclosure (+P = paint present, -L = limpets absent). D. Spring, non-paint control. E. Spring, paint control. F. Spring, limpet exclosure.
Figure 8.

NON-PAINT CONTROL (-P+L)  PAINT CONTROL (+P+L)  LIMPET EXCLUSION (+P-L)

A

B

C

D

E

F

TIME SINCE DISTURBANCE (MO)
less when copper paint was present (paint controls) than when it was absent (non-paint controls). Limpet abundances varied seasonally in both control treatments, declining in May (fall treatments) and again in January (both fall and spring treatments). Finally, average littorine abundances did not vary consistently between control treatments, but were greater in spring- than in fall-initiated treatments during the first 8 mo following initiation.

Primary Space

Herbivores had a strong effect on patterns of space availability. Average cover of total free space (which includes living and dead barnacles, barnacle scars, and dead coralline algal crusts, as well as bare rock) was similar in non-paint and paint control treatments (Figure 9A, B). From late December 1983 (the third month following initiation), total free space varied between 96 and 100 % mean cover in non-paint control plots and between 77 and 98 % in paint controls. In contrast, much less space was available in exclosures following initiation (Figure 9 C). Total free space was always less than 30 % mean cover and declined to less than 5 % immediately following initiation (November 1982) and again 9 mo after initiation (June 1983). Patterns of space availability among treatments did not differ between fall- and spring-initiated plots (compare Figure 9A-C, with D-F). Limpet grazing appeared to have a positive effect on
Figure 9. Effect of herbivore manipulation on abundance of free space. Mean ± standard error of transformed data are plotted in degrees and ordinates are back-transformed to cover (%). Error bars are not shown when they are smaller than the symbol. n = 6. "Total free space" includes living and dead barnacles, barnacle scars, and dead coralline algal crusts, as well as bare rock (also plotted separately). * = interpolated data included for total free space and bare rock for one replicate on this date. + = interpolated data included for total free space, only, for one replicate on this date. See Figure 8 caption for explanation of axes A-F.
Figure 9.

NON-PAINT CONTROL (-P,+L)

PAINT CONTROL (+P,+L)

LIMPET EXCLUSION (+P,-L)

- ○ TOTAL FREE SPACE
- ● BARE ROCK
- ▲ INITIATION OF TREATMENTS

TIME SINCE DISTURBANCE (MO)

FALL

COVER (%)
Figure 10. Effect of herbivore manipulation on abundance of barnacles. Mean ± standard error of transformed cover and density data are plotted. Ordinates are back-transformed. Error bars are not shown when they are smaller than the symbol. n = 6, unless noted. * = Cover interpolated data included for one replicate on each of these dates. See Figure 8 caption for explanation of axes A-F.
Figure 10.

**Figure A:** Non-Paint Control (-P,+L)

**Figure B:** Paint Control (+P,+L)

**Figure C:** Limpet Exclosure (+P,-L)

- **FALL**
- **COVER (%)**
- **SPRING**

**Legend:**
- *+-* Barnacle Cover
- *---* Barnacle Density
- *----* Initiation of Treatments

**Time Since Disturbance (MO):**

Before 2 4 6 8 10 12 14 16

**Density (g/100 cm²):**

0 50 100 150 200 250 300
colonization and growth of barnacles, although the results are confounded by an apparent paint effect (Figure 10). Maximum barnacle cover in fall-initiated non-paint controls (14% mean cover at 11 mo) was higher than in paint controls (3% at 12 mo) and exclosures (6% at 11 mo) (Figure 10A-C). Similarly, average barnacle densities were higher overall and reached higher maxima in non-paint controls (339 x 100^{-1} cm^{-2}) than in paint controls (59 x 100^{-1} cm^{-2}) or in exclosures (90 x 100^{-1} cm^{-2}).

In contrast, in spring-initiated plots, barnacle cover and density did not differ among the three treatments (Figure 10D-F). All spring treatments resembled fall-initiated paint control and exclosure plots, with lower maximum barnacle cover (<3% mean cover) and barnacle densities (mean <130 x 100^{-1} cm^{-2}) relative to fall non-paint controls. Barnacle density, but not cover, decreased by the final mid-winter monitoring in both fall- and spring-initiated plots, suggesting that small individuals suffered disproportionate mortality during this period.

Limpet grazing had a direct effect on early patterns of algal succession, but again the results were confounded by a paint effect. Peak abundance of microalgal film differed among the fall treatments, with 6% mean cover recorded in non-paint controls, 44% in paint controls, and 96% in exclosures (Figure 11A-C). The intermediate cover of microalgal film in paint controls probably reflects differential rates of limpet invasion among the treatments
Figure 11. Effect of herbivore manipulation on occupation of primary space by algal growth forms. * = data for upright perennial algae include interpolated data for one replicate on this date. + = interpolated data included for crustose and upright perennial algae for one replicate on this date. Also note that data for crustose algae and microalgal film were probably transposed during sampling on this date. See Figure 10 caption for other symbols and conventions.
Figure 11.

NON-PAINT CONTROL (-P,+L)

PAINT CONTROL (+P,+L)

LIMPET EXCLOSURE (+P,-L)

- MICROALGAL FILM
- CRUSTOSE ALGAE
- UPRIGHT PERENNIAL ALGAE
- INITIATION OF TREATMENTS

TIME SINCE DISTURBANCE (MO)
within the first few weeks following initiation. Limpets quickly invaded non-paint controls from all directions, but invaded paint controls from only three sides, because access was inhibited by the paint stripe at the top of the plot. Consequently, the heavy microalgal film which "bloomed" immediately after initiation was more quickly removed from non-paint than from paint controls, resulting in lower abundance by the first monitoring (1 mo following initiation). Microalgal film did not persist in non-paint controls—mean cover fell to <1 % in 3 mo (December 1982) and remained at or near zero percent cover for the duration of the study. Similarly, in paint controls, microalgal film remained low in abundance following the peak bloom, with <1 % mean cover on most sampling dates (except in August 1983, when it reached 5 %). In contrast, in exclosures microalgal film persisted throughout the 16 mo study period, with mean cover ranging between 14 and 66 % following the initial peak bloom.

Limpet grazing seemed to enhance initial rates of colonization of perennial crustose and upright algae, because they colonized and reached peak abundance earlier (February 1983) in non-paint and paint controls than in exclosures (late May 1983) (Figure 11A-C). Moreover, while crustose algae persisted and increased in cover in non-paint and paint control treatments (reaching 2 and 7 % mean cover, respectively), they remained at <1 % cover or were absent in exclosures. Although upright perennial algae
invaded non-paint and paint controls earlier than exclosures, by the end of the study they were more abundant occupants of primary space in exclosures.

Among *I. cornucopiae*, *Gigartina* spp., and other perennial algae, four patterns emerged in fall-initiated treatments (Figure 12A-C). First, *I. cornucopiae* and *Gigartina* spp. were relatively more abundant than other perennial algae in all treatments. Second, during the first 8 mo following initiation, *I. cornucopiae* was relatively more abundant than *Gigartina* spp. in non-paint and paint control treatments. Third, all three groups of algae declined in late summer in both control treatments. Fourth, in exclosures, *Gigartina* spp. colonized by 8 mo and grew rapidly to occupy an average of 5% cover in primary space by 16 mo. *Iridaea cornucopiae* and other perennial algae remained essentially absent in exclosures, occupying an average of <1% of primary space. In addition, recruitment of other upright perennials was delayed in exclosures until September 1983, 7 mo after they had first appeared in the two control treatments.

Among spring treatments, the pattern of abundance of microalgal film was similar to that in the fall treatments, dominating primary space in exclosures (Figure 11D-F). However, there was no consistent difference among spring treatments in occupation of primary space by perennial crustose and upright algae. In all three treatments, colonization by crusts and upright
Figure 12. Effect of herbivore manipulation on occupation of primary space by perennial algae. + = interpolated data included for one replicate on each of these dates. * = relative abundances of I. cornucopiae and Gigartina spp. include estimated data for some replicates on these dates. Note change in scale of ordinate. See Figure 10 caption for other symbols and conventions.
Figure 12.

NON-PAINT CONTROL (-P,+L)  PAINT CONTROL (+P,+L)  LIMPET EXCLUSION (+P,-L)

- P. CORNUCOPIAE
- GIGARTINA SPP
- OTHER PERENNIAL ALGAE
- INITIATION OF TREATMENTS

TIME SINCE DISTURBANCE (MO)

FALL

COVER (%)
perennials was delayed relative to fall plots, with maximum mean cover reaching <2 % for crusts and <<1 % for uprights.

In spring-initiated treatments, neither I. cornucopiae nor Gigartina spp. was observed during the 8 mo following initiation of treatments (Figure 12D-F). Other perennial algae (in particular, Endocladia muricata) became established in all three treatments, but with mean cover less than 1 % by the final monitoring.

Canopy

Limpet grazing also affected development of the canopy. Ephemeral algal canopy was more extensive in fall-initiated exclosures (up to 98 % mean cover, Figure 13C) than in non-paint controls (<3 %, Figure 13A). However, paint effects also confounded these results. In paint controls the canopy cover of ephemerals was intermediate between that in non-paint controls and exclosures (<18 %, Figure 13B).

Although perennial algae invaded and reached peak canopy cover later in exclosures than in non-paint and paint controls, exclosures had higher mean canopy cover of perennials by the end of the study period (Figure 13A-C, 14A-C). This was primarily due to colonization and growth of Gigartina spp. in three of the six fall-initiated limpet exclosures (Figure 14C).

Among the six replicates of the exclosure treatment, peak Gigartina cover in January 1984 correlated strongly
Figure 13. **Effect of herbivore manipulation on canopy cover of algal growth forms.** * = interpolated data included for upright ephemeral and perennial algae for one replicate on these dates. See Figure 10 caption for other symbols and conventions.
Figure 13.

FIGURE LEGEND:
A) NON-PAINT CONTROL (-P,+L)
B) PAINT CONTROL (+P,+L)
C) LIMPET EXCLUSION (+P,-L)

- UPRIGHT EPHEMERAL ALGAE
- UPRIGHT PERENNIAL ALGAE
- INITIATION OF TREATMENTS

CHARTS:
- FALL
- SPRING

TIME SINCE DISTURBANCE (MO)
BEFORE 2 4 6 8 10 12 14 16
Figure 14. Effect of herbivore manipulation on canopy cover of perennial algae. * = relative abundances of I. cornucopiae and Gigartina spp. include estimated data for some replicates on these dates. + = interpolated data included for one replicate on these dates. See Figure 10 caption for other symbols and conventions.
Figure 14.

NON-PAINT CONTROL (-P,+L)  
PAINT CONTROL (+P,+L)  
LIMPET EXCLUSION (+P,-L)

- IRIOAEA CORNUCOPIAE
- GIGARTINA SPP
- OTHER PERENNIAL ALGAE
- INITIATION OF TREATMENTS

TIME SINCE DISTURBANCE (MO)
Figure 15. Percent cover of Gigartina spp. (January 1984) and the presence or absence of barnacles (December 1982) in limpet exclosures. * = cover of Gigartina spp. in replicate 5 includes estimate of proportion of "red blade" (see Methods).
Figure 15.
Table 3. Correlations with January 1984 cover of *Gigartina* spp. in limpet exclosures.

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<thead>
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<th>Independent Variable</th>
<th>Slope</th>
<th>Intercept</th>
<th>r²</th>
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<td><strong>December 1982</strong></td>
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<tr>
<td>Barnacles (presence/absence)</td>
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<td>.91</td>
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<tr>
<td>(percent cover)</td>
<td>5.88</td>
<td>16.26</td>
<td>.55</td>
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<td>Bare space</td>
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<td>Microalgal film</td>
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<td>Ephemeral algae (canopy)</td>
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<td>.10</td>
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<td><strong>May 1983</strong></td>
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<td>Barnacles (density)b</td>
<td>10.96</td>
<td>-16.56</td>
<td>.52</td>
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<tr>
<td><strong>January 1984</strong></td>
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<tr>
<td>Barnacles (cover)</td>
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<td>.58</td>
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<td>Limpet invasion (cumulative)</td>
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<td>17.87</td>
<td>.20</td>
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<td>Littorine invasion (cumulative)</td>
<td>0.17</td>
<td>22.44</td>
<td>.19</td>
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</table>

a Regression model \( Y = a + bX \), unless noted. \( Y = \) percent cover of *Gigartina* spp., \( a = \) intercept, \( b = \) slope, \( X = \) independent variable.

b Regression model \( Y = a + b(\ln X) \).
with barnacle presence/absence and barnacle cover in December 1982, prior to the probable time of Gigartina settlement ($r^2 = .91$ and .55, respectively, Figure 15 and Table 3). Available space, microalgal film, and ephemeral algal canopy in December 1982 explained less of the variability in peak Gigartina cover ($r^2 = .13$, .10, and $1.1 \times 10^{-3}$, respectively). Invasion of exclosures by limpets and littorines explained little of the variation in final cover of Gigartina spp. ($r^2 = .20$ and .19, respectively). Barnacle density in May 1983, at the time of the initial appearance of Gigartina explained more of the variability ($r^2 = .52$, logarithmic model). Finally, barnacle cover in January 1984 also correlated with cover of Gigartina spp. at the same time ($r^2 = .58$).

In spring-initiated treatments, the relative abundance of ephemeral and perennial algae in the canopy were similar to those in fall-initiated treatments (Figure 13D-F). The canopy of ephemeral algae was more abundant, and that of perennial algae was less abundant, in exclosures compared to non-paint and paint controls. However, canopy cover of perennial algae was less in all three spring treatments than during a comparable period following initiation of fall treatments.
In summary, the effects of limpet grazers were

1. Grazers maintained high levels of free space on denuded substrata.

2. Barnacle abundances were probably not affected by limpet bulldozing in this system. It is not clear if limpet grazing enhanced barnacle colonization.

3. Establishment and persistence of microalgal film and upright ephemeral algae were limited by herbivores. In the absence of limpets, these algae held space throughout the year.

4. Following fall disturbance, establishment of crustose and upright perennial algae was initially enhanced by limpet grazing.

5. Establishment and growth of Gigartina spp. were eventually enhanced in the absence of limpet grazing. Barnacles appeared to facilitate Gigartina spp. establishment.

6. Season of initial disturbance affected early succession primarily through seasonal differences in the establishment of perennial algae. The response of ephemeral algae to herbivory did not change with season of disturbance.
DISCUSSION

Results of this study permit specification of switch-points in a model of succession in beds of *I. cornucopiae*. Established beds of *I. cornucopiae* appear to resist changes in abundance of dominant perennial algae due to "normal" physical disturbances (such as heavy wave action) and to invasion by ephemeral algae. If a disturbance produces a change in the community, however, three factors have been demonstrated to switch subsequent succession among alternate pathways. First, alternate trajectories may emerge, depending on whether or not perennial algae are able to vegetatively recover from basal structures. Second, the presence or absence of herbivores determines successional trajectories by altering relative abundances of ephemeral and perennial algae. Finally, season of initial disturbance affects establishment of perennial algae, switching succession between alternate pathways.

Community Structure and Resistance

Although *Iridaea cornucopiae* dominated both primary and canopy space in permanent plots at Whale Cove, abundant bare rock and barnacle-covered surfaces were available for algal colonization. Nevertheless, *Gigartina papillata*, *G. agardhii*, and other perennial algae were uncommon, while upright ephemeral algae were rare and microalgal film was essentially absent. Gastropod herbivores, on the other
hand, were present in high densities.

To adequately determine whether the observed community structure is at, or near, a stable equilibrium would require studies on a time-scale comparable to the mean generation time (time from germination to first reproduction) of the longer lived residents (Sutherland 1981; cf. Connell and Sousa 1983, who consider mean life-span to be the appropriate time-scale). It is possible that *I. cornucopiae* is extremely long-lived. While estimates of its longevity are not available Paine, et al. (1979), estimate that the crustose tetrasporophyte of the closely-related Gigartina spp. ("Petrocelis") may live 25 to 87 years. Mean generation time is probably much shorter. Less than two years after denudation, some individuals of *I. cornucopiae* that had recruited to denuded plots had become reproductive.

Using either of these criteria (mean generation time or life-span), however, the time scale of this study is too short to assess the global stability (Sutherland 1981) of *I. cornucopiae* beds. Nevertheless, one may observe the persistence (Margalef 1969, Sutherland 1981) of a "resident adult assemblage" (Sutherland 1981) and experimentally evaluate its resistance (Pimm 1984, Sutherland 1981; cf. Connell and Sousa 1983) to perturbations such as physical disturbance and invasion.

Beds of *I. cornucopiae* persisted in permanent plots, despite exceptionally heavy wave action during the first
winter (1982-1983) of this 16 mo study. Further, observations at this and other sites in Oregon (pers. obs.) and in Washington (R. T. Paine, pers. comm.) indicate that *I. cornucopiae* beds persist for at least three to 15 yr, respectively. Perhaps because it forms a short, compact turf, the canopy of *I. cornucopiae* was not as subject to strong seasonal fluctuations (Figure 4, pers. obs.) as are other members of the genus (e.g., *I. cordata*, Norris and Kim 1972, Hansen and Doyle 1976, Gaines 1985; *I. flaccida*, Foster 1982), most of whose blades senesce and disappear in winter. Occupation of primary space by crusts and the holdfasts of upright perennials together also remained relatively constant throughout the study period. Like stands of the closely-related *Chondrus crispus* in the low zone in New England (Lubchenco and Menge 1978, Lubchenco 1980), beds of *I. cornucopiae* appear to resist most mechanical disturbances such as heavy wave action at Whale Cove.

As Sutherland (1981) emphasizes, forces which remove organisms are not the only perturbations experienced by a community. Recruitment and immigration also potentially alter the resident community. During this study, heavy recruitment of ephemeral algae (including microalgal film and upright ephemerals) and of barnacles was observed on experimentally denuded surfaces. Yet in the established community, ephemeral algal cover remained constant and barnacle abundances fluctuated much less than in
experimental plots. I experimentally demonstrated that limpets control abundances of ephemeral algae on denuded substrata, so it is reasonable to assume that they do so in the natural community. However, limpet abundances in unmanipulated plots were less than, or equal to, those in experimental control plots where transitory blooms of ephemerals occurred, suggesting that the resident algae in the established community also inhibit ephemeral algal blooms. Lubchenco (1980) demonstrated that the crustose holdfast of *Chondrus crispus* and littorine grazers both inhibited establishment of fucoid algae. While I did not experimentally distinguish between pre-emption of space by resident algae and removal of invaders by consumers in the natural community, it is likely that a combination of these effects also accounts for the observed resistance of *I. cornucopiae* beds to invasion.

**Vegetative Recovery**

Some mechanical disturbances cannot be resisted by the community. An experimental disturbance of sufficient magnitude to remove the canopy, but leave the basal crust of *I. cornucopiae* and *Gigartina* spp. intact, resulted in rapid recovery by vegetative regeneration in the fall. As in the "undisturbed" community, establishment of ephemeral algae did not occur. Thus, within the range of natural disturbances (such as log-bashing) that remove canopy, but leave basal structures intact, the community was resilient

The effect of a mechanical disturbance on this community depends not only on its magnitude, however, but on the physical stresses effective at the time of the disturbance (Noble and Slatyer 1980). In spring, when the canopy removal was immediately followed by sunny weather during daytime extreme low tides, most crusts and holdfasts died. Those which survived did so in crevices. In contrast, significant mortality of crusts and holdfasts did not occur in the unmanipulated community during the same period. By the end of the study period, typical I. cornucopiae beds had not become established in the spring canopy removal plots, although limited vegetative regeneration from surviving crusts had occurred. On-going observations will determine whether the community will recover from this more severe disturbance or whether a different community structure will result.
Herbivory

Paint Effects

In studies of succession on marine hard substrata, cages or other methods for excluding consumers may themselves influence subsequent successional events (see a critical review of the marine fouling literature in Schmidt and Warner 1984). Consequently, researchers have attempted to control for the confounding effects of cages (e.g., Dayton 1971, Menge 1976, Lubchenco and Menge 1978) and of cageless methods of exclosure (Cubit 1975, 1984).

In previous studies using copper paint as a limpet barrier, the effect of the paint on colonization of experimental plots has not been quantified (Cubit 1975, 1984; Paine 1981). Paine (1981) did not report on controls for the possible effects of copper paint toxicity. Cubit (1975, 1984) appropriately controlled for paint effects by comparing results in limpet exclosures (with paint present and limpets absent) to those in paint controls (with both paint and limpets present). However, he did not compare results in paint controls to those in a non-paint control treatment (with paint absent and limpets present). Thus the effect of copper paint on colonization was not evaluated.

In the present study, I estimated both the magnitude and direction of paint effects on different classes of colonists by using non-paint, as well as paint, controls.
The effects of paint varied with growth form and season (Table 4). Most growth forms (and bare rock) were equally abundant in non-paint and paint controls for both seasons of initiation. Barnacles and herbivores were less abundant when paint was present in fall-initiated plots; limpet densities were also reduced in spring-initiated paint controls. The abundances of microalgal film, upright ephemeral algae, and Gigartina spp. were enhanced in the presence of copper paint, possibly due to the reduced limpet densities.

Reductions in barnacle abundance in the presence of copper paint were to be expected, since barnacles are capable of selecting the substratum on which they settle (Carefoot 1977) and since anti-fouling paint was originally designed to inhibit settlement of barnacles and other invertebrates. That this effect was observed in fall- but not spring-initiated treatments is more difficult to explain. Differences in rates of copper leaching between fall and spring treatments could partially account for the observed seasonal pattern. Different colors of anti-fouling paint were used for fall- and spring-initiated treatments. The brand name and copper concentration of the two paints were identical and both colors were equally effective in excluding limpets (Table 2, Figure 8). However, the paint applied to spring treatments developed a glossy surface that may have reduced rates of copper leaching.
Table 4. **Summary of paint effects.** Average abundance of free space, colonists, and herbivores in paint control (PC) relative to non-paint control (NPC) treatments. (+ indicates PC > NPC; 0, PC = NPC; -, PC < NPC)

<table>
<thead>
<tr>
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<th>FALL</th>
<th>SPRING</th>
</tr>
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<tbody>
<tr>
<td><strong>Free Space</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total Free Space</td>
<td>-</td>
<td>0</td>
</tr>
<tr>
<td>Bare Rock</td>
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<td>0</td>
</tr>
<tr>
<td><strong>Barnacles</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cover</td>
<td>-2</td>
<td>0</td>
</tr>
<tr>
<td>Density</td>
<td>-</td>
<td>0</td>
</tr>
<tr>
<td><strong>Algae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Primary Space Occupancy</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Microalgal Film</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Crustose Algae</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Upright Perennial Algae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Iridaea cornucophae</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Gigartina spp.</td>
<td>+</td>
<td>0</td>
</tr>
<tr>
<td>Other Perennial Algae</td>
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<td>0</td>
</tr>
<tr>
<td>Canopy</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upright Ephemeral Algae</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Upright Perennial Algae</td>
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</tr>
<tr>
<td>Iridaea cornucophae</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Gigartina spp.</td>
<td>+</td>
<td>0</td>
</tr>
<tr>
<td>Other Perennial Algae</td>
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<td>0</td>
</tr>
<tr>
<td><strong>Herbivores</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Limpets</td>
<td>0/- 3</td>
<td>-</td>
</tr>
<tr>
<td>Littorines</td>
<td>0/- 4</td>
<td>0</td>
</tr>
</tbody>
</table>

1. Total free space includes barnacles.

2. Note that while barnacle cover is decreased in paint relative to non-paint controls, it is also decreased relative to exclosures in the final eight months of the study period.

3. 0 = first eight months of study period; - = second eight months.

4. 0 = first twelve months; - = last six months (two sampling dates).
Reduced herbivore densities in paint relative to non-paint controls could be due either to (1) inhibitory effects of copper leaching into the sample space or to (2) direct limitation of limpet access from areas above the plot by the paint stripe across the top of the plot. Observational evidence supports the second hypothesis. Immediately following fall initiation, I observed a heavy bloom of benthic diatoms that averaged 96% cover in exclosure plots, but also appeared at a lower mean cover in non-paint and paint control plots (6% and 44%, respectively). Reduced cover in the two control treatments was clearly due to the invasion of limpets from the surrounding vegetation into the recently denuded plots. Areas invaded by limpets lacked the diatom film; areas where the film remained had not yet been invaded by limpets. In non-paint controls, the remnant patches of film were approximately circular and located near the center of the plot, whereas in paint controls, the patch extended down from the paint stripe in a "V" shape.

These patterns suggest that in non-paint controls, limpets invaded from all directions, while in paint controls limpets did not invade from above the plots (i.e., across the paint stripe). The observation that Collisella digitalis (the most abundant limpet in this system) tends to move vertically, rather than horizontally on the shore (Breen 1971, 1972) tends to support this interpretation. The entire plot, including the area immediately below the
paint stripe, was eventually invaded by limpets, suggesting that leaching of copper into the plots did not inhibit access of limpets from the sides and bottom. Thus, the direct effect of the paint stripe on limpet movement, rather than inhibitory effects of leaching copper, can account for the decreased limpet density in paint controls.

Increases in cover of microalgal film, upright ephemeral algae, and Gigartina spp. could be attributed to two factors: (1) enhancement of algal growth by copper leaching over the substratum or (2) reduced limpet abundances permitting more algal growth in paint control relative to non-paint control plots. It is unlikely that copper leachate enhances algal growth, because copper has been demonstrated to be toxic to many algae (Francke and Hillebrand 1980 and references therein). Although the diatom film discussed above was eventually removed by grazers from both control treatments, larger areas of the film persisted in paint controls, where limpet access was restricted. Consequently, an instantaneous measure of cover of microalgal film indicated higher cover in the non-paint control. Thus, increases in microalgal film, upright ephemeral algae, and Gigartina spp. could be explained by reduced limpet densities, rather than by the unlikely hypothesis that copper enhances algal growth.
Herbivore Effects

Successional pathways in communities similar to beds of *I. cornucopiae* are affected by herbivores in different ways, depending on the competitive relationships between ephemeral ("early") and perennial ("late") species (Lubchenco 1978, 1980, 1982, Lubchenco and Menge 1978, Sousa 1979, Foster 1982, Jara and Moreno 1984). If early successional species inhibit the establishment and growth of late species (the "inhibition" model of succession, Connell and Slatyer 1977), herbivory may accelerate succession by removing ephemeral species, permitting later perennial species to invade (e.g., Lubchenco 1978, 1980, 1982, Lubchenco and Menge 1978, Sousa 1979). In contrast, if later species are competitively superior to early successional species, eventually replacing them (the "competitive hierarchy" model, Horn 1981; also see Egler 1954, Connell and Slatyer 1977), herbivores may retard or locally re-initiate succession by removing competitively superior later species, permitting early species to invade (e.g., Foster 1982, Jara and Moreno 1984). During primary succession in beds of *I. cornucopiae*, different levels of herbivory similarly resulted in qualitatively different early successional pathways.

In the presence or absence of limpets successional trajectories were distinguished by differential fluctuations in the abundance of ephemeral and perennial
algae. Fluctuations in algal cover were exaggerated in the presence of grazers. The canopy of both ephemeral and perennial algae declined in summer. The decline in ephemerals occurred earlier, suggesting that grazers shifted to perennial algae when ephemerals were depleted. Eventually, ephemeral algae were totally removed and cover of free space was concomitantly high. Some perennial algae, however, persisted as basal crusts and holdfasts in minute crevices and as blades on small protruberances. At the beginning of the next growing season (January 1984), the canopy of perennials had begun to recover. Thus, perennial basal structures and escapes in space permitted perennial algae to persist through periods of intense grazing which eliminated ephemerals. In the presence of limpet grazers, the successional pathway was characterized by high levels of free space and persistence (although at low cover) of perennial algae.

In the absence of grazers, fluctuations in algal canopy were muted. The successional sequence was thus characterized by the persistence of ephemeral algae (both microalgal film and upright ephemerals) throughout the year, with concomitant low levels of free space. Cubit (1984) also found that seasonal fluctuations in the abundance of ephemeral algae were reduced in the absence of limpet grazers. The assemblage of ephemerals apparently resisted invasion by *I. cornucopiae* and other perennial algae, which colonized later and established more slowly in
the presence of ephemerals. These results are consistent with the inhibition model of succession—the presence or absence of herbivores switches succession between early pathways dominated by perennial or ephemeral algae, respectively.

By the end of the study period, Gigartina spp. had recruited and begun to dominate the canopy in the absence of limpet grazers. Gigartina cover in exclosures eventually exceeded that in controls. (I. cornucopiae and other perennial algae tended to remain suppressed in the absence of grazers.) Barnacles appeared to have facilitated the recruitment of Gigartina in the presence of high ephemeral algal cover. Thus, Gigartina spp. were probably not inhibited by ephemeral algae, at least in the presence of barnacles. Further, they may have been less tolerant of grazing than I. cornucopiae. As a consequence, the pattern establishment of Gigartina spp. in the present study parallels that of I. flaccida (Foster 1982) and I. boryana (Jara and Moreno 1984). These species established earlier and more quickly achieved dominance of the community in the absence of herbivores. These results are consistent with the "competitive hierarchy" model of succession—the presence or absence of herbivores switches succession between pathways characterized by increased dominance of the superior competitor.

In summary, the effect of herbivores on successional
pathways in beds of *I. cornucopiae* is complex, depending on the competitive relations among colonists and on whether the competitive dominant or subordinate is more affected by herbivory (e.g., Lubchenco 1978). High levels of limpet grazing may be a necessary condition for establishment of beds of *I. cornucopiae*. In the absence of limpets, ephemeral algae and *Gigartina* spp. dominate early successional assemblages.

**Season of Initial Disturbance**

In previous studies, differences in season of initial disturbance affected successional trajectories by influencing both the effectiveness of herbivores and the recruitment of colonists (e.g., Sousa 1979, Sousa et al. 1981, Jara and Moreno 1984). In beds of *I. cornucopiae*, however, season of disturbance did not change the effects of herbivory. Rather, season of initial disturbance affected succession mainly through seasonal patterns in the establishment of perennial algae. Species of ephemeral algae were able to recruit from spores and quickly pre-empt free space in both seasons of disturbance, but perennial algal establishment was highly seasonal. Although limpet grazing reduced ephemeral algal cover both in spring- and fall-initiated treatments, perennial algae did not become established until the end of the summer after spring denudation. *Iridaea cornucopiae* and *Gigartina* spp. were still absent in spring-initiated treatments at the end of
Mechanisms which could account for the failure of these dominant perennials to recruit in summer include (1) unavailability of spores or (2) intolerance of spores or new recruits to increased grazing or to the physical stresses of summer. Lack of spore availability is unlikely to explain the absence of summer establishment. Hasegawa and Fukuhara (1952) found that reproduction in four populations of *Iridophycus cornucopiae* (= *Iridaea cornucopiae*) peaked in May through July, while I observed reproductively mature individuals at Whale Cove throughout the year.

Increased limpet abundances alone also do not explain suppressed establishment of perennials in summer. Limpet density following spring-initiation was less than, or equal to, those in fall-initiated plots during the first eight months following disturbance (when *I. cornucopiae* and *Gigartina* spp. apparently recruited). However, consumer abundance is not necessarily proportional to intensity of consumption (Menge 1978a, 1978b; Cubit 1975, 1984). Cubit (1975, 1984) found that, despite decreased per capita consumption by limpets in summer, a larger proportion of the algal biomass was eaten because of lower rates of algal production during this more stressful season. During the present study, extreme low tides also fell during daylight hours in summer. Physical stresses of heat, light, and desiccation affecting germination and growth of perennial
algae would have been greater during summer months following spring disturbance than in winter months following fall disturbance. Herbivores (even at decreased densities) could have had a disproportionate effect on perennial algal establishment in summer. During a cool, wet summer, *I. cornucopiae* and *Gigartina* spp. might be able to recruit where limpet grazers reduced ephemeral algal cover.

In summary, although the removal of ephemeral species by herbivores may be a necessary condition for establishment of perennial algae, it is not sufficient. Space made available by grazers during physiologically stressful periods may be essentially unavailable for colonization by perennial algae, despite availability of their spores. If stress-tolerant species, such as *Endocladia muricata*, successfully recruit during such times, an entirely different successional trajectory may result.

Pathways of succession in beds of *Iridaea cornucopiae* and other systems appear to be very complex. By experimental manipulations, however, successional trajectories and the specific conditions which result in switches between alternate pathways can be defined for a particular community. Complex models of succession constructed in this manner suggest a general approach to succession which incorporates both deterministic and stochastic processes.

Arno, S. F., and D. G. Simmerman. 1982. Forest succession on four habitat types in western Montana (Review Draft). Fire effects research and development program. Intermountain Forest and Range Experiment Station, Missoula, Montana, USA.


Appendix I. Community structure.

<table>
<thead>
<tr>
<th>Parameters of Community Structure</th>
<th>Categories</th>
<th>Taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>FREE SPACE</strong></td>
<td>TOTAL FREE SPACE</td>
<td>Bare rock</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Barnacles (living, dead, scars)¹</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Bleached coralline crusts</td>
</tr>
<tr>
<td></td>
<td>BARE ROCK</td>
<td>Bare rock</td>
</tr>
<tr>
<td><strong>BARNACLES</strong></td>
<td>BARNACLE COVER</td>
<td>Barnacles (living)</td>
</tr>
<tr>
<td></td>
<td>BARNACLE DENSITY</td>
<td>Balanus glandula (living, dead)</td>
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<tr>
<td></td>
<td></td>
<td>Chthamalus dalli (living, dead)</td>
</tr>
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<td>PRIMARY SPACE OCCUPATION</td>
<td>Microalgal film</td>
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<td>CRUSTOSE ALGAE</td>
<td>Diatom film</td>
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<tr>
<td></td>
<td></td>
<td>Green algal film</td>
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<tr>
<td></td>
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<tr>
<td></td>
<td></td>
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<tr>
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<td></td>
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<td></td>
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<tr>
<td></td>
<td></td>
<td>Analipus japonica (crust only)</td>
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<td></td>
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<td>Red crust</td>
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<td></td>
<td></td>
<td>Coralline crust</td>
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<td><strong>PERENNIAL ALGAE</strong></td>
<td>Iridaea cornucopiae</td>
<td>Iridaea cornucopiae</td>
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<tr>
<td></td>
<td>Gigartina spp.</td>
<td>Gigartina papillata</td>
</tr>
<tr>
<td></td>
<td></td>
<td>G. agardhi</td>
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<tr>
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Appendix I.—(Continued)

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<tr>
<th>CANOPY</th>
<th>EPHEMERAL ALGAE</th>
<th>PERENNIAL ALGAE</th>
<th>HERBIVORES</th>
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<tr>
<td></td>
<td>Filamentous diatoms</td>
<td>Iridaea cornucopiae</td>
<td>Collisella digitalis</td>
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<td>Green filament</td>
<td>Gigartina papillata</td>
<td>C. pelta</td>
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<tr>
<td></td>
<td>Green blade</td>
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<td>C. strigatella</td>
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<td>Entermorpha sp.</td>
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<td>Notoacmea fenestrata</td>
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<td></td>
<td>Filament (Cladophorales)</td>
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<td>Littorina scutulata</td>
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<td>Petalonia sp.</td>
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<td>Blade (cf. Porphyra)</td>
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<td>Bangia fuscopurpurea</td>
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<tr>
<td></td>
<td>Porphyra spp.</td>
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</tbody>
</table>

- **Perennial Algae**
  - *Iridaea cornucopiae*
  - *Gigartina spp.*
  - *Other* See above

- **Herbivores**
  - **Limpets**
    - *Collisella digitalis*
    - *C. pelta*
    - *C. strigatella*
  - **Littorines**
    - *Notoacmea fenestrata*
    - *Littorina scutulata*
    - *L. sitkana*

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1 Barnacle cover data were not recorded by species.
2 Analipus Primary cover includes only the point of attachment of the upright. Crust data are included among crustose algae.
3 Cumagloia—perennial?
4 Polysiphonous red filament—perennial?
5 Canopy of perennials does not include *Cladophora*, whose intertwined filaments form a dense spongy mat on the substratum.