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# Temporal variation and succession in an algal-dominated high intertidal assemblage

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#### Abstract

We determined whether temporal variation and succession were similar among sites with similar species composition by sampling unmanipulated and cleared plots in a high intertidal assemblage dominated by *Endocladia muricata* and *Mastocarpus papillatus*. Sampling was done for 6 years at six sites spanning over 4° of latitude in California. Ten  $1 \times 2$ -m permanent plots were chosen in the central portion of the assemblage at each site. Four of these served as unmanipulated controls, three were cleared (scraped and burned) in the spring of 1985, and three were cleared in the fall of 1985. The cover of sessile and density of motile species were determined by subsampling within the plots from 1985 until 1991. Recovery of the clearings was determined by their similarity to the controls. The algae *E. muricata*, *M. papillatus*, and *Fucus gardneri*, and the barnacle *Balanus glandula*, were the most abundant sessile organisms in the control plots, although the latter never exceeded 12% cover at any site. The grazing gastropods *Littorina scutulata/plena*, various limpets, and *Tegula funebralis* were the most common mobile organisms. The species composition of the common species remained constant in the control plots over the study period and there were few large changes in relative abundance. Significant seasonal variation was detected in 11 species but variation was commonly site-specific.

Ephemeral algae were abundant during early succession at only two of the six sites, and barnacle cover was low (<15% cover) at four sites and moderate (15-50% cover) at the remaining two throughout succession. Recovery rate varied considerably among sites and between times of clearing (1-10%/month). Correlations between ephemeral algae and grazer abundance, and between these

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variables and recovery rate were not significant. The effects of grazers on recovery rate were only evident at one site where they appeared to reduce an initially high cover of ephemeral algae and delay the establishment of perennials. Some of the largest differences in recovery rate were between clearing times, associated with differences in the phenology of the dominant perennial algae. In spite of these differences, most plots recovered by the end of the study period.

These results indicate that the assemblages in the control plots at each site were relatively stable and, while successional pathways and processes varied, the assemblage at most sites still recovered. Current models, based largely on biological interactions, that attempt to explain within assemblage structure and succession were not broadly applicable.

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#### 1. Introduction

A current, major focus of community ecology is to understand the variation among natural communities and the processes that affect it. The focus on variation rather than consistency or average parameters has resulted from more detailed, long-term, and often experimental studies of how communities are organized. Rather than developing via predictable, facilitative interactions that produce a relatively homogeneous community structure in space and time (e.g. Clements, 1916; Odum, 1969), communities may be better described as a dynamic mosaic of species whose patchiness results from microsite differences and disturbances (reviews in Pickett and White, 1985). There is little evidence to determine if communities are stable (Connell and Sousa, 1983) and, rather than being driven by facilitation, succession within disturbed areas can vary with disturbance characteristics, dispersal, growth rates, and a variety of interactions among the species within a patch (Connell and Slatyer, 1977; Runkle, 1985; Dye, 1993; Sousa, 2001).

Intertidal assemblages on rocky shores have been a primary source of descriptive and experimental information on community dynamics (most recent reviews in Bertness et al., 2001). However, this present base of understanding is analogous to the patterns in communities and assemblages it attempts to explain; a patchwork of studies from different sites, assemblages, times, and approaches, the results of which are pieced together to develop broader scale generalizations concerning community structure and organization. In part because of this, the scientific foundations of many current generalizations are considered by some to be weak (Underwood and Denley, 1984; Underwood and Fairweather, 1986; Foster, 1990; Strong 1992). These foundations would be strengthened by more thorough, quantitative characterization of community structure and the associated abiotic environment over broader geographic regions, combined with multi-site experimental investigations (Underwood, 1986; Underwood and Kennelly, 1990; Underwood et al., 2000; Foster, 1990, 1991; Menge et al., 1994; Menge and Branch, 2001; Dye, 1998; Chapman and Underwood, 1988).

We examined variation in community structure and succession in a high intertidal assemblage dominated by the perennial red alga *Endocladia muricata* for 6 years at six sites spanning over 4° of latitude in California. Although the relative composition and vertical

distribution of species in this assemblage vary from site to site (Glynn, 1965; Foster, 1990; Farrell, 1991), the more common members occur on exposed and semi-exposed shores from Baja California, Mexico, to Alaska (Glynn, 1965; Abbott and Hollenberg, 1976; Ricketts et al., 1985). With the exception of the supratidal *Prasiola* assemblage found on rocks with bird guano (Anderson and Foster, 1999), the *Endocladia* assemblage is the highest intertidal assemblage in this geographic range with abundant, perennial macroalgae, including the red algae *E. muricata* and *Mastocarpus papillatus*, and the brown, fucoid algae *Fucus gardneri*, *Silvetia compressa* (*=Pelvetia fastigiata*; Serrão et al., 1999) and *Pelvetiopsis limitata* (Glynn, 1965; Foster et al., 1988; Farrell, 1991). Barnacles (*Balanus glandula, Chthamalus* spp.) may also be abundant at some sites, and Glynn (1965) characterized the assemblage as *Endocladia/Balanus*. Although there are only a relatively few species of abundant, perennial seaweeds, over 90 species of plants and animals have been found in the assemblage at sites in Monterey Bay, CA (Glynn, 1965).

Prior studies in the Endocladia assemblage have resulted in various models of assemblage structure and dynamics. Northcraft (1948) completely cleared 30-cm-wide strips through the assemblage at a site in Monterey Bay, and found that E. muricata had not recolonized after 37 months when observations ended. Glynn (1965) thoroughly described the assemblage and the population dynamics of the common species in the same area between 1959 and 1961. He concluded there was little seasonal and year-to-year variation in assemblage structure, and that E. muricata could recover in less than 6 months after clearing (holdfasts not removed). Recovery was especially rapid if clearing was done in late winter. Farrell (1991) explored successional processes in small clearings ( $6 \times 6$  to  $15 \times 15$  cm) in the assemblage at two sites in Oregon. He found a consistent successional sequence from barnacles to a mix of barnacles and perennial macroalgae, that the algae were dependent on the presence of barnacles for establishment, and that limpets delayed the establishment of both barnacles and algae. Few early successional, ephemeral algae settled in the plots, and variation in the rate of succession was attributed primarily to differences in the timing of barnacle settlement. Based on this and other studies, Farrell (1991) developed a model predicting the effects of consumers on the rate of succession given the different successional interactions proposed by Connell and Slatyer (1977), and found that his results supported the model. Sousa and Connell (1992) found that other relevant studies also supported Farrell's (1991) model.

Our objectives were to describe seasonal (spring and fall) and year-to-year variation in the assemblage, and to determine the effects of site and time of disturbance on the subsequent successional sequence and recovery rate. Complete clearing was chosen as the method of disturbance to produce a consistent, comparable degree of disturbance at all sites that eliminated possible effects from survivors. Successional pathways were based on observed changes in composition and abundance, and recovery rates on the similarities of cleared plots to controls. Possible mechanisms affecting these variables were largely based on other studies, and examined by correlation and observation. The 6-year timespan of the study was longer than most studies of disturbance and succession in the rocky intertidal zone, and allowed us to observe the effects of initial differences in species composition and associated processes (e.g. grazing) on recovery to control composition. The number of sites and their scale of distribution provided a relatively rigorous context for evaluating the generality of the results, and insights into how this assemblage may be regulated.

## 2. Sites, methods, and analyses

## 2.1. Sites and methods

Sites were chosen between Point Conception (34°42′N) and the California/Oregon border (41°05′N) based on similarity in assemblage composition, relatively even spacing in the geographic region, accessibility, and enough area of the assemblage to contain replicate plots. Potential sites were identified from low level aerial reconnaissance during low tides in February 1984. Twenty of these were identified and sampled between March and May 1984 (Foster, 1990) and, based on the above criteria, six sites were chosen for long-term study (Fig. 1).

Ten  $1 \times 2$ -m plots with qualitatively similar structures were chosen in the middle of the vertical distribution of the assemblage at each site in March and April 1985, with the



Fig. 1. Study sites along the central and northern California Coast.

restriction that adjacent plots were separated by at least 1 m. Four plots were randomly chosen as controls, three to be cleared in the spring, and three to be cleared in the fall. The spring-cleared plots were cleared in March and April 1985, and fall-cleared plots in October and November 1985. These two seasons represent the period of maximal (fall) and minimal (spring) standing stocks, reproduction, and recruitment for many of the intertidal algae in this region, and are before (fall) and after (spring) major storms in the region (Foster et al., 1988). We call our times of clearings "seasons" based on natural history information indicating that variation within these times is less than between them. However, we could not replicate clearings in different years, and thus resulting successional differences may simply be related to different times of clearings.

Plots were cleared by repeated scraping and heating (with a propane weed burner) until no visible organic matter remained. The substratum was heated to the point of boiling small pools of standing water and fracturing the rock-bits of encrusting organisms were turned to a white ash. Oxidized organic residues were washed from the plots with seawater after each burning. Damage to surrounding organisms was minimized by covering the borders of the clearings with wet towels and rugs. Controls and clearings were marked with stainless steel bolts secured with underwater epoxy into holes drilled into the rock.

Spring-cleared and control plots were sampled immediately before clearing in March-April, 1985 and 3 months after clearing (summer 1985). Spring-cleared, fall-cleared and control plots were sampled immediately before clearing the fall plots in October-November 1985. Fall-cleared and control plots were sampled 3 months after clearing (winter 1986). All plots were then sampled at 6-month intervals from spring 1986 to fall 1989, and at the end of a final 18-month interval between fall 1989 and spring 1991. Thus, control plots were sampled 13 times and, after clearing, spring-cleared plots 11 times and fall-cleared 10 times. During the course of the study, spring sampling occurred in March-April, summer sampling in June, fall sampling in October-November, and winter sampling in January. To minimize edge effects in these large clearings (most likely from grazers; reviewed by Sousa, 2001), only the center  $0.5 \times 1.5$  m area of each plot was sampled, leaving a 0.25-m border. This central area was further divided into 12 quadrats of  $0.25 \times 0.25$  m each. Three of these quadrats were sampled for the percentage of cover for all organisms and the density of motile animals at each sampling time. To maximize interspersion and independence of quadrats within plots, the quadrats were chosen at random for each sampling date with the restrictions that no more than one could be in a corner and all three could not be on one side of the plot. Furthermore, the same quadrat could not be sampled on two successive dates.

Control plots were sampled in the same manner as the cleared plots. Four control plots were established at each site in the event that one was catastrophically disturbed (e.g. buried by sand, cleared by rock fracture, etc.) during the course of the study. All were sampled on a rotating basis but only three on any one sampling date. No plots were catastrophically disturbed so none were excluded from the analyses.

Cover in each quadrat was determined by sampling 20 random points within the  $25 \times 25$  cm quadrats using the point quadrat described in Foster et al. (1991). Multiple contacts under a single point were sampled by moving aside successive layers or organisms. Multiple contacts of the same species under a given point were recorded as a single contact because of the difficulty of determining whether contacts represented more

than one individual when the organism, such as *E. muricata*, was densely branched. Motile molluscs and echinoderms greater than 0.5 cm long in any dimension were counted within each quadrat, and individuals 0.1-0.5 cm long were subsampled in a  $10 \times 10$  cm quadrat placed in the center of the larger quadrat. Densities of small motile taxa were adjusted to  $0.0625 \text{ m}^2$ . Algae were identified according to Abbott and Hollenberg (1976) and Scagel et al. (1989), and invertebrates according to Smith and Carlton (1975) and Lindberg (1986). Citations for more recent taxonomic changes are given where appropriate. Some organisms (e.g. small algal blades, small limpets) could not be identified to species, or were combined into larger groups for some analyses (e.g. limpets). The term "sp(p)." denotes organisms of either one or several unidentified species, and all taxa and groups of organisms are referred to as "species."

The tidal height of the center of each plot was determined using a transit and stadia rod relative to measured sea level that was corrected to predicted values from tide tables. Substratum characteristics were based on site observations and standard geologic analyses.

To determine possible relationships between succession and the reproductive phenology of the dominant perennial algae E. muricata and M. papillatus, the percentage of their blades (individual plants are difficult to determine in these species with spreading, intermixed holdfasts and numerous upright blades) bearing cystocarps with carpospores was assessed. These spores are generally produced after fertilization, are usually diploid, and develop into tetrasporophytes after settlement (haploid carpospores that develop into female gametophytes can be produced by *M. papillatus*; Polanshek and West, 1977). Data were obtained by randomly locating three 30-m-long transects within each site at each sampling date. For *M. papillatus*, the blade closest to each of 25 random points along each transect was selected. The proportion of these 25 blades with cystocarps was used to calculate the percentage of cystocarpic blades/transect, giving n=3/site/sampling time. Cystocarps were more sparsely distributed in E. muricata, so 10 randomly selected blades of this species were sampled within 50 cm of each random point. In this case, the percentage of cystocarpic blades was based on the number of such blades in each group of 10 points, giving n = 75/site/sampling time. For both species, a blade was cystocarpic if cystocarps were present and released carpospores when squashed. All sites but F were sampled, and sampling was done every other month from May 1985 through May 1986.

#### 2.2. Data presentation and analyses

As we were not interested in variation within control and cleared plots, the mean of the percent cover data from the three quadrats within a plot at any one sampling time and the sum of the motile animals counted (including scaled counts from the 0.01 m<sup>2</sup> quadrats) were used in analyses of abundance. Thus, densities of motile animals are per 0.1875 m<sup>2</sup> (0.0625 m<sup>2</sup> × 3), and each plot was a single treatment replicate unless otherwise noted.

Abundance data in figures are shown as the means through time of the four to five most abundant species of algae and barnacles, and the four most abundant mobile invertebrates based on their mean abundances at all sites, times and season of clearing. These 'species' include three lumped categories: "All Ephemerals," the summed abundances of all ephemeral algae (see Results for composition); "Chitons," the summed abundances of all chitons; and "Limpets," the summed abundances of all limpets. All data by species, site and time are in Kinnetic Laboratories (1992).

Temporal differences in the control plots at each site were evaluated with ANOVA with year and season as fixed factors. Using a subset of possible quadrats in a plot at each sampling date avoided temporal pseudoreplication (Hurlbert, 1984). Normality was assumed as the small sample size (usually n=3) precluded testing. Variances were either homogeneous or nearly so after transformation. Given that parametric ANOVA is robust to nonheterogeneity of variances (e.g. Zar, 1999) only parametric tests were used. Tukey's a posteriori test was used to evaluate differences among means.

Species sampled as percentage of cover were used to determine the recovery rate of cleared plots based on Bray–Curtis percent similarity (Bray and Curtis, 1957). The similarity of the control plots to each other (i.e. 1 vs. 2, 1 vs. 3, 2 vs. 3) at each sampling was used to calculate a control percent similarity envelope. The similarity of the cleared plots to the controls was calculated by taking the mean of the similarities of each cleared plot to each of the three control plots (n=9 comparisons). The mean and range of the cleared plot similarity values were then plotted relative to the control envelope. Recovery rate (percent/month) was calculated for each recovered cleared plot by dividing 100 by the number of months that it took the cleared plot to fall into the control percent similarity envelope. For those plots that had not recovered by the last sampling date, recovery rate was calculated by dividing the percent similarity for a given cleared plot by the percent similarity of the least similar pair of control plots (i.e. the comparison defining the lower limit of the recovery envelope at a given time), multiplying by 100 and dividing by the number of months to the last sampling date.

# 3. Results

## 3.1. Site characteristics and control plots

The sites spanned  $4^{\circ}23'$  of latitude along wave-exposed sections of the coast, with the greatest distance (1°20' latitude) between sites at Bolinas (Site C) and Pescadero Rocks (Site D, Fig. 1). The mean tidal position of plots within a site varied between +0.7 and +1.9 m above Mean Lower Low Water (MLLW). This variation may reflect differences in wave exposure that affect the ability of organisms to live at different tidal positions (e.g. Lewis, 1964), but because of the complex topographic variation on the rocky benches where sites were located, we did not attempt to measure differences in wave exposure among the sites.

Most sites were composed of extensive, gently sloping rock platforms or benches. The bench at Site B was composed of wide ridges with tidal channels between, and Site D was a wall of approximately  $45^{\circ}$  slope that graded into a rock platform below. While all sites were on the exposed coast, most were bounded on their seaward edge by extensive intertidal platforms and were up to 100 m from the sea at low tide. The substratum was hard rock at all sites except Sites C and F where the fractured surfaces were commonly observed to flake off. Losses of harder inclusions in the conglomerate resulted in occasional, small (2–5 cm diameter) natural clearings at Site D. Overall, 49.3% (SE=5.3; all sites and dates combined; n=78) of the substratum in the control plots

was unoccupied rock. Of this 49.3%, 15.4% was rock with no overstory. The remaining 33.9% was covered by an overstory canopy, and microalgae and bacteria no doubt covered the surfaces of all the rocks.

Based on data from all sites and surveys, *E. muricata* was the most abundant alga overall (mean = 45.8% cover; n = 78), and at all sites except Site C (5.4%; n = 13). *M. papillatus* was second most abundant overall (21.2%; n = 78) but did not dominate any site. The brown alga *F. gardneri*, the third most abundant plant overall (13.1%; n = 78), was the most abundant alga at Site C (43.7%; n = 13), and was more abundant at the northern sites than at the southern sites (A, B, and C vs. D, E, and F; Fig. 2). The crustose red alga *Petrocelis* sp(p)., some species of which are the tetrasporic phase of *Mastocarpus* spp. (Guiry et al., 1984), was the fourth most abundant (7.6%; n = 78). While *Silvetia*–*Pelvetiopsis* sp(p). (lumped because of the difficulty of distinguishing juveniles of the former from adults of the latter in the field) can be a common associate in some areas (Farrell, 1991), it exceeded 10% cover only at Site C (12.6%, n = 13). Sessile animal cover



Fig. 2. Cover of abundant algae and barnacles in control plots at the six sites. Data are means of three plots/site.

was relatively low. *B. glandula*, the most common barnacle and the assemblage codominant at Glynn's (1965) sites in Monterey Bay, had an overall mean abundance of 4.1% cover with a maximum of 12% cover at Site C.

Molluscan grazers were by far the most abundant motile animals counted at all sites, and densities of some species spanned an order of magnitude among sites (Fig. 3). *Littorina scutulata/plena* was the most abundant of all grazers at Sites A, C, D, and especially Site E, while limpets were most abundant at Site B and these plus *Tegula funebralis* at Site F.

Species richness, based on the sum of all species found in all surveys, ranged from 34 at Site E to 71 at Site B.

The species composition of the dominant sessile and motile species remained the same at all sites during the study. Absolute abundances varied within sites, but there were few large changes in relative abundance at the end vs. the beginning of the study. These were a



Fig. 3. Density of abundant mobile invertebrates in control plots at the six sites. Data are means of three plots/site. Note log scale.

decline in *E. muricata* and increase in *M. papillatus* at Site A (Fig. 2), an increase in *F. gardneri* at site C (Fig. 2), and a decrease in *L. scutulata/plena* at Site B (Fig. 3).

The number of species per site with significant spring-fall seasonal variation ranged from two at Sites A, D, and E, to five at Site C (Table 1). Of all the occurrences of significant seasonal variation among sessile species, the majority (10/14) of the highest

| Table 1  |  |
|--|--|
| Species in control plots with significant ( $p \le 0.05$ ) temporal variation based on ANOVA |  |

| Site                  | Species                                 | Temporal variable   |                                       | Interaction $Y \times S$ |
|-----------------------|---|---------------------|---------------------------------------|--------------------------|
|                       |   | Season <sup>a</sup> | Year <sup>b</sup>                     |                          |
| Kibesillah Hill (A)   | Cladophora columbiana                   | 0.022 (F)           |                                       |                          |
|                       | Tegula funebralis                       | 0.021 (S)           |                                       |                          |
| Sea Ranch (B)         | Fucus gardneri                          | 0.004 (F)           |                                       |                          |
|                       | limpets                                 |                     |                                       | 0.009                    |
|                       | Littorina scutulata/plena               | 0.017 (F)           |                                       |                          |
|                       | Mastocarpus papillatus                  | 0.002 (F)           |                                       |                          |
|                       | Nucella emarginata/ostrina <sup>c</sup> |                     | 0.008 (89 86 91 87 85 88)             |                          |
|                       | Ralfsia sp(p).                          | 0.005 (S)           | · · · · · · · · · · · · · · · · · · · |                          |
| Bolinas (C)           | Cryptosiphonia woodii                   | 0.002 (S)           |                                       |                          |
|                       | Fucus gardneri                          | < 0.001 (F)         | < 0.001                               | 0.044                    |
|                       | Littorina scutulata/plena               |                     |                                       | 0.023                    |
|                       | Mastocarpus papillatus                  | 0.037               | 0.016 (85 88 87 91 86 89)             |                          |
|                       | Mazzaella splendens <sup>d</sup>        | 0.028 (F)           |                                       |                          |
|                       | Petrocelis sp(p).                       |                     | 0.014                                 | 0.031                    |
|                       | Ralfsia sp(p).                          |                     | 0.020 (89 91 88 87 86 85)             |                          |
|                       | <i>Silvetia–Pelvetiopsis</i> sp(p).     | 0.023 (F)           | ·                                     |                          |
| Pescadero Rocks (D)   | Cladophora columbiana                   | < 0.001 (F)         |                                       |                          |
|                       | green crust                             |                     | 0.008 (85 87 86 88 89 91)             |                          |
|                       | limpets                                 |                     | 0.013 (91 88 89 86 87 85)             |                          |
|                       | Littorina scutulata/plena               | 0.10 (S)            |                                       |                          |
| Pt. Sierra Nevada (E) | Balanus glandula                        |                     | 0.015 (85 86 87 88 91 89)             |                          |
|                       | Endocladia muricata                     | < 0.001 (S)         |                                       |                          |
|                       | Littorina keenae                        |                     |                                       | 0.039                    |
|                       | Littorina scutulata/plena               | < 0.001 (F)         | 0.002 (85 87 86 88 91 89)             | 0.009                    |
| Diablo Canyon (F)     | limpets                                 | 0.008 (F)           |                                       |                          |
|                       | Littorina scutulata/plena               |                     | 0.029                                 | 0.010                    |
|                       | Mastocarpus papillatus                  | 0.031 (F)           | 0.010 (88 85 89 91 86 87)             |                          |
|                       | Mazzaella splendens <sup>d</sup>        | 0.005 (F)           | 0.010 (88 89 87 85 91 86)             |                          |
|                       | Nucella emarginata/ostrina <sup>c</sup> |                     | · · · · · · · · · · · · · · · · · · · | 0.012                    |
|                       | Petrocelis sp(p).                       |                     |                                       | 0.016                    |
|                       | Ralfsia sp(p).                          | 0.025 (F)           | 0.015                                 | 0.050                    |

Season: fall vs. spring, Year: 1985–1991, Y × S: Year × Season interaction. Numbers are p values. Blank space indicates p>0.05.

<sup>a</sup> (F)=fall>spring, (S)=spring>fall.

<sup>b</sup> Multiple comparisons among years done if p value significant and interaction not significant. Mean values for each year ranked from greatest to least (left to right). Similar font or underline indicates years not significantly different from each other based on Tukey's test. Because fonts and underlining overlap, the pattern of significant differences among years cannot be identified.

<sup>c</sup> N. emarginata is now recognized to contain two species whose distribution overlaps in central California (Marko, 1998).

<sup>d</sup> Formerly Iridaea splendens (Hommersand et al., 1994).

abundances were in the fall. There were only five cases of significant seasonal variation in abundance among motile species and, of these, two were most abundant in the spring and three in the fall (Table 1).

There were few consistent seasonal patterns in the dominant species among sites. Seasonal variation in the cover of *E. muricata* was significant only at Site E (Fig. 2; Table 1). *M. papillatus* was significantly more abundant in the fall at Sites B, C, and F. However, seasonal variation in this species was not significant at Site D although its cover was consistently high at this site (Fig. 2). Among motile species, there was significant seasonal variation in *T. funebralis* only at Site A (Table 1), even though it was also abundant at Sites C and F (Fig. 3). Seasonal differences in *L. scutulata/plena* abundance were significant at two (D and E) of the four sites where it was abundant, and at Site B where it was relatively rare (Table 1). When significant, *L. scutulata/plena* was most abundant in the fall at two sites (B and E) and in the spring at Site D (Table 1).

There were 13 cases of significant year-to-year variation in abundance in the control plots (Table 1). However, with the exception of the red alga *M. papillatus* and the brown alga *Ralfsia* spp. at Sites C and F, and *L. scutulata/plena* at Sites E and F, none of the species were significantly different at more than one site.

## 3.2. Succession in cleared plots

Changes in plant species composition during succession in the cleared plots followed two general patterns regardless of when plots were cleared. At Sites A, C, E, and F there was a very low cover of ephemeral species (Figs. 4 and 5) such as *Ulva* spp., *Enteromorpha* spp., *Urospora* spp., *Porphyra* spp., and benthic diatoms that have often been found to colonize and grow rapidly during the early stages of intertidal succession (e.g. Northcraft, 1948; review in Foster et al., 1988). There was a bloom of ephemerals composed almost entirely of diatoms in the fall clearings at Site C (Fig. 5), but it persisted for less than 6 months. At sites with low ephemeral colonization, one or more of the dominant plants in the control plots usually settled early and increased rapidly (e.g. *E. muricata* in the spring clearings at Sites A, and F; *M. papillatus* in the spring clearings at Site C (Fig. 4), and fall clearings at Sites A, C, and F (Fig. 5)). In contrast, Sites B and D had very high initial covers of ephemeral species in both fall and spring clearings, and the appearance of a high cover of the dominant plants at Site B and D except for the lack of *Enteromorpha* spp. at Site B.

Sessile animal cover during succession in the cleared plots was generally low. Sites B and C were the only locations where barnacles, the most abundant sessile animal, exceeded 15% cover during succession. Barnacles, particularly *B. glandula*, tended to be most abundant 1 or 2 years after clearing (Figs. 4 and 5). Sites B and C were also the only ones where *Chthamalus* spp. cover exceeded 10% (highest=27%; Kinnetic Laboratories, 1992).

*L. scutulata/plena* generally reached extremely high abundances in the cleared plots within 3–6 months after clearing (Figs. 6 and 7), probably from immigration. Littorines were common at all sites except Sites B and F where these animals were relatively rare in the control plots (Fig. 3). Limpet abundance tended to peak at 2–3 years after clearing and then, in most cases, declined to near levels found in the controls (e.g. Fig. 7, Site B). *T.* 



Fig. 4. Cover of abundant algae and barnacles in plots cleared in the spring at the six sites. All ephemerals is the combined cover of rapidly growing, short-lived algae (see Results for species). Data are means of three plots/site.

*funebralis* occupied the cleared plots at Sites A, B, C, and F soon after clearing. Its densities were highly variable but generally increased with successional age (e.g. Fig. 7, Site C). Like the littorines, *T. funebralis* densities in the clearings were highest at those sites where it was also abundant in the control plots (Fig. 3 vs. Figs. 6 and 7).

The total number of all species found in the spring clearings was positively and significantly correlated with the total number of all species in the controls ( $r_6$ =+0.94, p=0.002). A similar correlation with the fall clearings was also positive but the coefficient was lower and not significant ( $r_6$ =+0.52, p=0.315).

# 3.3. Succession and time of clearing

Species composition of colonists varied little between the two clearing times; most differences were in relative abundance. Of the very abundant ephemeral species (>30%



Fig. 5. Cover of abundant algae and barnacles in plots cleared in the fall at the six sites. All ephemerals is the combined cover of rapidly growing, short-lived algae (see Results for species). Data are means of three plots/site.

cover at any time at any site), only *Urospora penicilliformis* and diatoms varied greatly in cover between spring clearings and fall clearings within a site. The former was abundant at Site B in the spring but not the fall clearings, and at Site D in the fall but not the spring clearings. Diatoms were abundant at Site B in the fall but not in the spring clearings, and at Site D in the spring but not in the fall clearings. Of the less abundant species, *Porphyra perforata* tended to be common in the fall but not the spring clearings at Site A (Kinnetic Laboratories, 1992).

There were some clear differences in abundance of the dominant, perennial algal species related to season of clearing, and some of these persisted through the last survey. *E. muricata* was significantly more abundant in the spring clearings (paired-sample *t*-test using spring and fall data from a site as a pair, n=6, p=0.048) while *M. papillatus* was significantly more abundant in the fall clearings (paired-sample *t*-test, p=0.05). This was particularly evident at Sites A and F but not at other sites (Fig. 4). In contrast, the



Fig. 6. Density of abundant mobile invertebrates in plots cleared in the spring at the six sites. Data are means of three plots/site. Note log scale.

abundance of *F. gardneri* was not significantly different between plots cleared at different times (paired-sample *t*-test, p = 0.09).

#### 3.4. Recovery rate

While recovery rate varied among sites and between season of clearing, all except the fall-cleared plots at site F were recovered or nearly so by the end of the study (Fig. 8). Mean recovery rates of the three plots at each site and season ranged from a high of 10.3%/month in the spring-cleared plots at Site A to a low of 1%/month (no plots recovered as of spring 1991) in the fall-cleared plots at Site F (Fig. 8). The slow rate of recovery of the fall-cleared plots relative to the spring-cleared plots at Site A was associated with the high cover of *M. papillatus* that developed in the fall-cleared plots and



Fig. 7. Density of abundant mobile invertebrates in plots cleared in the fall at the six sites. Data are means of three plots/site. Note log scale.

the slow increase of *E. muricata* (Fig. 5), the dominant in the control plots. Recovery rates in spring and fall clearings within a site were similar at Sites B, C, and D, with highest rates at Site C (Fig. 8). The rapid recovery at Site C was associated with the more rapid establishment of *F. gardneri* and *M. papillatus* (Figs. 4 and 5), the dominants in the control plots at this site.

Recovery at Site D was slow in both sets of clearings (Fig. 8). The controls remained fairly constant in composition and similarity to each other during the course of the study, with a very high abundance of *E. muricata* (Fig. 2). Both *E. muricata* and *M. papillatus* were slow to colonize both seasonal clearings (Figs. 4 and 5). This delay was associated with the high abundance of ephemerals at this site, as well as the persistent, high abundance of limpets ( $\sim 100-200/0.1875 \text{ m}^2$ ) in the clearings (Figs. 6 and 7) which, at its lowest, was nearly twice the overall mean abundance in the controls (50.6/0.1875 m<sup>2</sup>).



Fig. 8. Recovery of plots cleared in spring and fall. Data are Bray–Curtis percent similarities (see Data presentation and analyses). The gray area is the range of similarities among the control plots (n=3). Points are mean (range) of similarities of the cleared plots (n=3) to the mean of the control plots. Spring clearings were made in spring 1985, and fall clearings in fall 1985 (0's on elapsed months axes). S and F are mean (SD, n=3) recovery rates/month for spring and fall, respectively.

Recovery at Site E was highly variable; the similarities among the controls fluctuated greatly during the study and there was considerable variation among cleared plots (Fig. 8). Although plots were at about the same tidal height as those at Site D, our observations indicated that at Site E they were more subject to episodic, intense desiccation. As discussed above, *E. muricata* died back in some of the quadrats in the control plots at Site E in fall 1986, resulting in the distinct drop in the control similarity envelope. Because the plants rapidly regrew, we considered the "recovery" of cleared plots in fall 1986 an

anomaly, and did not use it to calculate recovery rates. This site also had an extremely high and variable abundance of *L. scutulata/plena* in the clearings (Figs. 6 and 7).

Similarity of spring-cleared plots to controls increased rapidly at Site F but recovery of fall-cleared plots was much slower, with none of them recovered by spring 1991 (Fig. 8). Control plots at site F were dominated by *E. muricata*, and this alga settled and increased rapidly in the spring clearings (Fig. 4). Similar to what occurred at Site A, however, *M. papillatus* settled early in the fall clearings at Site F and remained abundant, while *E. muricata* underwent a very slow increase (Fig. 5).

The differences in recovery rates among sites and seasons of clearing were significant, as was the interaction between site and season (two-way Model 1 ANOVA; site, F = 11.79, p = 0.0001; season, F = 6.94, p = 0.015; interaction, F = 6.53, p = 0.0006). Inspection of the means (Fig. 8) indicates relatively high recovery rates in the spring at sites A and F, a higher recovery rate in the fall at site E, and little seasonal difference in recovery at the remaining three sites. Regression analyses indicated that 30% of the variation in recovery in the spring clearings (primarily a result of rapid recovery at site A), and only 12% in the



Fig. 9. Percentage of branches of *E. muricata* and *M. papillatus* with fertile cystocarps at five sites, each sampled every other month for one year. (\*) No data for site A on this date.

fall clearings, was accounted for by latitude. The slope of the regression was significantly different from zero for spring (p=0.02), but not fall clearings (p=0.15).

To explore the general relationship between the abundance of grazers and ephemeral algae, and between these abundances and recovery rate, the maximum grazer density (all grazers combined) and maximum cover of ephemeral algae at any time after clearing in the spring-cleared and fall-cleared plots at each site were correlated with recovery rate. All correlations were weak and none were significant (Pearson product moment correlation; grazers vs. ephemeral algae,  $r_{12} = 0.028$ , p > 0.5; grazers vs. recovery rate,  $r_{12} = -0.455$ , p > 0.1; ephemeral algae vs. recovery rate,  $r_{12} = -0.44$ , p > 0.1).

# 3.5. Reproductive phenology

There were very distinct seasonal patterns in cystocarp abundance on blades of *E. muricata* and *M. papillatus* at the five sites sampled (Fig. 9). The former species produced these reproductive structures primarily in the spring and summer, the latter did so in the fall and winter.

# 4. Discussion

#### 4.1. Control plots

The *Endocladia* assemblage differed in richness and relative abundance of species from site to site, but exhibited relatively little seasonal (spring-fall) or year-to-year variation in the abundances of the common species (Table 1). Most species in the control plots that had significant seasonal variation in abundance were more abundant in the fall, presumably a result of the preceding favorable climatic conditions (Foster et al., 1988; Murray and Horn, 1989). Similar seasonal variation has been found in the only other long-term study of this assemblage in central California (Foster et al., 1988). Some species exhibited seasonal variation between other seasons (e.g. summer–winter), but this was only examined during the first year of this study. There were fewer significant year-to-year differences in abundance, and those that were significant varied among years and sites such that no patterns were apparent. However, lack of significant year-to-year differences was no doubt partly due to low within year replication (n=2).

In contrast to the view that disturbance is important to rocky intertidal community structure (see Introduction), disturbance at the sites and spatial and temporal scales we sampled did not appear to be particularly important in maintaining assemblage structure. There were no substantial changes in species composition and few large changes in relative abundance in control plots over 6 years. Total bare space (rock with and without overstory) was high. Contrary to the often stated generality that space is an important limiting factor in intertidal communities (e.g. Connell, 1972; Paine, 1974; Carefoot, 1977; Ricketts et al., 1985; Menge and Branch, 2001), it is unlikely that space, as measured by us and usually by others, was an important limiting resource for macroscopic sessile organisms in the *Endocladia* assemblages at the spatial scales sampled at our sites or other, similar sites within this geographic range (Foster, 1990). Moreover, we did not

observe even occasional patches of ephemeral algae in control plots at Sites B and D that might indicate recent disturbance, although these plants were abundant in the clearings at these sites. This suggests that there are differences between 'new' and 'old' space (e.g. presence of grazers, biofilms, overstory) such that bare space as usually measured is not necessarily 'available' space.

This assemblage in California is not subject to battering by logs as described at sites in Washington (Dayton, 1971) and, in contrast to Sousa's (1979) sites where plants grew on cobbles and boulders that could be overturned by waves, our sites were solid rock. We have observed natural disturbances of the size and severity of our clearings created by rock fracture, rock slides, and scour by sand and cobble, but not within the study areas during the study. The primary disturbances appeared to be from large waves, and high air temperatures when low tides occurred during clear, warm days. Given our data and the perennial nature, morphology, and strong attachment of the dominant algae, the result was probably only partial loss of fronds.

## 4.2. Successional patterns and causes

The successional sequence of species varied among sites and recolonization by the dominant, perennial algal species varied with season of clearing. Sites B and D had a high abundance of ephemeral species early in succession regardless of the time of clearing (Figs. 4 and 5), and a trend toward delayed development of the perennial species that dominated the control plots. Ephemerals were rare at the other four sites, and clearings at these sites were more rapidly colonized by perennial species. However, the overall correlation between ephemeral abundance and recovery rate was not significant, most likely because ephemerals were only abundant at two sites. The causes of these differences in ephemerals among sites are not clear, and were not obviously related to biological or physical site characteristics. Grazer densities were not particularly low at Sites B and D relative to other sites, and correlation found no significant relationship between grazer abundance and ephemeral algal cover. As noted by Cubit (1984) and Foster (1992), algal abundance in the high intertidal zone is a function of grazing as well as suitability of conditions for algal growth, and we know little about variation in the latter at our sites.

While molluscan grazers were variable in abundance from site to site and with time in the cleared plots, their effects on succession were obvious only at Site D. Following the initial bloom of ephemerals at this site, limpets (primarily new recruits) became very abundant (Figs. 6 and 7), ephemerals declined (Figs. 4 and 5) and, although bare rock increased, occupation by perennials was very slow. Extremely high abundances of *L. scutulata/plena* may also have been responsible for some of the variability in recovery at Site E (Fig. 8).

The correlative evidence for lack of grazing effects on recovery is admittedly weak. However, while only the maximum grazer density at any time was used in the correlations, at most sites, this maximum occurred within 1.5 years of clearing (and during the period when ephemeral algae were most abundant), and densities remained high after this peak (Figs. 6 and 7). This suggests that maximum grazer density is a reasonable measure of 'grazing' at a site. Recovery during the first 4 years was examined plot by plot in the fall and spring clearings using maximum grazer densities scaled by species-specific consumption rates. These correlations were negative but low (r = -0.49 and -0.43), and only significant for the spring clearings (Foster, 1992). Thus, although weak, the evidence suggests that neither ephemerals nor grazers had large effects on recovery.

Season of clearing affected the relative abundance patterns of *E. muricata* and *M. papillatus* at some sites, and these abundance patterns no doubt influenced seasonal differences in recovery rates at Site A, and especially at Site F. Control plots at both of these sites were dominated by *E. muricata*, and this alga quickly colonized the spring plots soon after clearing (Fig. 4). However, foliose *M. papillatus* quickly colonized the fall clearings either by haploid carpospores or tetraspores (not assessed). These differences in colonization were similar to those found by Glynn (1965) and Sousa (1984) for these species, and were associated with differences in reproductive phenology (Fig. 9). They may reflect seasonal variation in recruitment. However, no such clear relationship was seen at the other sites between A and F.

Recovery rates varied from the complete recovery in 1 year of all spring-cleared plots at Site A to lack of complete recovery of any fall-cleared plots at Site F in 6 years (Fig. 8). Recovery rates thus differed among sites, and between seasons at some sites. Like many of the other factors examined (e.g. temporal variation in abundance in the control plots), there was no consistent relationship between recovery and latitude. Overall, these successional patterns were remarkably similar to those found by Chapman and Underwood (1998) in a similar study on low, wave-exposed shores in New South Wales.

# 4.3. Models of succession

We found significant site and seasonal variation in community structure during succession among the six sites. Observations and correlations suggest processes such as inhibition by ephemerals, variation in reproductive timing, and grazing may affect these patterns but only at particular sites and times. In contrast to Farrell's (1991) results from this assemblage at two sites in Oregon, there were no consistent interactions during succession that affected recovery at all sites. In particular, the facilitation of algae by barnacles in the presence of limpets was not observed. Data in Farrell (1989) suggest that limpet densities at his sites were higher than at our sites, but overall grazing rates are difficult to compare as other grazers were also abundant at many of our sites. Relative to Farrell's (1991) sites, barnacle abundance, especially B. glandula, at our sites was low, perhaps related to the effects of geographic-scale oceanographic differences on recruitment (Connolly et al., 2001). Our results do not support the suggestion by Connolly et al. (2001) that, because of nearshore larval retention, barnacle recruitment may be higher between San Francisco and Monterey Bay. Site B with high barnacle recruitment was well north of this region, and recruitment at Site D, slightly south of Monterey Bay, was low (Figs. 4 and 5).

Grazing can directly affect succession in various ways via the removal of ephemeral and/or perennial algae (Sousa, 1979; Lubchenco, 1983; Dye, 1993; review in Sousa and Connell, 1992). Farrell (1991) suggested that the lack of ephemerals at his sites was probably the result of grazing. As previously discussed, however, effects of ephemerals and grazers, and their interaction, appeared to be minimal at our sites.

Moreover, Tarpley (1992) excluded molluscan grazers from cleared plots at Site C in the same area where ephemerals were rare in our study, and still found low ephemeral recruitment. Other observations at sites with low ephemeral cover (e.g. similar ephemeral cover in the centers vs. periphery of cleared plots) suggest that the abundances of these algae were affected by other, undetermined site characteristics. Some of these differences between our and other studies, especially grazer effects, may also be related to differences in patch size and severity of disturbance (e.g. Sousa, 1984; Dye, 1993).

Similar to the findings of Benedetti-Cecchi and Cinelli (1994), our results indicate that factors such as abiotic site characteristics and seasonal differences as they affect reproduction, dispersal, recruitment, and growth may be more important to successional changes in species composition and differences in recovery rate than variation in biological interactions. This is further suggested by the large seasonal differences in recovery rate at Sites A and F. Site F is particularly illustrative as it had high grazer densities during succession (especially limpets and *T. funebralis*; Figs. 6 and 7), but the greatest seasonal difference in recovery rate.

The critical examination of successional processes by Connell and Slatyer (1977) and subsequent tests of these processes have provided a strong scientific foundation for the refutation of the universal facilitative nature of succession and the relationship of facilitation to the organization of communities. However, our data suggest that further elaboration and dissection of the successional models proposed by Connell and Slatyer (1977) and others (e.g. Berlow, 1997; Jenkins and Buikema, 1998; Benedetti-Cecchi, 2000) may not provide insights into the causes of variation in successional rates and sequences, at least in the relatively well defined and structurally simple *Endocladia* assemblage. As pointed out by Farrell (1991), different species at the same stage of succession can respond to different successional processes (e.g. inhibition vs. facilitation). This plus differences among local sites (as also found by Chapman and Underwood, 1998), variation in available species and recruitment, and size and severity of disturbance (review in Sousa, 2001) will make non-trivial predictions of natural successional pathways and rates using these models very difficult.

Biotic variations arising from facilitative and other interactions, and variations in these interactions caused by consumers, may be only small ripples on the large waves of variation caused by site-specific determinants of the demographic attributes (e.g. fecundity, recruitment success) of the dominant sessile organisms and their subsequent effects as facilitators and habitat modifiers (reviewed by Bruno and Bertness, 2001). This may be particularly true in assemblages dominated by marine plants as these organisms are generally not dependent on other organisms for successful reproduction, recruitment, growth, or dispersal, and are thus unaffected by many processes that affect the demographic attributes of animals and many land plants. The relationship between seasonal differences in reproduction and recruitment of perennial algae at a few of our sites suggests that if predictive successional models proliferate further, they may be more realistic if they incorporate variation in the demographic features of the dominant plants (see also Kennelly and Underwood, 1993). Unfortunately, such variation, let alone its causes, is largely undescribed in marine macroalgae. Our understanding of intertidal succession would also be sharpened by explicit recognition that the function, as well as the structure, of a mid-

intertidal zone dominated by mussels no doubt differs from the algal-dominated zones that commonly occur above and below them.

# 4.4. How is the Endocladia assemblage organized?

Much of the literature on community organization has been devoted to the determination of whether or not communities are at equilibrium, and what processes affect this equilibrium or lack thereof (e.g. Petraitis and Dudgeon, 1999). Connell and Sousa (1983) pointed out that measurements at time scales that allow at least one complete turnover of all individuals, and at spatial scales that are sufficient for their turnover to occur, are prerequisite for resolving these issues. We do not know the lifespans and turnover rates of most of the common species in the *Endocladia* assemblage, but the dominant macroalgae did settle, grew to maturity, and reproduced during the course of the study. It is likely that the clearings were sufficiently large for replacement as the dominant species recolonized them after clearing, and can also recolonize smaller clearings (e.g. Farrell, 1991).

Assuming these observations do indicate adequate scales to evaluate equilibrium or stability and using the similarity indices as the measure of these properties and elasticity (recovery), our results suggest that this assemblage is in equilibrium at the scales studied. With few exceptions, the structure of the control plots remained similar over the study period and, while rates of recovery differed, most clearings had recovered in 6 years. The most obvious exception to this generality were the fall clearings at Site F where *M. papillatus*, not *E. muricata*, colonized early and persisted. This exception could be called an alternative state. If so, then in contrast to Petraitis and Dudgeon's (1999) and Dudgeon and Petraitis's (2001) findings that alternative communities at their sites arise from a critical threshold related to the interaction of disturbance size and predator densities, its different state was related to the timing of disturbance, and only occurred at one site. While there were numerous interactions during succession, their importance varied among sites and none appeared to be particularly strong (sensu Paine, 1980) except the ability of late successional species to prevent the establishment of ephemerals (as indicated by ephemeral colonization of clearings but not controls).

If there are generalizations about the organization of this assemblage, they may most efficiently arise from an examination of the population biology of the dominant species, and the factors that affect it, over a number of sites where these species vary in abundance.

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