

Development of a subtidal epibenthic community: factors affecting species composition and the mechanisms of succession

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Summary. Macroinvertebrate grazers and temporal variability were found to strongly influence species composition of communities that developed subtidally on plexiglas panels. On panels exposed to the naturally high densities of sea urchins and sea stars, only grazer-resistant algal crusts, a diatom/blue-green algal film and short-lived filamentous algae became abundant. On those panels protected from grazers, however, other algae and sessile invertebrates were also common. Both the effects of grazing and the abundance of individual taxa differed on panels immersed at different times of the year.

Resident species also affected subsequent recruitment. Some colonists were found more frequently on panels with established communities than on recently immersed plates. Others became more abundant on younger than on older panels. Considerable small-scale spatial variation in the abundance of species was also found among panels within treatments and appeared to persist throughout the 13 months of the study.

I suggest that since the interactions that determine which mechanisms are important in succession occur between individuals (generalized here to species), not between successional stages, factors such as those examined that can determine which species will interact, indirectly determine the mechanisms that are important in the development of a community. Models that deal with interactions between successional stages may lack the detail necessary to predict or explain changes in species composition in diverse communities.

species can inhibit recruitment of a later species by pre-empting space (direct interaction). Yet, the earlier species may eventually be replaced because individuals of later successional species that do manage to recruit, survive longer than individuals of earlier ones (e.g. Sousa 1979).

Effects of early residents on recruitment, growth and survival of later successional species can range from essential to detrimental (reviews in Drury and Nisbet 1973, Connell and Slatyer 1977; see also Dean and Hurd 1980, Day and Osman 1982). In benthic marine habitats, both enhancement and inhibition of later colonists have been shown to occur within single communities (Boyd 1972; Dean and Hurd 1980, Osman 1981, Turner 1983a). Whether the overall effect of earlier stages on later ones is enhancement or inhibition may depend on the net outcome of many inter- and intraspecific interactions. Since these interactions occur between individuals rather than successional stages, models that describe the mechanisms of community change in terms of successional stages may obscure the complexity involved.

Predation (including grazing), stochastic events and other factors may indirectly alter the balance between enhancement and inhibition of later colonists by determining the species that are to interact. For example, grazing by sea urchins often results in a high percent cover of encrusting coralline algae (Paine and Vadas 1969, Vance 1979, Ayling 1981, this study; review by Lawrence 1975). These algae appear to inhibit recruitment of many sessile species (Breitburg 1984, Masaki, et al. 1982, Padilla 1981, Kitting and Morse, in prep.). Thus in heavily grazed areas, the net outcome of resident:recruit interactions may be inhibition of later successional stages because grazing indirectly determines a suite of negative interactions between crustose coralline algae and potential recruits of later species.

In the present study of a subtidal epibenthic community, I manipulate two factors that may influence species composition, and therefore the balance between enhancement and inhibition of later colonists during the first year of succession: (1) grazing by large mobile invertebrates and (2) time of year that succession begins. I also examine temporal patterns of abundance of common sessile species to see if the presence of an established community affects the abundance of later colonizing species, or the ability of earlier successional species to recolonize. "Earlier" and "later" successional species are used as relative terms. They simply distinguish species under discussion by their times of peak abundance.

Succession may be defined as changes in species composition and community structure through time (Pickett 1976). These changes can result from direct interactions between earlier and later colonizers, or from indirect effects by which earlier residents make the physical environment more favorable or less favorable for later arrivals. Succession may also result from non-interactive processes such as chance introduction of propagules or differences in growth rates and longevity among species (Clements 1916, Gleason 1927, Foster 1975a, reviews in Drury and Nisbet 1973, Connell and Slatyer 1977). Often, succession may involve more than one of these mechanisms. For example, earlier successional

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Study site

The study site was located at a depth of 15 m at the western edge of Naples Reef, located approximately 1.6 km offshore and 24 km west of Santa Barbara, California (34°25' N, 119°57' W). Shallow parts of the 2.2 ha reef (described in Ebeling et al. 1980) supported a diverse assemblage of algae and invertebrates during this study. However, the particular area of the reef used as my study site has not supported kelp or other erect macroalgae since early 1978 (A. Ebeling, pers. commun.). Most of the rock substrate at the study site was covered by encrusting coralline algae. The ahermotypic corals *Balanophyllia elegans*, *Paracyathus stearnsii* and *Astrangia lajollensis* were also common. The sea urchins, *Strongylocentrotus franciscanus* and *S. purpuratus*, and the omnivorous sea star *Patiria miniata* were the most abundant large invertebrate grazers.

Methods

Settling plates were used to examine the effects of grazing, temporal variability and the presence of an established community on species composition during early development of the sessile community. Plates measured 14.5 × 14.5 cm and were constructed of plexiglas roughened by sand-blasting. Plastic cable ties were used to attach plates to concrete block platforms.

Three treatments were used to examine the effects of grazing by benthic macroinvertebrates on the establishment of the sessile community: no cage, cage-roofs and complete cages. Cages and cage-roofs were made of 1.3 cm mesh galvanized hardware cloth and measured 19 × 19 × 19 cm. They were cleaned biweekly to minimize reduction of light and water flow due to fouling. The uncaged treatment permitted grazing by all invertebrates and fish. Cages excluded invertebrates and fish too large to fit through the wire mesh (e.g. most sea urchins and sea stars). Plates fitted with mesh roofs only were used to control for shading caused by cages. This treatment opened plates to both large and small invertebrates but closed them to medium and large sized fishes, which could not orient vertically to feed on the substrate.

Two series of plates, one started 7 months before the other, were used to examine the temporal patterns of succession. Each series consisted of the three treatments described above. Since series were not replicated within seasons, the differences found may reflect chance temporal variation in, e.g., recruitment and physical factors rather than predictable seasonal trends.

Six replicates of each treatment were initiated on August 28, 1979 ("August series" of succession plates). However, severe storms with swell heights of up to 6 m (Craig Fusaro, pers. commun.) during February 1980 destroyed two cage-roof plates, two uncaged plates, and all replicates of the caged treatment. The lost caged plates were replaced with four other caged plates that had been submerged at the study site since September 6, 1979 and had been returned to the lab twice prior to the storms. Handling and age of the replacements were thus quite similar to that of the lost plates. The second series of plates (six replicates of each treatment) was set out on March 14, 1980. Both March and August series were examined every six to eight weeks, depending on diving conditions. Both series were terminated in October 1980. The August and March series were

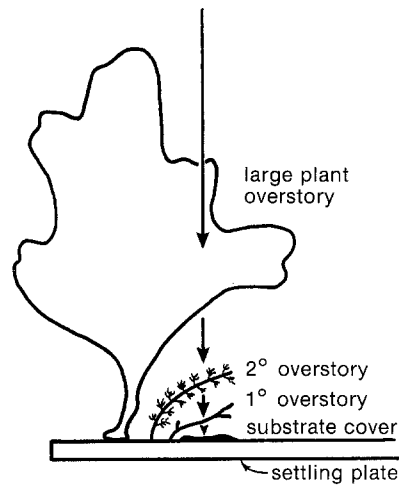


Fig. 1. Counting technique used to determine space occupation. Species attached directly to the panel (or an encrusting organism) below the point being examined (indicated by arrows) were counted as substrate cover. Small sessile organisms whose erect portions fell below the point but were attached elsewhere were counted as overstory cover. Area covered by erect portions of large algae was visually estimated and scored as large plant overstory

maintained for 13 and 7 months and examined 8 and 4 times, respectively.

To further examine the influence of macroinvertebrate grazers on community structure, I provided a temporary refuge from grazing. Eight caged plates were set out in March 1980. After 21 weeks they were examined and returned to the field; four randomly chosen plates were returned with cage-roofs instead of complete cages. All plates were re-examined 15 weeks later, in November 1980.

Another series of caged plates ("recruitment plates") was used to compare recruitment onto recently bare substrate with recruitment into established communities (March and August series succession plates). A clean set of five or six recruitment plates was set out every four to eight weeks. Species or species groups were recorded as present or absent on each plate; no percent cover estimates were performed.

In the laboratory, all plates remained submerged in running filtered sea-water while they were observed with a dissecting microscope. Except on recruitment plates, percent cover of sessile organisms was estimated by a point intercept technique. A 1 cm mesh grid was randomly positioned over the plate and all intersection points falling within a 12.5 × 12.5 cm area were examined. The outer 1 cm margin of the plates was excluded from examination to avoid an "edge effect" (Foster 1975b). Approximately 150 points were counted on each plate; the exact number depending on the position of the counting grid on the plate.

Three separate estimates of percent cover were made for each plate: substrate cover, overstory cover and large plant overstory (Fig. 1). Substrate cover was estimated from organisms that were attached directly to the substrate, or to an encrusting organism, at each intercept. Diatom/blue-green algal film was counted only where it occupied primary substrate (the plate surface) – not at points where it was an epibiont. At points falling on other species, both the epibiont (if present) and the species attached directly to the substrate were counted. Total substrate cover could therefore exceed 100%.

Overstory cover was estimated from all points falling directly over the erect portions, rather than the attachment sites, of small (≤ 2.5 cm tall) individuals that were not overlapping other individuals of the same species. Where multiple layering of different erect species occurred, points were recorded as primary overstory, secondary overstory, etc. Cover of large plants (> 2.5 cm tall) was estimated subjectively by viewing completely submerged plates because flattening large plants against the plate with the counting grid would impose a large sampling bias.

Whenever the August series of succession plates was sampled, large invertebrate grazers were censused in permanent 16 m^2 quadrats, surrounding each of the two platforms that held the settling plates. I counted all individual grazers large enough to be excluded by cages. These included all mobile species that feed on attached prey.

Statistics, species groupings and tests of methodology

Unless otherwise noted, all statistical analyses were done with either two-way analyses of variance or t-tests using SAS programs (SAS User's Guide: Statistics). Percent cover data were arcsin transformed for all ANOVAs and for t-tests on the same data sets. Otherwise, untransformed data were used. The p values I report for t-tests reflect either the t-statistic or the approximate t-statistic, depending on whether variances were equal or not equal by the F-test. In ANOVAs, the effects of temporal variation were examined by comparing August and March series plates of similar ages. The effects of the age of a community were explored by comparing August and March series plates on similar sample dates and thus, at different ages.

Most species were grouped into "taxa" for statistical analyses and description of trends in community development. Each taxon consisted of a group of morphologically similar and taxonomically related species whose combined abundance comprised at least 5% substrate or overstory cover in at least one treatment on at least one sample date. The category "space bare of macrobiota" (SBOM) consisted of substrate that appeared totally bare under a dissecting microscope plus substrate covered only by a visible film. The main components of this film were diatoms and blue-green algae. It is recognized that even the "totally bare" space was, in fact, occupied by microbiota. The main difference between space designated "totally bare" and that considered to be occupied by the diatom/blue-green algal film was probably the density of cells.

Taxa (or other descriptive categories) were included in the statistical analysis only on those dates when their mean cover equalled or exceeded 5% in at least one of the treatments being considered. Data are presented in tables and text as the mean ± 1 SE.

Cages and cage roofs did not significantly alter water flow as measured by Plaster of Paris blocks (Day 1977) but did reduce light by 8% compared to levels on uncaged plates. Differences in the community developing on cage-roof and uncaged plates were few and not consistent with expected effects of shading (only 2 of 33 statistical comparisons of the percent cover of abundant taxa indicated significant differences at the 0.05 level; Wilcoxon two-sample test, Sokal and Rohlf 1969). However, to be conservative, all comparisons to determine the effects of grazing were made between the caged and cage-roof treatments rather than

between caged and uncaged plates. The effects of handling plates were determined by comparing caged plates left undisturbed in the field for 21 weeks with the others brought back to the lab and examined twice prior to the 21 week sample date. The handling effects found were minor compared to differences between experimental treatments. (See Breitbart 1982 for details on tests of methodology.)

Results

Graser densities

Density of large grazers on the two 16 m^2 quadrats surrounding the experimental platforms was high during the 13 months of this study (Fig. 2). The sea urchins *Strongylocentrotus franciscanus* and *S. purpuratus*, and the omnivorous sea star *Patiria miniata* were most abundant. Several other mobile benthic invertebrates, large enough to be excluded by cages, were also present. These included the sea urchin *Lytechinus anamesus*; the sea stars *Dermasterias imbricata*, *Orthasterias koehleri*, *Pisaster giganteus* and *P. brevispinus*; the sea cucumber *Parastichopus parvimensis*; the gastropods *Astrea undosa*, *Cypraea spadicea* and *Kellia kellitii*, the crab *Cancer antennarius* and the spiny lobster *Panulirus interruptus*. Grazer density (based on total number present in 32 m^2 sampled) ranged from a high of 17.2 individuals/ m^2 in May 1980 to a low of $9.9/\text{m}^2$ in October 1980, the last sampling date.

Pattern of succession on grazed (cage-roof) August-series plates

During the 13 months in which the grazed, August-series plates were examined, only four taxa reached a mean cover of 5% or more for even a single sample date. These four were encrusting coralline algae, diatom/blue-green algal film, erect filamentous diatoms, and filamentous brown algae. Nearly all of the cover of filamentous brown algae in this and the other treatments was made up of *Giffordia granulorum*. All other taxa of macroscopic algae and all invertebrate species combined never exceeded 3% mean substrate cover on the grazed panels.

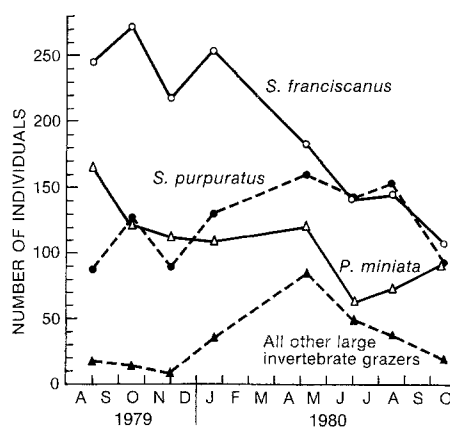


Fig. 2. Total number of large invertebrate grazers on the two permanent 16 m^2 quadrats. All individuals too large to fit through the 1.3 cm mesh of the cages were included in the count

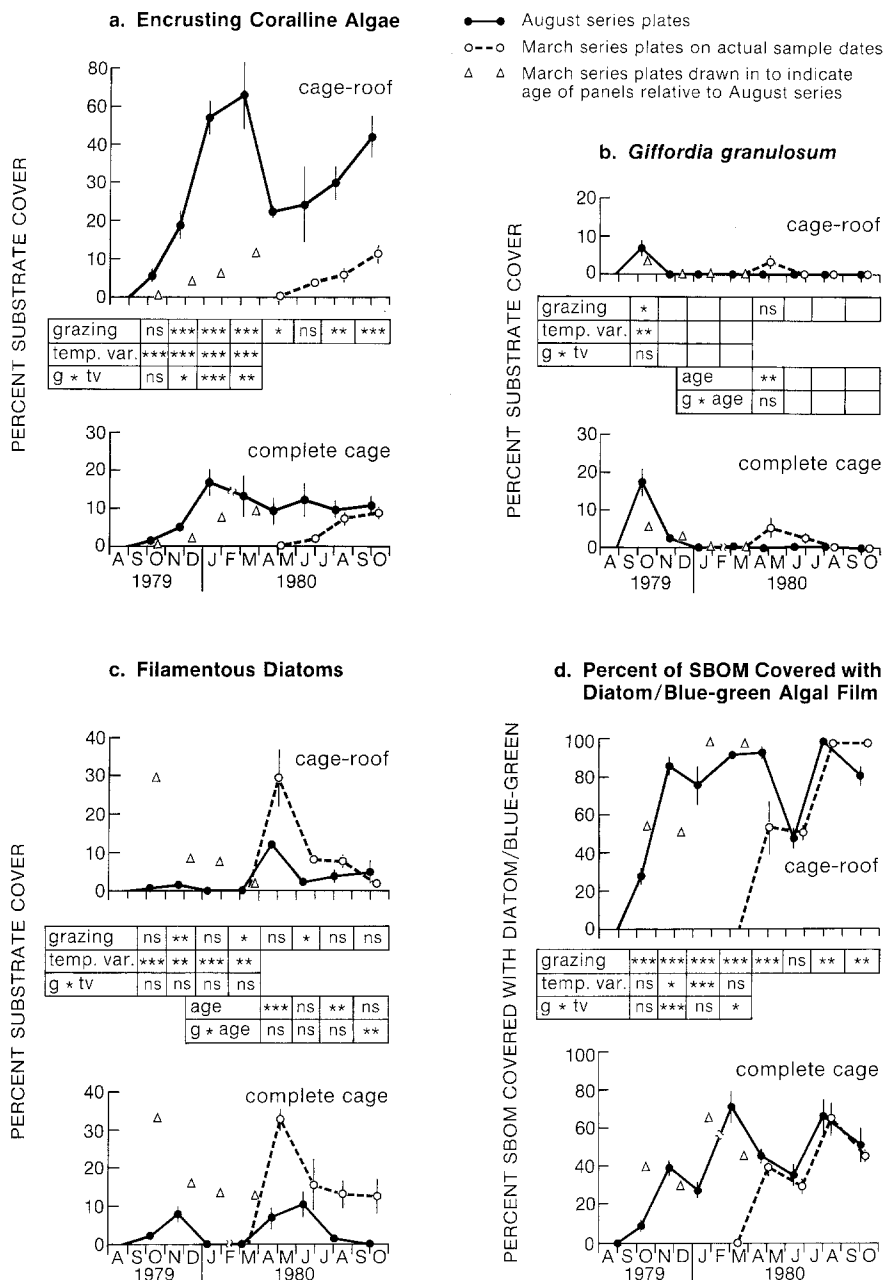


Fig. 3a-d. Abundance of taxa that reached $\geq 5\%$ substrate cover on both grazed and caged treatments of the long-term successional pattern plates. Data are $\bar{X} \pm 1$ SE. March series plates are drawn to indicate age relative to August series plates (unconnected triangles) as well as their actual sample dates (open circles) to facilitate between series comparisons. The break in the line for August series caged plates indicates the loss of the original plates. The inserted tables indicate the results of statistical comparisons between cage-roof and completely caged plates: two-way ANOVAs when 2 main effects and an interaction are indicated and t-tests when only the effect of grazing was considered. All dates tested (See text for explanation) are indicated by significance levels: *** = $P \leq 0.001$, ** = $P \leq 0.01$, * = $P < 0.05$, ns = $P \geq 0.05$

Encrusting coralline algae (Fig. 3a) recruited rapidly, and reproductive patches were observed on six week old plates. Substrate cover of coralline crusts gradually increased and these algae persisted as an abundant component of the community throughout the study. In contrast, abundance of *Giffordia* (Fig. 3b) and filamentous diatoms (Fig. 3c) fluctuated considerably. *Giffordia* peaked once in October 1979 and then disappeared from the plates while filamentous diatoms were most abundant in April 1980.

Space bare of macrobiota fluctuated but remained high throughout the study in this series, averaging between 45 and 78% of the substrate. However, on 13 week through 13 month-old plates (except in June 1980) 75% or more of this SBOM was comprised of a visible film of diatoms and blue-green algae (Fig. 3d).

Overgrowth by epibionts was uncommon and never exceeded $2.2 (\pm 1.0$ SE)% of the plate surface. Overstorey growth was also sparse. Overstorey cover rose to

$10.6 \pm (2.3)\%$ in October reflecting the fall bloom of *Giffordia* and then declined to only 0–3% cover for the remainder of the study.

Effects of grazing on species composition

1) *Comparison of grazer exclusion cages and cage-roof treatments (August-series)*. More taxa were abundant on plates from which large grazers were excluded than on grazed plates. In addition to the four that were also abundant on grazed plates, the following taxa (and, indicated by parentheses, individual species or genera within those taxa) exceeded 5% mean substrate cover on at least one sample date: filamentous red algae (*Polysiphonia* sp.), hydroids (*Obelia dichotoma* and *Lovenella* sp.), encrusting cyclostome bryozoans (*Tubulipora* spp.), encrusting cheilostome bryozoans (*Aetea anguina*), barnacles (*Balanus pacificus*) and tubicolous amphipods (not keyed to species). Over 90%

of the encrusting cyclostome bryozoa and barnacle cover was composed of *Tubulipora* spp. and *Balanus pacificus*, respectively. The sums of algae and of all invertebrates, other than the taxa mention above, never exceeded 5% substrate cover in this treatment.

On August series caged plates, the mean substrate cover of all algae (excluding diatom/blue-green algal film) averaged 21% and remained fairly constant through time. However, the abundance of sessile invertebrates increased throughout the study reaching $60.7 (\pm 9.4)\%$ cover by October 1980. As invertebrate cover increased, SBOM decreased so that during summer and fall of 1980, levels were only half of that found on grazed plates.

Encrusting coralline algae covered more substrate, and the percent of SBOM covered by a diatom/blue-green algal film was higher on grazed plates (Fig. 3a and d), but most other algal taxa were more abundant in the absence of large grazers. During their fall peaks both *Giffordia* and filamentous diatoms were more abundant on caged than on grazed plates ($P < 0.05$ for both comparisons (Fig. 3b and c). However, both time of year plates are initially immersed and age of the community on the plates also affect the abundance of *Giffordia* and diatoms. Inhibitory effects of the established community appeared to negate the advantage of protection from large grazers (see below).

Filamentous red algae and red, blade-forming algae also occasionally became abundant on caged plates immersed in August. Filamentous red algae were abundant in winter 1979, reflecting the cover of *Polysiphonia* spp., and peaked again in August 1980 when several other genera of ceramiales were also common (Fig. 4a). Red, blade-forming algae dominated the large plant (> 2.5 cm high) overstory. However, the pooled percent substrate cover of red blades, brown blades and all green algae, remained low (\bar{X} always $< 3\%$ cover).

Sessile animals were very much more abundant when large grazers were excluded. The abundances of the various invertebrate taxa in grazed and caged treatments were not compared statistically, however, because the mean total invertebrate cover on grazed plates was so low (always $< 2\%$). On caged plates, substrate cover of most invertebrate taxa increased with time, but peaks occurred during different seasons (Fig. 4b-f). The January peak of bryozoans reflected the high abundance of *Tubulipora* spp., while a subsequent increase during the summer was due to the increasing abundance of encrusting cheilostomes and arborescent species. Barnacles and tubicolous amphipods reached their greatest cover earlier in the year than did polychaetes. The abundance of individual hydroid species varied widely among plates, even though the total cover of hydroids remained fairly constant. *Obelia dichotoma* peaked in winter 1979 but by March 1980 was abundant on only one of the four caged plates (22.9% vs. $0.4 (\pm 0.4)\%$ cover on the other three plates). *Lovenella* sp. comprised over 50% of the total hydroid substrate cover in March 1980 and 100% from April-October 1980. It was a major part of the primary overstory as well.

It is not clear that any single measure accurately describes the amount of space available for colonization in a diverse community like the one that developed on caged plates. Space bare of any visible growth declined to less than 25% of the substrate on 6 through 13 month old plates. An additional $11.5 (\pm 3.4)$ to $26.5 (\pm 6.0)\%$ of the primary substrate was covered only by a film of diatom/

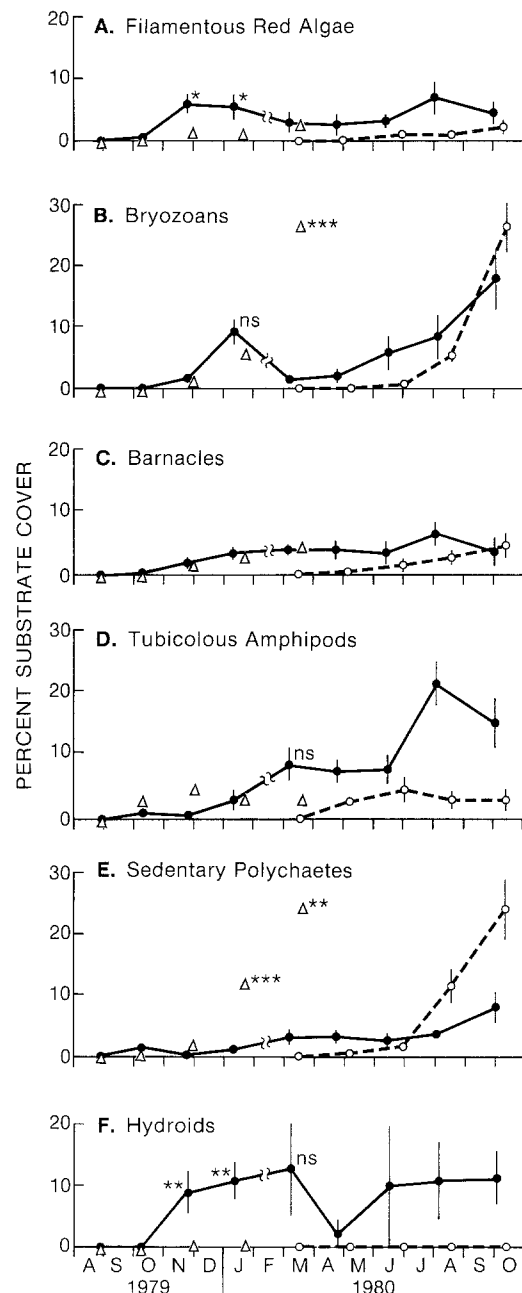


Fig. 4A-F. Percent substrate cover of taxa that were abundant ($\geq 5\%$ mean substrate cover) on caged panels but rare in grazed treatments. Data are $\bar{X} \pm 1$ SE. Asterisks or ns in graphs indicate significance level for comparison of August and March series plates of similar ages. March series plates are drawn to indicate age relative to August plates as well as their actual sample dates to facilitate between series comparisons. The break in the line for August series caged plates indicates the loss of the original plates. All dates tested (see text for explanation) are indicated by significance levels: *** = $P \leq 0.001$, ** = $P \leq 0.01$, * = $P < 0.05$, ns = $P \geq 0.05$

blue-green algae (Fig. 3d). Non-living biotic substrate (calcium carbonate and sand tubes, barnacle tests and scars, and dead coralline algae) increased to $39.2 (\pm 5.1)\%$ cover by August 1980 (Fig. 5). During 1980, furthermore, substrate cover of dead invertebrates and algae fluctuated between $5.0 (\pm 3.0)$ and $15.4 (\pm 4.4)\%$, suggesting that bare patches were constantly being regenerated.

Another determinant of space available for colonization

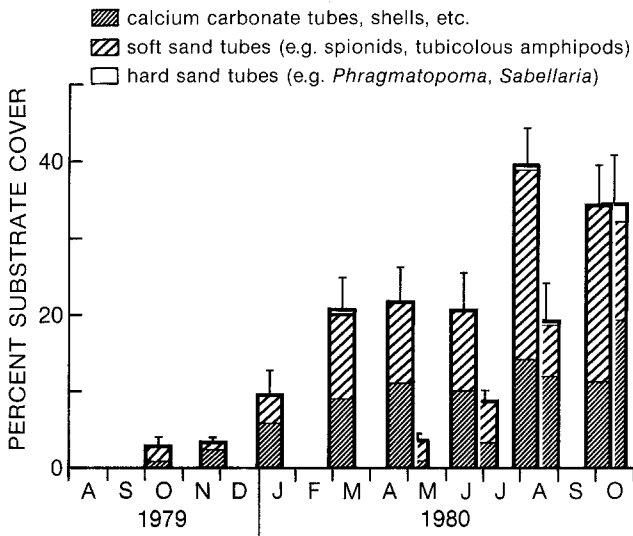


Fig. 5. Secondary space on August and March series caged plates. Data are mean for each type of substrate ± 1 SE of total mean. Where bars are paired, the second bar represents the March series plates

is vertical structure. Low encrusting species always made up most of the substrate cover but stoloniferous and non-stoloniferous erect species were common. Although variable in cover, primary overstory overlaid an average of 16.3 (± 3.1)% of the substrate during the 13 months. Occasionally, two or more layers of different species (secondary overstory) were present. In addition, large blade-forming algae increased from $<3\%$ cover August 1979 – August 1980 to 40.0 (± 5.9)% overstory cover on 13 month old plates. Direct overgrowth of one species by another increased to 7.3 (± 2.0)%.

2) *Temporary refuge from grazers.* A comparison of plates that were caged for 5 months and then exposed to large grazers for 3, with plates that remained caged for the entire

8 months (March–November 1980), indicated that grazers were able to remove established invertebrate individuals and colonies. Grazers significantly reduced both number of individuals or colonies, and the area covered by abundant sessile invertebrates on plates that had previously been protected by cages (Table 1). In contrast, percent substrate cover of encrusting coralline algae and SBOM increased on grazed plates.

Effects of temporal variability on species composition

Here I compare communities that have developed for similar lengths of time but that were started on different dates (August and March) as an example of the effects of temporal variability on species composition. Qualitatively, the development of the assemblage on grazed plates that were immersed in March resembled that on plates of similar ages immersed in August. Uncaged and cage-roof plates of both series showed early peaks of filamentous diatoms and *Giffordia*, and a gradual increase of encrusting coralline algal cover. Most of the SBOM on 21 and 29 week plates was covered with diatom/blue-green algal film. Substrate cover of all other species combined remained low, never exceeding 3.1 (± 0.8)% on either treatment. Direct overgrowth was rare and filamentous diatoms and *Giffordia* comprised most of the overstory.

Quantitatively, however, the two series differed in many ways. On March plates, encrusting coralline algae, *Giffordia* and filamentous red algae were less abundant than on August plates of similar ages (Fig. 3a and b). In contrast, filamentous diatoms peaked earlier and persisted at higher densities on March plates (Fig. 3c). Percent of SBOM covered with diatom/blue-green algal film differed inconsistently between the two series (Fig. 3d).

The effects of excluding large grazers depended on time of year treatments were started. Unlike the August series plates, such exclusions on March plates generally did not significantly affect abundance of coralline algae, or, during its early peak, filamentous diatoms (Figs. 3a–c). Like Au-

Table 1. Effect of caging plates for 21 weeks prior to exposure to large grazers. Data are presented as mean ± 1 SE number of individuals and/or percent substrate cover at 21 weeks (just prior to exposing experimental plates to grazers) and at 35 weeks. T-Tests were used to test for differences in abundance of common taxa on experimental and control plates at 21 weeks and for the change in number or percent cover between 21 and 35 weeks. There were no significant differences between experimental and control plates for any of the species test at 21 weeks ($P > 0.18$ for all comparisons)

	Experimental plates		Controls		Change in no. of individuals or percent cover $P =$
	21 weeks	35 weeks	21 weeks	35 weeks	
Number of individuals/plate					
<i>Vermeliopsis bififormis</i>	206.3 \pm 37.1	10.5 \pm 1.6	183.5 \pm 11.7	161.8 \pm 17.3	0.017
<i>Tubulipora</i> spp.	58.3 \pm 9.9	0.3 \pm 0.3	84.3 \pm 30.7	63.0 \pm 19.8	ns (0.083)
<i>Rhynchozoon rostratum</i>	23.5 \pm 0.3	0.3 \pm 0.3	16.8 \pm 3.9	24.8 \pm 5.4	0.006
<i>Microporella</i> spp.	8.5 \pm 0.6	0.0	11.8 \pm 4.4	11.0 \pm 2.0	0.002
<i>Cauloramphus spinifera</i>	11.3 \pm 2.5	0.0	9.5 \pm 3.8	13.8 \pm 2.3	0.002
<i>Pododesmus cepio</i>	19.8 \pm 7.5	0.0	12.3 \pm 2.5	5.5 \pm 2.2	ns (0.156)
Percent substrate cover					
<i>Vermeliopsis bififormis</i>	8.6 \pm 2.1	1.1 \pm 0.4	7.4 \pm 2.2	12.3 \pm 1.7	0.007
<i>Tubulipora</i> spp.	3.7 \pm 0.9	0.2 \pm 0.2	5.1 \pm 1.7	8.2 \pm 2.7	0.020
encrusting cheilostomes	3.4 \pm 1.5	0.2 \pm 0.2	5.5 \pm 1.3	13.9 \pm 3.6	0.009
encrusting coralline algae	7.6 \pm 1.6	27.4 \pm 2.4	13.3 \pm 8.6	11.5 \pm 3.6	0.012
available space	48.9 \pm 5.3	63.8 \pm 4.0	49.3 \pm 8.4	19.7 \pm 5.5	0.0004

gust plates, however, grazed plates had more SBOM covered with diatom/blue-green algal film (Fig. 3d) and drastically reduced densities of sessile invertebrates.

Patterns of abundance of the various invertebrate taxa on caged plates also varied between March and August series caged plates of similar ages. On August plates, *Tubulipora* dominated bryozoan cover, while encrusting cheilostomes were rare ($\leq 0.5 (\pm 0.3)\%$ substrate cover) during the first 27 weeks of growth (Fig. 6a and b). On March plates, however, the two taxa were about equally abundant and bryozoan cover reached higher levels (Fig. 4b). Dominant polychaete species also differed between the two series. Cover of *Vermeliopsis bioformis* reached $11.1 (\pm 2.2)\%$ on March plates but was always close to zero on August plates (Fig. 6c). *Chaetopterus variopedatus* also tended to be more abundant on March plates reaching $4.3 (\pm 3.0)\%$ cover. Total substrate cover of sedentary polychaetes was higher on March series caged plates (Fig. 4c). In contrast, hydroids were far less abundant on March plates (Fig. 4f). Neither series supported much cover of barnacles or tubicolous amphipods during their first 7 months of immersion (Fig. 4c and d).

Totally bare space on plates of both series declined rapidly – on March plates to $13.1 (\pm 1.8)\%$ at 7 months, when the diatom/blue-green algal film covered an additional $15.5 (\pm 4.4)\%$ of the substrate. By the same date, the secondary substrate of calcium carbonate and sand-tubes increased to $34.5 (\pm 6.2)\%$ cover (Fig. 5).

Two measures of community complexity—percent overstory and percent overgrowth—differed at times between the August and March series. Although March plates generally had 10–20% overlay by overstory species, 13 and 19-week August plates had higher, primarily due to the abundance of *Polysiphonia* and *Obelia* ($P < 0.01$).

Evidence of inhibition on caged plates

To examine whether the presence of an older, established community might negatively affect the abundance of (inhibit) various taxa, March and August-series caged plates were compared at similar sample dates. The recruitment and/or growth of species (or higher taxa) found to be more abundant (higher percent substrate cover) on young (March) plates than on older (August) ones was considered to be inhibited by the earlier resident community.

Tubulipora spp., encrusting cheilostome bryozoans, *Vermeliopsis biformis* (Fig. 6a–c), filamentous diatoms and *Giffordia granulorum* (Fig. 3b and c) were significantly more abundant on younger plates than on older ones examined on similar dates. The evidence for inhibition of cheilostome bryozoans is somewhat weaker than that for the others because the trend was not apparent until the last sample date.

Encrusting coralline algae are one component of the established community that may depress the abundance of other taxa. They inhibit recruitment of *Vermeliopsis* and bryozoans (Breitburg 1984). They have also been reported to inhibit recruitment of filamentous diatoms (Padilla 1981). To examine the relationship between coralline algae and filamentous diatoms in this community, I calculated the number of points at which diatoms grew directly on coralline algae vs. on some other substrate. I compared this with the number of times diatoms were expected to be on or not on coralline algae based on the proportion

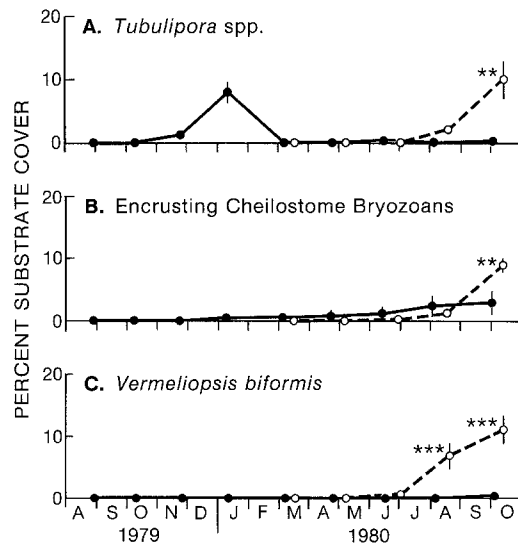


Fig. 6A–C. Percent substrate cover of species that appeared to be inhibited by the presence of an established community ($\bar{X} \pm 1$ SE). See also Fig. 3b and c (filamentous diatoms and Giffordia) for a similar pattern. The break in the line for August series caged plates indicates the loss of the original plates. All dates tested (see text for explanation) are indicated by significance levels: *** = $P \leq 0.001$, ** = $P \leq 0.01$, * = $P < 0.05$

of the substrate covered by coralline algae. This expected value was calculated separately for each plate of the August series during the peak of the spring diatom bloom (April for cage-roof and uncaged plates and June for caged plates) to maximize the sample size. Observed and expected values were then summed over all plates for the X^2 calculation. Diatom recruitment directly onto crustose coralline algae was very similar to that expected (observed = 40 points with diatoms on coralline algae, 184 points on other substrates; expected = 38.6 on coralline, 185.4 not on coralline algae; $X^2 = 0.057$, ns). Since the overall abundance of filamentous diatoms was lower than expected on the older plates, it appears that coralline algae alone depressed the abundance of filamentous diatoms as much as did the average of all other components of the community combined. Other species on the caged plates, however, may have a greater potential to inhibit filamentous diatom recruitment/survival. On August plates during the June 1980 peak in filamentous diatom abundance, only $1.0 (\pm 1.0)\%$ of the filamentous diatoms were growing on sand-tubes, which covered $10.6 (\pm 3.9)\%$ of the substrate; only $2.4 (\pm 1.4)\%$ were growing on calcium carbonate surfaces, which covered $9.9 (\pm 2.6)\%$ and only $2.1 (\pm 2.1)\%$ were growing on all other live plants and animals combined. The remaining 94.5% of the diatom cover was made up of plants attached to substrate that appeared bare of other macrobiota.

Unlike the above species whose abundance is depressed on plates with established communities, encrusting coralline algae tended to be less abundant on younger plates than on older ones ($P < 0.01$ in April and June/July 1980). However, they too appear to be adversely affected by some components of the established community. Coralline algae rarely recruited onto or overgrew soft (e.g. spionid) or hard (e.g. *Phragmatopoma*) sand tubes although they were frequently found on calcium carbonate polychaete tubes and barnacle tests. Their lateral spread may also be restricted since they tend to be the losers in overgrowth interactions

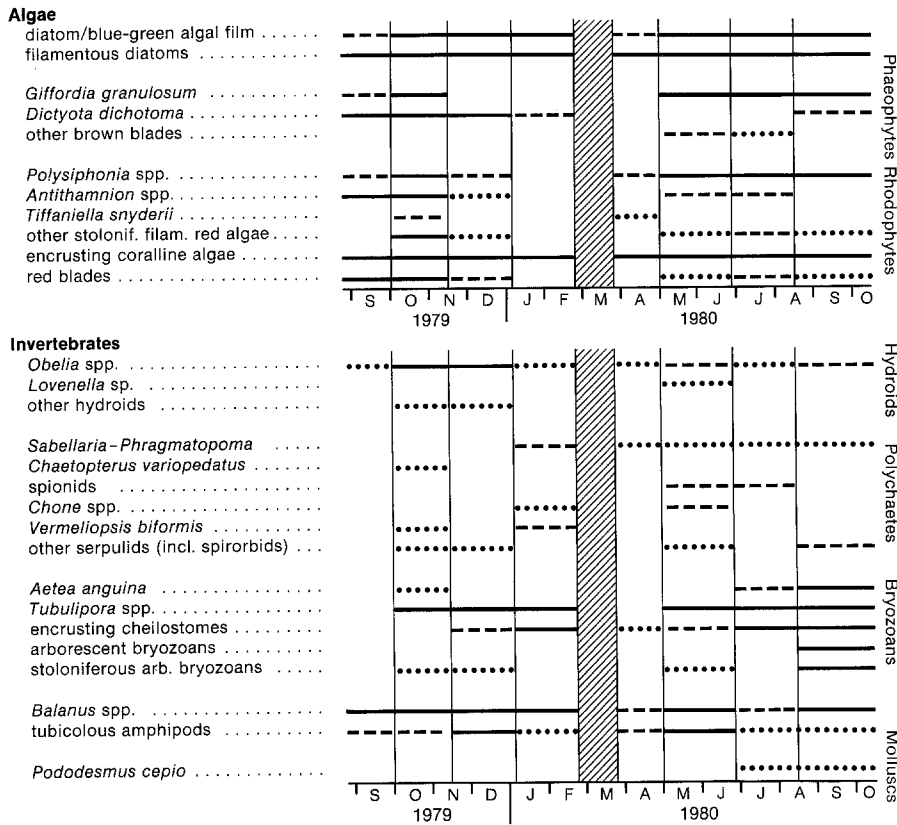


Fig. 7. Summary of recruitment of algae and sessile invertebrates. Solid, dashed and dotted lines indicate that a taxon occurred on all, 3–4 or 1–2 of the five recruitment plates used for each sample period, respectively. Since two of the plates used during Jan.–Feb. 1980 were lost, the solid, dashed and dotted lines indicate that a taxon was present on 3, 2, and 1 plate, respectively, during this period

with other encrusting organisms in this community (Breitburg 1984).

Evidence for enhancement

Recruitment and/or growth of several species appeared to be enhanced by the presence of an established community. A new set of filamentous diatom species appeared on caged March plates in fall 1980, where they preferentially recruited onto sand tubes. The three plates with higher percent covers of sand-tubes (25.0 (± 3.1) vs 1.0 (± 0.4)% on the other three plates) also had higher percent covers of diatoms (22.9 (± 2.2) vs. 2.7 (± 1.7)% cover, respectively). More diatoms were found growing directly on sand-tubes than expected by the proportion of the substrate covered by the tubes ($X^2 = 148.4$, $P \ll 0.005$).

While sand-tube building polychaetes may enhance recruitment of certain filamentous diatoms, these polychaetes and other taxa may in turn be enhanced by other components of the epibenthic community. To examine this possibility, recruitment onto the short-term “recruitment panels”, was compared to that onto the regular caged panels with established communities. Sample size in the following examples varies depending on whether the time period considered includes both the lost ($n = 6$) and replacement ($n = 4$) August series caged plates or only the replacement plates.

Several taxa that rarely recruited to the recruitment panels occurred on many of the regular caged plates. By March 5, 1980, spionids had recruited to seven of ten August plates, but to no recruitment panels; *Chone* spp. to eight of 16 August + March plates (by October 1980) but to only one recruitment panel; arborescent bryozoa (excluding *Filicrisia*) to nine of ten August + March plates (during

March–August 1980) but to no recruitment panels. *Lovenella* never appeared on recruitment panels but was present on three of the four August series plates that survived the severe storm of February 1980.

Seasonality of recruitment

The series of “recruitment panels” revealed no general seasonal trends in recruitment. Some taxa recruited most frequently at different times of the year; others recruited abundantly year round (Fig. 7). Fewer of the algal taxa recruited to panels during January–May 1980 than at other times, perhaps because of the unusual storm damage during this period.

Discussion

Factors that influence species composition

Four factors that affect species composition, and therefore can influence the interactions that occur during succession, have been identified for this community. They are: (1) the influence of residents on recruiting species and (2) grazing by large benthic invertebrates as well as (3) temporal and (4) small-scale spatial variation in the abundances of species. These same four factors were also cited by Turner (1983b) as important agents that increase the complexity of succession in a rocky intertidal surfgrass community.

1) *Effects of prior residents.* Established residents can alter the suitability and amount of space available for further colonization (e.g. Russ 1980, Dean and Hurd 1980, Dean 1981, Grosberg 1981 and Osman 1982 in marine systems; Keever 1950, Bazzaz 1975, Gant and Clebsch 1975 and

Pinder 1975 in terrestrial communities). The other three factors examined – grazing, time colonization begins and patchiness of recruitment – each have direct effects on species composition. However, they have an additional, perhaps equally important effect. By having directly influenced species composition in the past, they influence the biotic environment into which currently recruiting species can settle, and thus determine which resident:potential recruit interactions can occur.

Whether space suitable for colonization is available may depend on the type of structure created by species already present. Resident species can provide secondary space, or modify surrounding substrate, to create conditions that are (1) more favorable for settlement of later colonizers (enhance recruitment), (2) worse or unsuitable for later colonizers (inhibit recruitment) or (3) conditions equivalent to that of bare space (no effect).

Exactly what constitutes space available for colonization depends on the specific requirements of the colonizing species. Any particular kind of space, even substrate free of any visible growth, is not equally preferred by all colonists. Of the taxa that covered $\geq 5\%$ of the substrate on at least one plate, several recruited much less frequently onto panels left in the field for only 6–8 weeks than onto panels with established communities and less bare space. These included the sand-tube building polychaetes *Chaetopterus variopedatus*, *Chone* spp. and spionids, as well as arborescent bryozoans (excluding *Filicristia*), and the hydroid *Lovenella* sp. In a similar study, Osman (1982) found that fully 40% of the species that grew on experimental panels with established communities never occurred on recruitment panels that were exposed for less than two months. Haderlie (1974) also found that many species do not recruit onto panels until much of the substrate is occupied by other organisms.

Specific associations may be required for recruitment of some species. For example, in this study, all 62 recruits of *Petalonochus montereyensis* (a vermetid gastropod) occurred on *Rhynchozoon rostratum*, which itself never occupied more than 3.2 (± 0.6)% of the substrate in any treatment. (However, in the field, I have also found *Petalonochus* recruits on a few other cheilostome bryozoan species.)

Other favorable interactions may be more general. Erect species increase vertical structure. This in turn may increase microhabitat diversity, and thus species number (Bazzaz 1975, Russ 1980, Dean 1981, Osman 1982). Erect species, especially hydroids and filamentous diatoms, also trap considerable amounts of sediment (personal observation; Osman 1982). On caged plates, I observed both spionid polychaetes and tubicolous amphipods pulling sediment off hydroid uprights and incorporating the particles into their tubes. Thus the presence of hydroids and diatoms may enhance the recruitment of animals that build sand tubes.

However, these same effects of erect species – sediment entrapment and increasing three dimensional structure – may have adverse effects on other potential recruits. For example, only a fine layer of sediment is required to inhibit development of *Macrocystis pyrifera* gametophytes (De Vinny and Volse 1978). Erect portions of *Obelia dichotoma* have been shown to inhibit recruitment of barnacles, possibly by reducing water flow or physically interfering with larval settlement (Standing 1976). In addition, erect plants and animals may shade out subsequent plant colonists, while filter-feeding invertebrates, which covered as much

as 60% of the substrate on caged plates, may ingest larvae and algal spores.

Species also modify their environment simply by occupying space. However, whether these residents monopolize this space exclusively or provide secondary substrate that can be colonized by others varies among species. Few organisms recruited onto established forms such as encrusting bryozoans whose surface is mostly covered by a feeding apparatus (see also Kay and Keough 1981). More recruitment was found onto species with more benign surfaces such as solitary tunicates, and onto species that build tubes, shells etc. But even among these species, the influence of residents on recruits varied.

A given resident species may influence the abundance of the various later colonizers in different ways and to different degrees, and, conversely, later colonists can respond differently to different residents. For example, in this study the abundance of some later colonizing filamentous diatoms was enhanced by established tubicolous amphipods and polychaetes, whose sand-tubes provided substrate for the diatoms' attachment. However, at the same time, diatoms occurred less frequently than expected on bryozoans or calcium carbonate tubes. In contrast, coralline algae frequently recruited and grew on calcium carbonate tubes but never on tubes constructed of sand. Elsewhere it has been shown that crustose corallines inhibit recruitment of many sessile invertebrates, but don't affect the common barnacle species in this system and actually enhance a common bryozoan (Breitburg 1984). The allelochemicals of some diatoms inhibit growth of other diatom species (Chan et al. 1980), although a diatom film may enhance recruitment of some sessile invertebrates (Scheer 1945, but see Connell 1972). Similarly, Turner (1983a) found that survival of surfgrass seedlings varied depending on the species of algae to which they were attached.

2) *Grazing*. As in many other marine communities (e.g. subtidal kelp beds: Breen and Mann 1976, Duggins 1980, Choat and Schiel 1982; rocky intertidal: Dayton 1971, Paine 1974, Menge 1978, Robles and Cubit 1981; soft bottoms: Virnstein 1977, Woodin 1978, 1981; coral reefs: Sammarco et al. 1974, Porter 1974), species composition varied dramatically with exposure to macroinvertebrate grazers. Only four taxa – filamentous diatoms, *Giffordia granulorum*, encrusting coralline algae and diatom/blue-green algal film – ever exceeded 5% cover on grazed plates.

At least some species in all of these taxa are rapid colonizers and reproducers. *Giffordia* and representatives of the three other taxa colonized plates immersed for only 10 days. Reproductive *Giffordia* and coralline algae were seen on 6 week old plates in October 1979; diatoms presumably can propagate by binary fission from time of settlement. However, the four common taxa differ in persistence of their individuals as well as their ability to withstand grazing. Filamentous diatoms and *Giffordia* are ephemerals and are not known to have any chemical or mechanical anti-herbivore defences. They are readily eaten by grazers such as urchins (Irvine 1973). In contrast, encrusting coralline algae live longer and resist grazing, presumably because they have calcified thalli. They are among the algae least preferred by sea urchins (Irvine 1973).

Taxonomic richness in the grazed community was low for at least two reasons: (1) grazers remove sessile species and (2) residents inhibit recruitment. When cages were re-

moved from plates after 21 weeks, the only taxa that did not decrease in abundance were those that also persisted on plates that had always been grazed. Urchin toothmarks and fragments of bryozoan colonies and polychaete tubes were common on these unprotected plates, suggesting that the sessile organisms were removed by grazers. Thus, by increasing mortality, grazing decreases the mean lifespan of individuals and increases the importance of repeated recruitment to prevent local extinctions.

At the same time, however, grazing provides a favorable environment for the proliferation of other species who then decrease recruitment of many of the susceptible ones. The two most abundant taxa which persist on grazed panels, encrusting coralline algae and benthic diatoms, inhibit recruitment of other species (Scheer 1945, Breitburg 1984, Padilla 1981, Masaki et al. 1982, Kitting and Morse, in prep.).

Thus the linking of grazing with species that inhibit recruitment may create a depauperate community. In combination with macroinvertebrate grazing, coralline algal cover may totally preclude recruitment of many bryozoans and several polychaetes (Breitburg 1984). Among grazer-susceptible species, the only ones that became abundant were rapidly growing ephemerals. And of these, filamentous diatoms, at least, appear to be adversely affected by the presence of the grazer-resistant coralline crust.

3) *Temporal variability.* Because recruitment and growth rates of many species (1) vary seasonally and (2) may depend on the composition of the established assemblage, the time of year at which succession begins can influence species composition of a community (see e.g. Foster 1975a, Osman 1977, Sutherland and Karlson 1977). In this study, filamentous diatoms, bryozoans and polychaetes tended to be more abundant on plates started in the spring, while most other algae and hydroids became most abundant on comparably aged caged plates begun in August. Seasonal variation in abundance and feeding rates of macro- and micrograzers may also contribute to the observed temporal differences.

4) *Small-scale spatial variation.* Within treatment variance in the abundance of many species was high, indicating small-scale differences in settlement, growth and/or survival of colonists. Patchiness of recruitment has frequently been noted in marine communities (Coe and Allen 1937, Denley and Underwood 1979, Keough 1983, Turner, in press, Swarbrick in prep.). In this study, considerable among plate variation in the abundance of taxa was evident even on very young plates. For example, substrate cover of *Giffordia* ranged from 3 to 27% on six week old caged plates of the August series. By twelve weeks, substrate cover of filamentous diatoms ranged from 2–14% while that of *Obelia* varied from 2–23%. Similar degrees of variation in the abundances of species were found in all treatments and in both series.

Considerable among plate variation in species composition was also evident on older plates. For most taxa, variance:mean ratios remained greater than one throughout the study. Variation in the influence of early colonists due to among plate variation in their abundances, as well as variation in recruitment and mortality of later colonists, independent of interactions with prior residents, may both be important contributors to the maintenance of small-scale spatial variation in species composition.

Mechanisms of succession

Synthesizing previous data and ideas on community development (see especially Clements 1916, Egler 1954, Drury and Nisbet 1973), Connell and Slatyer (1977) proposed three models to describe the process of succession: facilitation, tolerance and inhibition. The effect of early successional species on the establishment of later ones is positive and essential in facilitation, neutral in tolerance and negative in inhibition. Conversely, the effect of later successional species on individuals of early successional species that have already colonized is negative in both the facilitation and tolerance models, and neutral in the inhibition model. Dean and Hurd (1980) have pointed out that these processes form a continuum, not a trichotomy. Early successional species can enhance the growth and/or recruitment of later species without being necessary for their establishment. In addition, Day and Osman (1981) noted that it may be common for early successional species to initially depress the abundance of (partially inhibit) later colonizing species but still eventually be outcompeted by them (see also Keever 1950, Breitburg 1984).

The specific mechanisms embodied in the Connell/Slatyer models all appear to have influenced the community studied here. Residents enhanced, had no effect on, and/or inhibited recruitment of later colonizers. However, the kinds of interactions that occurred varied among pairs of resident and colonizing species. The magnitude and kinds of processes involved were generally unrelated to the successional stage in which the species involved were most abundant. In fact, the only recurrent pattern was of eventual inhibition of several short-lived early-colonizing species (e.g. *Giffordia*, certain filamentous diatoms and *Tubulipora*); they tended to be poor invaders of an established community.

In general, as taxonomic richness and structural complexity of a community increase, the probability that outcomes of all pairwise interactions between resident and colonizing species will be of equal direction and magnitude should decrease. Explanations of succession in complex communities that are based on general interactions between earlier and later stages, rather than on particular interactions between earlier and later species, may prove inadequate because they do not provide sufficient detail. They may be useful only insofar as they can predict the effects of early colonizers on rates of succession by averaging out the results of the various pairwise interactions. To predict changes in species composition, however, interactions between the various pairs of early and later colonizers must be taken into account. This is because of the potential importance of early residents affecting the relative abundance of later colonizing species.

An early colonizing species potentially affects all later colonizing species. An abundant early successional species could, therefore, strongly influence community diversity by determining which later species, if any, become dominant (considerably more abundant than other species). This could happen even if only the magnitude – not the direction – of the effect varied among later colonists. For example, a species could become dominant even though it was inhibited by an earlier resident if other late colonizing species are more strongly inhibited by the earlier resident. Alternatively, species evenness could be at least temporarily increased during later stages if the ability of later species

to recruit in the presence of an early colonizer is inversely related to the later species' abilities to compete among themselves. By affecting different later species to different degrees, an early successional species may alter both the rate and also the pattern of succession.

Similarly, each of the various early successional species may affect a given later colonist in different ways. Thus history and timing may be important. Early dominance by species A may favor (later dominance by species B either by facilitating it, by having no effect on it if species B is a superior competitor, or by inhibiting other species more strongly. However, if at another time or place initial conditions favor early dominance by another species (X), B may fare poorly and C might become the later successional dominant by any of the alternative processes. A diverse early successional community could thus create a patchwork of varying influences that promotes small scale variation in abundance of later species. Viewed on a larger scale, this small scale patchiness could lead to high diversity in later successional stages.

Because of the variety of potential effects of different residents on different later colonists, stochastic or deterministic events that influence species composition during early stages of community development may indirectly influence the species composition of later stages in increasingly complex ways (Gleason 1927, Osman 1977, Breitburg 1984). The unpredictability of the course of succession can increase enormously at each stage, as chance and historical events alter the probability of any particular interaction occurring.

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