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SUBSTRATE CHARACTERISTICS, FISH GRAZING, AND EPIBENTHIC REEF ASSEMBLAGES OFF HAWAII

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ABSTRACT

Potentially important determinants of whether artificial reefs or settling plates will support relatively "natural" epibenthic communities are the surface texture (smooth or rough), chemical composition, and small-scale relief (flat or irregular) of the chosen substrate. Holding texture constant, this study investigated the effects of the latter two characteristics upon subtidal epibenthic reef assemblages which developed under several fish-grazing treatments in situ off Oahu, Hawaii. Some 1,200 settling surfaces were sampled without replacement during the yearlong course of the experiment.

With relief held constant, we tested the hypothesis regarding chemical composition that a nontoxic artificial substrate (polyvinyl-chloride plastic) would support the same assemblages as the natural substrate in our reef-crest system (dead coral rock). Comparisons of invertebrate abundance, detritus and sediment load, algal biomass, coverage, diversity, and species composition usually supported this hypothesis. However, several significant differences were evident, especially at high grazing intensities. These were apparently due to the relative softness and porosity of the coral.

With chemical composition held constant, we tested two independent hypotheses regarding small-scale relief by comparing assemblages that developed on flatly-cut coral-rock plates versus unaltered, irregularly-contoured pieces of coral rock. The first prediction, that irregular natural coral would support greater benthic diversity than flat coral only at low grazing intensities, was based on the hypothesis that natural coral provides only spatial heterogeneity allowing enhanced microhabitat partitioning among potentially competing benthic species. This hypothesis was rejected. The second prediction, that natural coral would support greater diversity only at high grazing intensities, was based on the hypothesis that natural coral provides only refuges from predation. This hypothesis was supported.

Previous research has shown that rough surface texture is important for enhancing benthic settlement on artificial substrates. Our findings additionally suggest that, for artificial reefs designed to provide a food source for fishes, an irregular substrate may provide refuges for settling benthic organisms. Such refuges may prevent colonizing fishes from overgrazing early successional benthic assemblages, thus allowing the establishment and persistence of a diverse and sustainable food source.

Characteristics of marine hard substrates that can potentially influence the structure of attached epibenthic communities are surface texture, chemical composition, and small-scale relief (review by Foster and Sousa, in press). Surface texture has been known for some time to strongly influence settlement patterns of sessile organisms, with rough surfaces usually enhancing settlement relative to smooth surfaces (Pomerat and Weiss, 1946; Ogata, 1953; Tippett, 1970; Harlin and Lindbergh, 1977; Borowitzka et al., 1978).

Chemical composition and small-scale relief have been less well studied. Controlling texture and relief, previous investigators have suggested or assumed that the chemical composition of a substrate has little effect on which species will colonize and survive, provided of course that the substrate is not toxic (Foster, 1975a; Osman, 1977; Sousa, 1979). These studies indicated that the species compositions of sessile assemblages on artificial surfaces were similar to those on nearby natural surfaces in the same habitat. However, such comparisons have often been reported superficially or anecdotally, with the main thrust of each study usually focusing on biological interactions. The final substrate characteristic, small-scale relief (i.e., flat vs. irregular surface contours), has received the least attention. To our knowledge, only Foster (1975b) has investigated the effects of small-scale relief while simultaneously controlling both surface texture and chemical composition. Others have manipulated substrate relief by attaching objects to otherwise flat surfaces (Brock, 1979; Russ, 1980). The results of these studies have been mixed (see Discussion).

These characteristics of settling surfaces have important ramifications for both basic and applied marine studies. For basic ecological research, artificial substrates allow the investigator to control the size and location of a surface, the impact of biological and physical factors, and the timing and extent of replication (reviews by Osman, 1982; Schoener, 1982). Despite these advantages, the resulting patterns observed on these surfaces are relevant to natural systems only to the extent that they reflect the processes occurring on natural substrates. In this regard, simultaneous comparisons of the benthic assemblages on natural and artificial substrates are essential (Kennelly, 1983).

For applied marine sciences, artificial reefs provide a potential opportunity to create habitats not only for enhancing commercial and sport fisheries, but also for mitigating the effects of deleterious coastal alterations. Unfortunately, the materials used to construct artificial reefs often seem to be chosen on the basis of economic rather than biological considerations. Given the obvious importance of sessile reef organisms as a source of food and shelter for fishes and other fauna, comparisons of natural and artificial substrates are again essential for determining to what extent an artificial reef will support a relatively natural benthic community.

The goal of this paper is to report experimental tests of several general hypotheses on the importance of substrate characteristics in determining the structure of epibenthic reef assemblages. Because of the well-documented importance of rough surface texture, our study held this factor constant and separately investigated the effects of chemical composition and small-scale relief. Our experimental design further controlled substrate size and location, impact of environmental factors, and time in the field. The hypothesis regarding chemical composition was that, if texture and relief were both controlled, a nontoxic artificial substrate (polyvinyl-chloride plastic) would support the same epibenthic assemblages as the natural substrate at our study site (dead coral rock).

The hypotheses regarding small-scale relief concerned the mechanism(s) by which this characteristic might influence benthic community structure. Two mechanisms seemed possible (Brock, 1979): (1) irregular surface relief may simply provide spatial heterogeneity, thus enhancing local diversity through small-scale microhabitat partitioning among potentially competing benthic species (Schoener, 1974); and/or (2) irregular relief may provide small-scale prey refuges, thus enhancing local diversity by decreasing effective predation intensity (Menge and Sutherland, 1976). By manipulating both small-scale surface relief and grazing intensity by fishes, while controlling substrate texture and chemical composition, we were able to determine which (if either) of these mechanisms were operating in our system.

In the system we studied, the prevalent sessile species (algae) exhibit apparent linear competitive hierarchies for the use of space that are the reverse of hierarchies based on resistance to grazing. That is, while erect algae are dominant competitors, prostrate and crustose algae are often more resistant to grazing (review by Lubchenco and Gaines, 1981). Under these circumstances, the above hypotheses provide independent predictions (Hixon, in press and in prep.). If only the spatial-partitioning hypothesis was true, then irregularly-contoured natural coral surfaces would support a considerably greater diversity of benthic species than flatly-cut coral surfaces only where grazing intensity was low (i.e., where competitive interactions were common). At low grazing intensities, species would partition the crevices and exposed surfaces of the irregular natural substrate, while relatively few species would be able to coexist on the homogeneous flat substrate. At high grazing intensities, only the grazer-resistant species would persist regardless of surface relief. If only the prey-refuge hypothesis was true, then irregular natural surfaces would support greater benthic diversity only at higher grazing intensities, with no differences expected where predation intensity was low. At low intensities, the competitively dominant nonresistant species would cover all surfaces regardless of small-scale relief. At high intensities, grazer-resistant species would occupy exposed surfaces, with the others refuging in the crevices of the irregular natural substrate. Only the grazer-resistant species could persist on the flat substrate at high grazing intensities. If both mechanisms were operating (presumably additively), then natural surfaces would support greater benthic diversity at both high and low grazing intensities. Of course, if neither hypothesis was true, no differences would be expected throughout.

METHODS

Study System.—Our study site was located along a 600-m section of the subtidal windward reef crest at the Coconut Island Marine Refuge, located in Kaneohe Bay, Oahu, Hawaii (21°26′N lat., 157°47′W long.). Water depths at this site averaged about 1 m. The natural substrate consisted of a flat bench of dead *Porites compressa* coral rock, which was mostly covered by crustose coralline algae.

The dominant grazers in this system were parrotfishes (Scaridae) and surgeonfishes (Acanthuridae), which were by far the most abundant fishes on the reef (Brock et al., 1979). Sea urchins and other large invertebrate grazers were rare. Scattered throughout the site were the territories of individual yelloweye damselfish (*Stegastes fasciolatus*). Like other damselfishes (Brawley and Adey, 1977; Lassuy, 1980; Lobel, 1980; Montgomery, 1980), the yelloweyes defended small patches of substrate (about 1 m^2) from other fishes, thereby allowing the growth of distinct mats of filamentous algae. Thus, the exposed substrate in this system was occupied by two basic kinds of benthic assemblages: (1) those outside damselfish territories, exposed to intense grazing by parrotfishes and surgeonfishes, and dominated by crustose coralline algae; and (2) those inside territories, exposed to moderate grazing by the resident damselfish and dominated by filamentous algae, a pattern originally documented by Vine (1974). Hixon and Brostoff (1982; 1983) provide quantitative measurements of relative fish grazing intensity in these two subhabitats (see below).

Experimental Design.—Testing the chemical-composition hypothesis required comparisons of nontoxic substrates with identical surface texture and small-scale relief, but different composition. We chose to compare natural coral rock with gray polyvinyl-chloride (PVC) plastic because the latter was artificial, nearly inert chemically, and also used in previous studies off Hawaii (Long, 1974; Rastetter and Cooke, 1979). We controlled small-scale relief by cutting pieces of sun-dried coral rock into flat plates, and controlled surface texture by roughly sanding flat PVC plates until their texture resembled the flatly-cut coral. Both substrates were cut into 50-cm^2 squares, an area which preliminary field tests had shown to approximate adequately the asymptote of species-area plots (Pielou, 1974: 309).

Testing the spatial-partitioning and prey-refuge hypotheses required comparisons of substrates with identical texture and composition, but different small-scale relief. We accomplished this by comparing our flat coral plates with unaltered pieces of sun-dried coral rock, which were approximately the same size, but irregularly contoured.

Our experimental tests further required not only simultaneous controls of the location and orientation of the plates in the field, but also different plates being exposed to different fish-grazing intensities. We accomplished this by mounting 1,152 of our plates (384 of each substrate type) horizontally on 96 concrete blocks. This arrangement allowed groups of four flat-plastic plates, four flat-coral plates, and four natural-coral plates to be exposed to virtually identical conditions in situ. Thus, each block supported 12 plates and constituted a single reef module (Fig. 1). In September 1980, all modules were distributed in the field simultaneously and evenly among three fish-grazing treatments: (1) high (exposed to grazing by parrotfishes and others outside damselfish territories); (2) moderate (exposed inside territories mostly to damselfish grazing); and (3) low intensity (protected from fish grazing within cages). Hixon and Brostoff (1982; 1983) measured relative grazing intensity in these treatments as the "standing crop" of fish bite marks. The mean values were: 269.6 (high, outside territories), 14.9 (moderate, inside territories), and 0.0 bites/50 cm^2 (low intensity, caged).

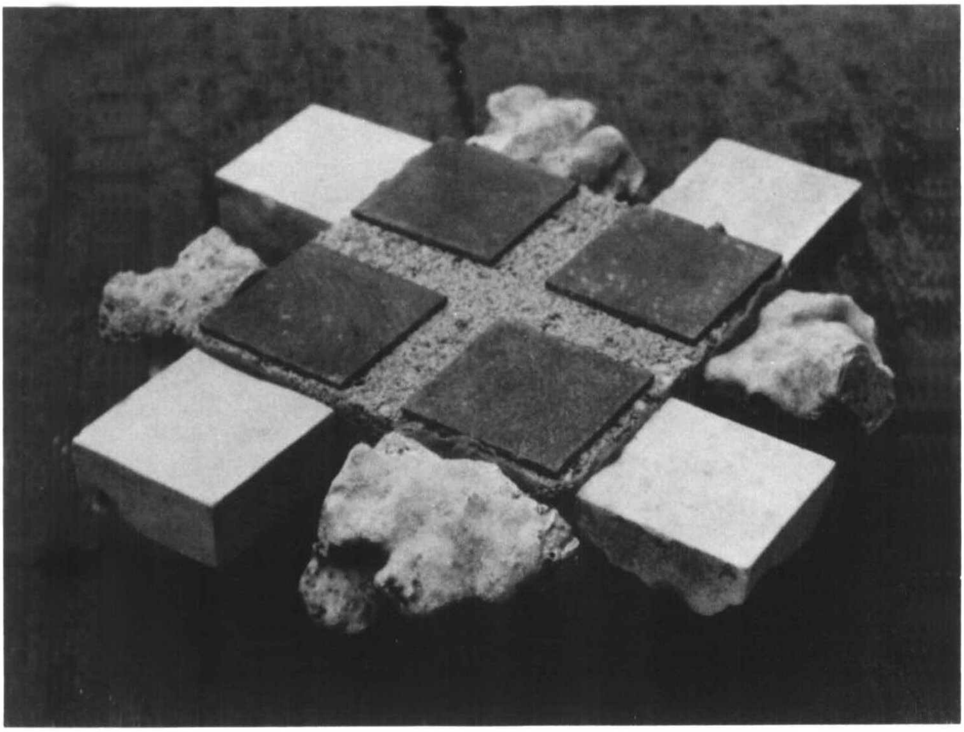


Figure 1. One of the "reef modules" used in the experiment, showing the spatial arrangement of settling plates on a concrete block. Four roughly-sanded PVC-plastic plates were mounted on top of the block; four flatly-cut coral plates and four irregular natural coral pieces were mounted around the upper edge of the block. The flat-plastic and flat-coral plates measured 50 cm^2 each; the natural coral pieces were approximately the same size, but had irregular surface contours.

The cages were constructed of 1.3 × 1.3 cm galvanized wire mesh and were 60 × 60 × 30 cm in volume, so no plate was mounted closer than 15 cm from the wall of a cage. Exterior cage surfaces were prevented from fouling by the intense grazing activity of fishes, while interior surfaces were periodically cleaned by divers. A separate cage-control experiment, which included wall-only (no roof) and roof-only (no wall) cages, tested the importance of these and other potential secondary effects. Because the present paper considers only comparisons within treatments (i.e., within-cage comparisons as opposed to caged vs. uncaged comparisons), the results of the cage-control experiment will not be detailed here. Basically, the cage controls demonstrated that the secondary effects of caging were negligible compared to the primary effect of inhibiting fish grazing (Hixon and Brostoff, in prep.).

Laboratory Analyses.—Seventeen times during the yearlong experiment, a sample of 63 plates (3 substrate types from 1 reef module × 3 grazing treatments × 7 replicates) was removed from the field without replacement to compare the attached epibenthic assemblages. After being photographed, each plate was rinsed free of loose detritus and sediment (which were analyzed separately), and all macroscopic animals (a consistently minor component) were removed and counted. The relative abundance of prostrate noncoralline and crustose coralline algae was estimated visually as percent cover. Because the remaining algae were morphologically similar and grew in mixed-species stands, they were scraped from the plate into a glass petri dish, wet weighed, examined microscopically to estimate relative species abundances (see below), dry weighed, and finally ash weighed. The naturally-contoured coral plates were examined microscopically only, since accurate area measurements were impossible. Drying was at 60°C for at least 72 h, until constant weight was attained, and ashing was at 500°C for 16 h.

During microscopic examinations, the algae from each plate were first spread uniformly within the petri dish and scanned to determine the total number of species present. To estimate the relative abundance of each species, 100 random points within the dish were then examined under 100-power magnification, and the alga occupying the central point of each ocular field was recorded (Jones, 1968). The total number of species per plate observed by this method was almost invariably identical to that

Table 1. Detritus-sediment weights on each substrate type at each grazing intensity. Each value gives the mean (g/50 cm^2) and 95% confidence interval for seven settling plates removed from the field after 1 year. All differences between adjacent means are not significant ($P > 0.05$, t-tests, or approximate t-tests where variances are not homogeneous)

Parameter	Grazing intensity	Substrate	
		Flat coral	Flat plastic
Dry weight	High	0.768 ± 0.026	0.731 ± 0.035
	Moderate	0.835 ± 0.069	0.887 ± 0.291
	Low	2.482 ± 0.397	2.384 ± 0.263
Ash-free dry weight	High	0.753 ± 0.024	0.719 ± 0.032
	Moderate	0.753 ± 0.026	0.819 ± 0.288
	Low	1.650 ± 0.040	1.629 ± 0.039
Sediment-ash weight	High	0.014 ± 0.005	0.012 ± 0.005
	Moderate	0.082 ± 0.067	0.069 ± 0.069
	Low	0.833 ± 0.361	0.755 ± 0.227

determined by complete scanning, indicating that we had adequately sampled the local species "universe" (Peet, 1974).

Mathematical Indices.—To minimize the bias associated with any one species diversity index (review by Peet, 1974), we analyzed our relative abundance data using seven different diversity measures (Hixon and Brostoff, 1982). Because all indices suggested the same patterns, we present here only species number or richness (S), Pielou's evenness index (J), and the well-known Shannon-Wiener index (H'), which combines richness and evenness (Pielou, 1974). We measured the similarity of paired samples of plates in terms of species composition using the "coefficient of community" and species relative abundances using the "percent similarity" index (Pielou, 1974). Expressed as percentages, both indices attain a value of 100% when species lists and relative abundances, respectively, are identical, and a value of 0% when samples have no species in common. All confidence intervals presented in this paper are based on the t-distribution. Comparisons of differences between means were accomplished by t-tests, except where variances were not homogeneous. In such cases, approximate t-tests (Sokal and Rohlf, 1981) or nonparametric tests were used.

RESULTS

General Patterns.—Throughout the experiment, algae were the dominant organisms on all plates. Substrates exposed outside damselfish territories to intense grazing by parrotfishes and surgeonfishes became dominated during the course of the year by several prostrate forms, predominantly the crustose coralline *Hydrolithon reinboldii.* Substrates exposed to moderate grazing within the defended territories of damselfish became dominated mostly by filamentous species, including *Centroceras clavulatum, Taenioma perpusillum, Ectocarpus indicus,* and *Polysiphonia rhizoidea.* Those protected from fish grazing within cages became dominated mostly by coarsely branched species, such as *Tolypiocladia glomerulata* and *Acanthophora spicifera.*

Invertebrates were a minor component of these benthic assemblages. Sessile forms, such as spat of the coral *Pocillopora damicornis* and small oysters, recruited only sporadically and exhibited low survival. Small mobile forms included polychaete worms, harpacticoid copepods, amphipods, and the postlarvae of various invertebrates. Larger invertebrate grazers, such as limpets, were very rare. Thus, our data analyses focus primarily on algae. Also, because the late successional stages of the epibenthic assemblages are most relevant to our hypotheses, we confine most of our present analyses to our final 1-year sample of 63 plates. Finally, note that the present hypotheses are tested by comparisons within each grazing-intensity treatment. Comparisons between grazing treatments are presented elsewhere (Hixon and Brostoff, 1981; 1982; 1983; in prep.).

Table 2. Percent cover by crustose and prostrate algae on each substrate type at each grazing intensity. Each value gives the mean (% cover) and 95% confidence interval for seven settling plates removed from the field after 1 year. Symbols give significance levels of differences between adjacent means (*t*-tests, or approximate *t*-tests where variances are not homogeneous)

		Substrate				
Algal type	Grazing intensity	Natural coral		Flat coral		Flat plastic
Crustose corallines	High	8.1 ± 5.5	ns	13.3 ± 13.4	*	38.6 ± 15.5
(*Hydrolithon reinboldii*)	Moderate	1.4 ± 1.5	ns	1.4 ± 1.0	*	3.1 ± 1.3
	Low	0.0 ± 0.0	ns	0.4 ± 0.5	ns	0.8 ± 0.6
Prostrate greens	High	5.7 ± 6.6	ns	15.3 ± 9.2	*	30.0 ± 7.5
(*Enteromorpha* holdfasts)	Moderate	2.4 ± 3.5	ns	1.4 ± 0.5	*	19.8 ± 19.7
	Low	0.0 ± 0.0	ns	0.0 ± 0.0	ns	0.4 ± 0.5

* $P < 0.05$; ns: $P > 0.05$ (not significant).

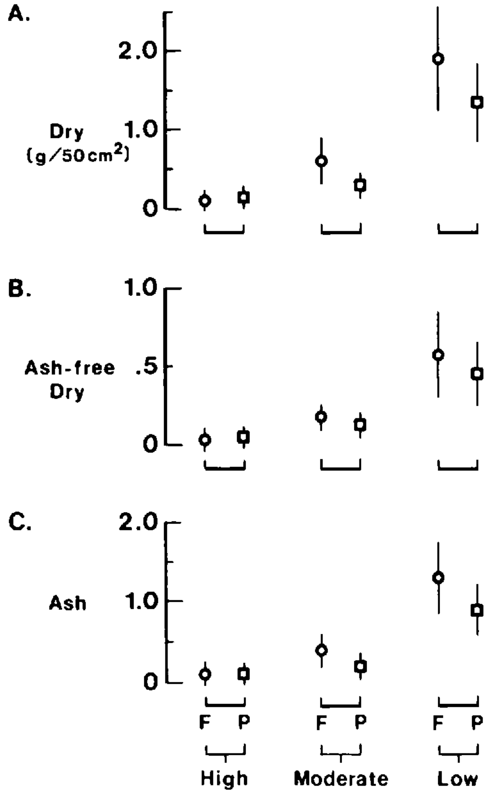
Chemical Composition Effects.—The hypothesis that the chemical composition of a nontoxic substrate does not affect the structure of attached epibenthic assemblages was tested by comparing the results on the flat-plastic plates to those on the flatly-cut coral plates. After one year in the field, both algal biomass (Fig. 2) and the amount of sediment and detritus (Table 1) on these two substates were not significantly different ($P > 0.05$) within each grazing treatment. Similarly, the number of associated invertebrates per plate was not significantly different, except at the lowest grazing intensities, where for unknown reasons the plastic plates supported more animals (Fig. 3).

At moderate and high grazing intensities, the flat-plastic plates exhibited significantly greater coverages of crustose coralline and prostrate noncoralline algae than the flat-coral plates (Table 2). This difference appeared to be caused by parrotfish bites penetrating the surface of the coral plates, removing more biomass per bite than on the relatively impenetrable plastic surfaces.

Within each grazing treatment, total algal species richness on each sample of seven plastic plates was very similar to that on each corresponding sample of flat-coral plates throughout the experiment (Fig. 4). Nonparametric paired comparisons of these data within each grazing treatment determined that there were no significant differences overall between these substrates in the total number of algal species per seven-plate sample ($P \gg 0.1$, Wilcoxon Signed-Ranks Tests). Closer inspection of the final 1-year samples determined that the overall percent similarity between the plastic and flat-coral plates in terms of algal species composition (measured by the coefficient of community) was relatively high (greater than 75%) at all grazing levels (Table 3A). The overall percent similarity in terms of species abundances (measured by the percent similarity index) was also quite high (greater than 57%) at all grazing levels (Table 3A).

After 1 year, within-plate (alpha or local) algal species diversity within each grazing treatment was usually not significantly different between the plastic and flat-coral substrates (Fig. 5). However, at high grazing intensities, the evenness component was very low on the plastic plates (Fig. 5C), resulting in significantly lower Shannon-Wiener diversity (Fig. 5B) despite no significant difference in the richness component (Fig. 5A). Among-plate (beta or global) diversity patterns were similar (Table 4). The difference between the substrates in the evenness of species relative abundances at high grazing intensities, despite identical species composition (Table 3A), appeared to be due to differences in surface porosity. In particular, blue-green algae were more abundant on the coral plates, where they actually penetrated the porous surface.

In summary, for most measured parameters, the epibenthic assemblages on the



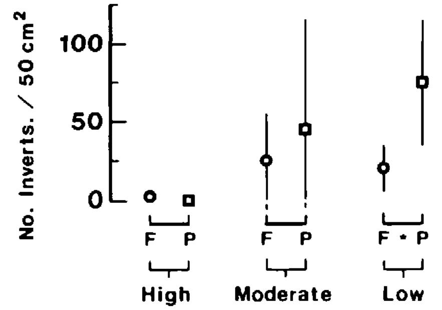


Figure 2. (Left) Noncoralline algal biomass in terms of, A, dry weight, B, ash-free dry weight, and C, ash weight for each substrate type (F, flat coral; and P, flat plastic) at each fish-grazing intensity (high, moderate, and low). Each symbol gives the mean (g/50 cm^2) and 95% confidence interval for seven settling plates removed from the field after 1 year. All differences between adjacent means in each grazing treatment are not significant ($P > 0.05$, t-tests, or approximate t-tests where variances are not homogeneous).

Figure 3. (Right) Densities of all sessile and motile invertebrates found on each substrate type (F, flat coral; and P, flat plastic) at each fish-grazing intensity (high, moderate, and low). Each symbol gives the mean (No./50 cm^2) and 95% confidence interval for seven settling plates removed from the field after 1 year. All differences between adjacent means in each grazing treatment are not significant ($P > 0.05$), except that indicated by the asterisk ($P < 0.05$, t-tests, or approximate t-tests where variances are not homogeneous).

chemically artificial (flat-plastic) substrates were statistically indistinguishable from those on the chemically natural (flat-coral) surfaces. However, at higher grazing intensities, the coral substrates exhibited lower coverages of crustose and prostrate algae and greater evenness of algal relative abundances. These differences appeared to be due to the relative softness and porosity of the coral.

Small-scale Relief Effects.—The hypotheses regarding the effects of small-scale surface relief upon epibenthic communities concerned the species diversity of those assemblages under different levels of fish-grazing intensity. These hypotheses were tested by comparing the results on flatly-cut coral plates to those on irregularly-contoured natural coral substrates. Figure 4B and C shows that, at both moderate and low grazing intensities, respectively, algal species richness on the flat plates was very similar to that on natural substrates throughout the experiment. Overall, there were no significant differences ($P > 0.1$, Wilcoxon Signed-Ranks

Table 3. Similarity of noncoralline algal species composition (by coefficient of community, CC) and relative abundances (by percent similarity, PS) between substrate types at each grazing intensity. Each index value compares two data sets, each set pooled from seven settling plates removed from the field after 1 year

	Similarity index	
Grazing intensity	CC (%)	PS (%)
A. Flat plastic vs. flat coral		
High	100.0	66.9
Moderate	75.9	57.2
Low	85.7	60.9
B. Flat coral vs. natural coral		
High	37.5	48.9
Moderate	83.9	61.2
Low	72.0	58.2

Tests). However, after three weeks at high grazing intensities, natural substrates consistently exhibited greater species richness ($P < 0.001$), with the flat plates supporting the same number of species in only three samples between the sixth and tenth week of the experiment (Fig. 4A).

This same pattern was evident in the more detailed analyses of the final 1-year sample. Within-plate algal species diversity on flat coral was not significantly different from that on irregular natural coral at both low and moderate grazing intensities (Fig. 5). However, both species richness and Shannon-Wiener diversity were significantly greater on the higher-relief natural coral plates at high grazing intensities (Fig. 5A, B), despite no significant differences in evenness (Fig. 5C). Among-plate diversity comparisons suggested the same pattern (Table 4). The percent cover of crustose and prostrate algae was not significantly different on the different coral substrates (Table 2).

Reflecting the same general pattern, the overall percent similarities between the flat and irregular natural coral plates in terms of algal species composition were relatively high at low and moderate grazing intensities (coefficients of community exceeding 70%), but very low (37.5%) at high grazing intensities (Table 3B). The overall percent similarities in terms of species relative abundances exhibited the same pattern: relatively high (about 60%) under low and moderate grazing and relatively low (about 50%) under high grazing (Table 3B).

In summary, virtually all measures suggested that both within- and between-plate algal species diversity was greater on irregularly-contoured natural coral surfaces than on flatly-cut coral surfaces at high grazing intensities, with no differences at low and moderate grazing intensities. This pattern was reflected in species composition and relative abundance measures on the two substrates being least similar at high grazing intensities.

DISCUSSION

Chemical Composition Hypothesis.—The hypothesis that, controlling for surface texture, small-scale relief, and other factors, a nontoxic artificial substrate will support the same epibenthic assemblages as a natural surface was partially supported for our system. Roughly sanded PVC-plastic plates usually supported the same invertebrate abundance, detritus and sediment load, algal biomass, coverage, species composition, and diversity as flatly-cut plates of coral rock at each of three different intensities of fish grazing. However, the coral supported fewer invertebrates at low grazing intensities (Fig. 3), and exhibited lower coverages by prostrate

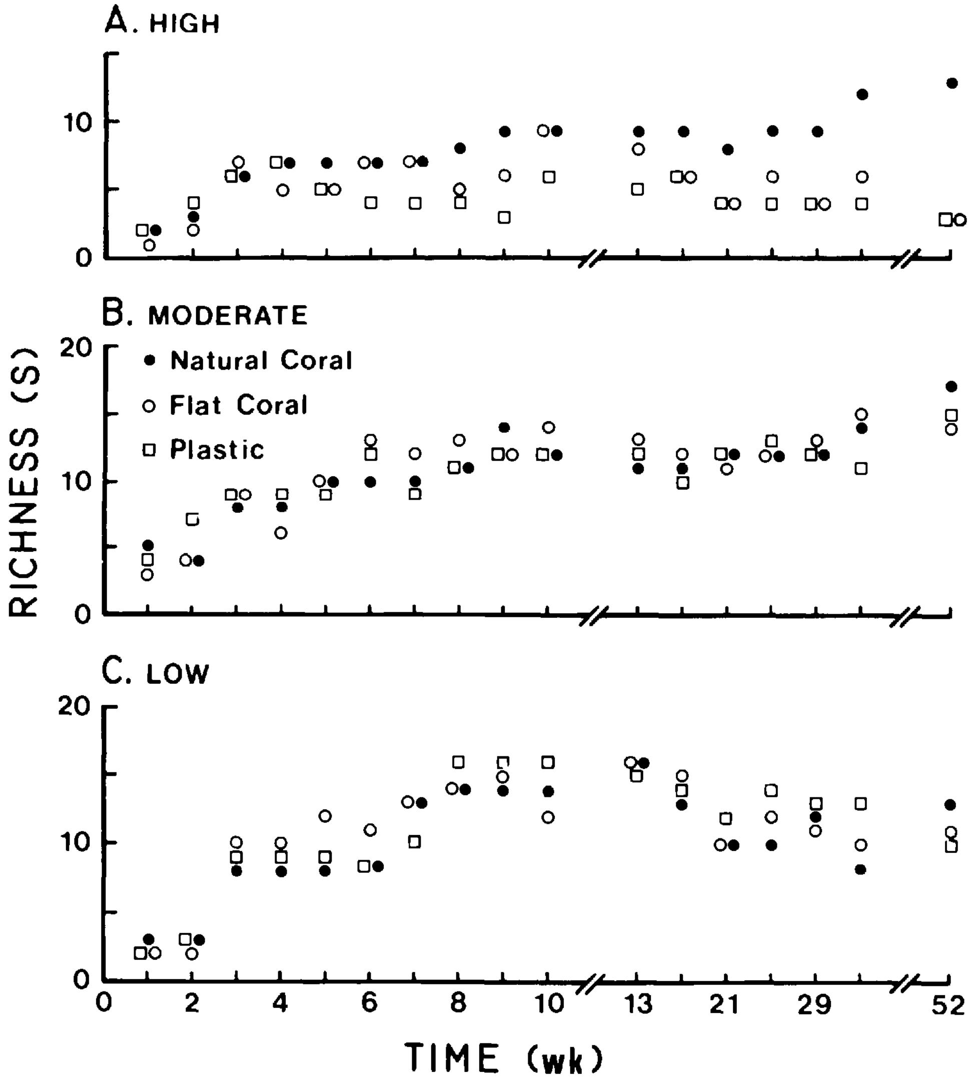


Figure 4. Total noncoralline species richness for each pooled seven-plate sample of each substrate type at each fish-grazing intensity (A, high; B, moderate; and C, low).

and crustose algae (Table 2) and greater evenness of species relative abundances (Fig. 5C) at higher grazing intensities. These differences appeared to be mainly due to the relative softness and porosity of the coral.

These results generally support previous studies that have invoked the same hypothesis, albeit for different substrates and different systems. For example, despite previous suggestions (MacGinitie and MacGinitie, 1968) that potentially lethal chemicals leach from concrete, Foster (1975a) and Sousa (1979), respectively, found that the pattern of subtidal and intertidal algal succession off California was nearly identical on concrete blocks and natural rock surfaces. Similarly, our general findings lend credence to Osman's (1977) contention that slate plates adequately mimicked natural granite rocks as settling surfaces off New England.

In general, it appears that epibenthic organisms will readily settle and grow on any nontoxic substrate exhibiting suitable surface texture. However, before in-

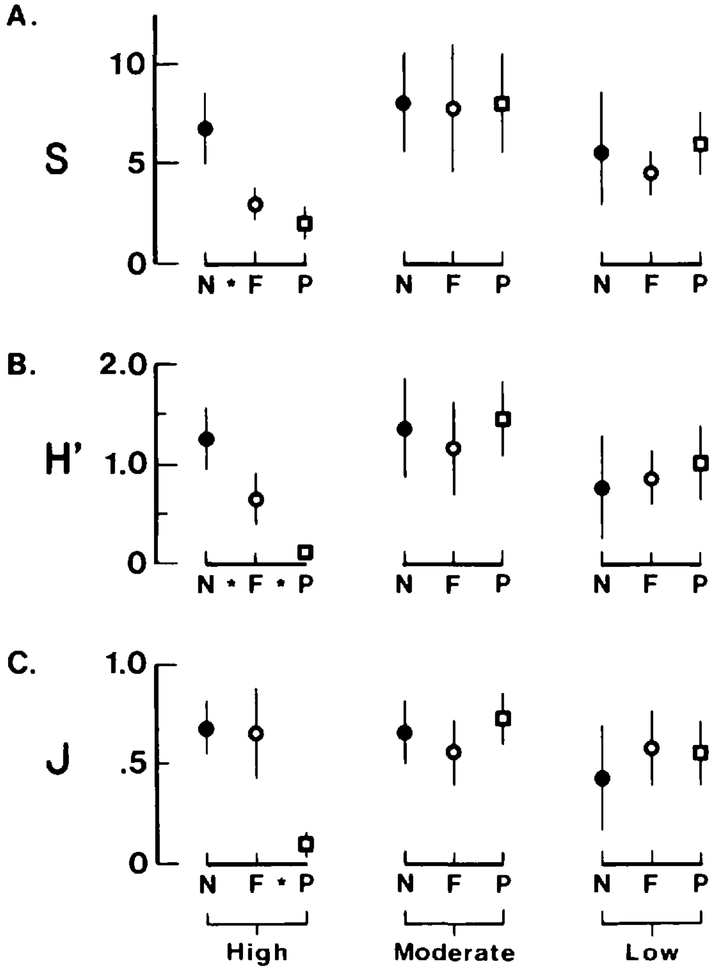


Figure 5. Within-plate (alpha or local) noncoralline algal species diversity measures (A, richness [S]; B, Shannon-Wiener diversity [H']; and C, Pielou's evenness [J]) for each substrate type (N, irregular natural coral; F, flat coral; and P, flat plastic) at each fish-grazing intensity (high, moderate, and low). Each symbol gives the mean index value and 95% confidence interval for seven settling plates removed from the field after 1 year. All differences between adjacent means in each grazing treatment are not significant ($P > 0.05$), except those indicated by asterisks ($P < 0.01$, Mann-Whitney *U*-tests).

vestigators use results such as these to further justify employing man-made substrates in studying natural systems, two notes of caution seem prudent. First, there were some significant differences between the plastic and coral plates in this study, especially at high grazing intensities. Second, in benthic systems exhibiting a considerable infaunal component, such as coral reefs (Bailey-Brock et al., 1980), interactions between infaunal and epibenthic organisms should not be dismissed a priori. Obviously, natural chemical composition will be more crucial to the infauna. Due to these and other unknown factors, we agree with Kennelly (1983) that it would be wise in general for researchers to use as natural a settling substrate as possible in any benthic study.

Spatial Partitioning Hypothesis.—This hypothesis states that, controlling surface texture, chemical composition, and other factors, an irregularly-contoured surface

Table 4. Among-plate (beta or global) noncoralline species diversity measures for each substrate type at each grazing intensity. Each index value was calculated from data pooled from seven settling plates removed from the field after 1 year

		Substrate		
Diversity index	Grazing intensity	Natural coral	Flat coral	Flat plastic
Richness (S)	High	13	3	3
	Moderate	17	14	15
	Low	14	11	10
Shannon-Wiener (H')	High	1.59	0.80	0.22
	Moderate	2.35	1.68	1.98
	Low	1.68	1.46	1.57
Evenness (J)	High	0.62	0.73	0.20
	Moderate	0.83	0.64	0.73
	Low	0.64	0.61	0.68

will support a greater diversity of benthic organisms than a flat surface only because the spatial heterogeneity of the former increases the potential for microhabitat partitioning among species (Schoener, 1974). If this hypothesis was true and certain other conditions characteristic of our particular system were met (see Introduction), then the natural coral substrates would have exhibited considerably greater algal diversity than the flat-coral plates only where grazing by fishes was inhibited by cages, that is, where competition for space among algal species was important. This was not the case; this hypothesis was rejected for our system. In fact, species diversity on these two substrates was statistically indistinguishable at all but the greatest fish grazing intensities.

Local species diversity has been shown to be correlated with habitat spatial heterogeneity in a number of terrestrial systems, especially for birds (MacArthur and MacArthur, 1961; Recher, 1969; Karr and Roth, 1971). The general explanation is that increased spatial complexity provides a greater number of microhabitats, allowing increased resource partitioning among potentially competing species, thereby enhancing local coexistence. In our system, all but several of the approximately 40 algal species encountered during the experiment were very similar morphologically. This similarity, combined with the fact that plants usually require the same general resources, may have precluded small-scale microhabitat partitioning at the scale of the crevices and exposed surfaces on our irregularly-contoured coral plates (Schoener, 1974).

Prey Refuge Hypothesis.—This hypothesis states that an irregularly-contoured surface will support a greater diversity of benthic organisms than a flat surface only because the crevices and depressions in the former provide refuges from predation (Menge and Sutherland, 1976). If this hypothesis was true, then the natural coral substrates would have exhibited greater algal diversity than the flat-coral plates only where grazing by fishes was intense, with no differences expected where grazing was low. This hypothesis was supported for our system.

The mechanisms underlying this hypothesis are straightforward. At high grazing intensities, coverage by prostrate noncoralline and crustose coralline algae was much greater than in the other grazing treatments (Table 2). Such species are known to be highly resistant to grazing (Littler et al., 1983), but otherwise poor competitors for space against erect algae (reviews by Paine, 1980; Lubchenco and Gaines, 1981). Under these circumstances, erect species were found abundantly only in the crevices and depressions of the irregular natural-coral plates, the flatly-cut plates providing no such refuges. The same pattern has been observed on natural substrates off Panama (Menge and Lubchenco, 1981). Thus, the irregular and flat substrates exhibited strikingly different algal diversity (Figs. 4 and 5; Table 4) and species composition (Table 3B) where grazing intensity was high. At lower grazing intensities, the coverage of grazer-resistant forms was very low, with all space on both kinds of substrates being dominated by erect algae. In these cases, the differences between the two substrates were negligible.

Synthesis with Previous Studies.—The only other study we know of which also varied small-scale surface relief while simultaneously controlling both surface texture and chemical composition is that of Foster (1975b). Conducted subtidally off California, his study compared the algal assemblages which developed on unaltered flat concrete blocks to those on blocks with alternating ridges and grooves. Foster observed no significant differences between the assemblages occurring on the two surfaces after 472 days in the field, but also determined through caging experiments that direct grazing of algae was not extensive in his system. Thus, his data also appear to reject the spatial-partitioning hypothesis at the scale of surface relief he studied, but do not bear directly on the prey-refuge hypothesis.

Two other studies have investigated the effects of surface complexity on the impact of grazing by reef fishes, both involving refuge-like objects attached to otherwise flat settling surfaces. Using microcosm tanks at the same site as our study, Brock (1979) compared benthic diversity on terracotta tiles covered by three different sizes of plastic mesh and exposed to nine different parrotfish densities for 36 days. His results were qualitatively identical to ours, supporting the prey-refuge hypothesis. At low parrotfish densities and grazing intensities, all refuge sizes supported similar epibenthic species richness. At high parrotfish densities and grazing intensities, those refuge (mesh) sizes affording greater protection from grazing supported greater epibenthic diversity.

In a study off Australia, Russ (1980) constructed artificial "bryozoans" from tufted pieces of nylon net and attached these to bakelite panels. Comparing these complex substrates to bare panels after seven months revealed no significant differences in epibenthic diversity regardless of whether the two substrates were both exposed to fish grazing or both caged. Thus, Russ's data also appear to reject the spatial-partitioning hypothesis. Overall, his exposed panels exhibited greater epibenthic diversity than caged panels, suggesting that fish grazing intensity in this system was perhaps not sufficiently high to result in a significant prey-refuge effect.

Ramifications for Designing Artificial Reefs.—If the rationale for constructing an artificial reef is to provide as natural a habitat as possible for fishes, care must be taken to also provide a suitable substrate for the benthic assemblages which constitute a source of food and shelter for such "target" species. The results of this and previous studies suggest criteria for determining the appropriate characteristics of artificial-reef substrates. First, rough surface texture is known to enhance the settlement of sessile species (see Introduction). Second, provided the substrate is nontoxic, chemical composition per se appears to be of minor importance if only epibenthic species are considered (Long, 1974). However, in habitats where infaunal assemblages are often abundant, such as coral reefs (Bailey-Brock et al., 1980), natural substrates should be duplicated as far as possible. Third, small-scale surface relief appears to generally enhance local benthic species diversity where fish grazing is relatively intense. It seems reasonable that such high grazing intensities might be common during the early development of an artificial reef community, when colonizing fishes may tend to overgraze the early-successional low standing crop of attached benthos. Under such conditions, small-scale refuges from fish predation may be essential for the initial establishment and persistence of some ecologically important benthic species that might otherwise be excluded. In any case, assuming that sessile reef species in any given area have adapted to the prevailing natural substrates, duplicating all characteristics of these surfaces as closely as possible may be the most prudent means of reproducing natural reef communities.

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