Disturbance in Marine Intertidal Boulder Fields: The Nonequilibrium Maintenance of Species Diversity

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DISTURBANCE IN MARINE INTERTIDAL BOULDER FIELDS: THE NONEQUILIBRIUM MAINTENANCE OF SPECIES DIVERSITY[1]

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Abstract. The effects of disturbance on local species diversity were investigated in an algal-dominated intertidal boulder field in southern California. In this habitat, the major form of disturbance occurs when waves, generated by winter storms, overturn boulders. These natural physical disturbances open space, interrupt successional sequences, and determine local levels of species diversity. Because small boulders are more frequently overturned than larger ones, the plants and sessile animals of boulder fields are distributed in a patchwork of successional stages.

Boulders which are subjected to intermediate disturbance frequencies are usually less dominated than those which are very frequently disturbed, and always less dominated than those which are seldom disturbed. In all seasons most small boulders have fewer species than those of intermediate size. Large boulders also usually have fewer species, except in the spring, when defoliation of the algal canopy during the previous winter has opened space for colonization. Species richness on these boulders declines during summer months, and is less than that on boulders of intermediate size in the fall.

Small boulders, with a shorter disturbance interval, support only sparse early successional communities of the green alga, *Ulva*, and barnacles. Large, infrequently disturbed boulders are dominated by the late successional red alga, *Gigartina canaliculata*. Intermediate-sized boulders support the most diverse communities composed of *Ulva*, barnacles, several middle successional species of red algae, and *Gigartina canaliculata*. Comparison of the pattern of succession on experimentally stabilized boulders with that on unstable ones confirms that differences in the frequency of disturbance are responsible for the above patterns of species composition.

The frequency of disturbance also determines the degree of between-boulder variation in species composition and diversity. Small boulders which are frequently overturned sample the available pool of spores and larvae more often. As a result, a greater number of different species occur as single dominants on these boulders. Boulders with an intermediate probability of being disturbed are most variable in species diversity. Assemblages on these boulders range from being dominated by a single species to being very diverse while most communities on boulders which are frequently or seldom disturbed are strongly dominated.

Observations on the local densities of three species of middle successional red algae over two year-long periods indicate that most of these are variable in time. More local populations went extinct or became newly established on boulders than remained constant in size. These species persist globally in the boulder field mosaic by colonizing recent openings created by disturbances. These results lend support to a nonequilibrium view of community structure and, along with other studies suggest that disturbances which open space are necessary for the maintenance of diversity in most communities of sessile organisms.

Key words: algae; coexistence; competition; disturbance; dominance; equilibrium; local extinction; patchiness; rocky intertidal; species diversity; stability; succession.

INTRODUCTION

There are two major opposing viewpoints with regard to the organization of natural communities. The first and older view is that local populations of a species and the communities of which they are a part, are in equilibrium. In this context, a community is in equilibrium when the absolute and relative abundances of species in a local area remain relatively constant or undergo regular cyclic oscillations over many generations. The density of individuals in local populations is "balanced" by a number of intra- and interspecific interactions, including competition (Nicholson 1933, 1957) and attacks by natural enemies, which decrease the chance of survival and/or the rate of reproduction of the average individual as the density of the population increases.

A number of equilibrium hypotheses have been proposed to explain the local coexistence of species in natural communities (Connell 1978). High diversity is maintained near equilibrium because: (1) Each species is specialized on, and competitively superior in exploiting a particular subdivision of the available resources (e.g., food or habitat) thereby lessening the level of interspecific competition. Diversity is a function of the total range of resources and the degree of specialization of the species to parts of this range (MacArthur 1972, Schoener 1974). (2) The competitive hierarchy at equilibrium is not linear and transitive, as often presumed. Each species uses interference mechanisms to win over some competitiors but loses in turn to others. This prevents any one species from becom-

ing so abundant that it excludes all others (Gilpin 1975, Jackson and Buss 1975, Buss and Jackson 1979). (3) Natural enemies or selective physical disturbances cause proportionately greater mortality of the species which ranks highest in competitive ability and thus prevents lower ranked species from being competitively excluded locally (Paine 1966).

The second view of natural communities is that though they may be in a state of global equilibrium (i.e., most species persist for many generations over a large area) these assemblages are rarely in equilibrium locally. The species composition in any area is usually changing and local populations of a species often go extinct. Equilibrium is prevented by periodic or stochastic disturbances or more gradual changes in the physical environment. Natural systems are characterized by strong interactions and local disequilibria, rather than being fine-tuned or biologically accommodated (sensu Sanders 1968, 1969).

Disturbances are heterogeneous in time and space and generate patchiness in natural systems. They renew limiting resources and promote the local coexistence of species. Migration between patches ensures the global persistence of species that go extinct locally (Hutchinson 1951, Andrewartha and Birch 1954). The range of life history traits exhibited by different species reflects in part their evolutionary responses to the spatio-temporal heterogeneity in resource availability generated by localized disturbances. Differences in the composition of neighboring patches are a direct result of differences in the intensity, periodicity, and exact history of the disturbances to which each is subjected (Jones 1956, Peterkin and Tubbs 1965, Jackson 1968, Lewontin 1969, Henry and Swan 1974, Niering and Goodwin 1974, Sutherland 1974, Levin 1976).

In the absence of disturbance, the diversity of assemblages of sessile organisms often declines rather than remaining high as equilibrium hypotheses would predict. The process of successional replacement leads to the local monopolization of space by the competitively dominant and/or most long-lived species. This pattern has been demonstrated or inferred for a wide variety of associations; forests (Eggeling 1947, Horn 1974); coral reefs (Connell 1973, 1976, 1978, Loya 1976, Glynn 1976), rocky intertidal algal communities (Dayton 1975, Menge 1975, Lubchenco and Menge 1978); marine epifaunal invertebrates (Osman 1977) and rocky intertidal invertebrate communities (Connell 1961, 1970, Paine 1966, 1974, Dayton 1971 and others).

However, recurrent patchy disturbance is characteristic of most natural systems. Examples include fires in terrestrial plant communities (Jackson 1968, Loucks 1970, Hanes 1971, Heinselman 1973, Taylor 1973, Wright and Heinselman 1973, Wright 1974; for numerous examples see the annual Proceedings of the Tall Timbers Fire Ecology Conference, Tall Timbers Research Station, Tallahassee, Florida, USA), hurricanes and wind throws in forests (Niering and Goodwin 1962, Henry and Swan 1974, Whitmore 1974, Williamson 1975, Connell 1978), storms over coral reefs (Connell 1973, 1976, 1978), the burrowing activity of badgers in prairie grasslands (Platt 1975), drift logs which batter the marine intertidal (Dayton 1971), large waves which open patches in intertidal mussel beds (Levin and Paine 1974), and the damage caused by grazing elephants in East Africa (Laws 1970).

I have studied algal succession following a disturbance in marine intertidal boulder fields in southern California, a system which conforms more closely to the nonequilibrium model of community structure. In a companion paper (Sousa 1979) I describe in detail the patterns of recolonization and the mechanisms which drive successional sequences. When a surface is cleared either by a natural disturbance or experimentally, it is first colonized by the green alga, *Ulva*, and the barnacle, *Chthamalus fissus*. In the fall and winter of the 1st yr after clearing, several species of perennial red algae, *Gelidium coulteri*, *Gigartina leptorhynchos*, *Rhodoglossum affine*, and *Gigartina canaliculta* colonize the surface. If there is no intervening disturbance, the late successional species, *Gigartina canaliculata*, gradually dominates, holding 60 to 90% of the space after a period of 2 to 3 yr. During succession, diversity increases initially as species colonize bare surfaces but declines later as one species monopolizes the space.

However, as in the examples above, this sequence is often interrupted. Boulders are overturned by storm waves, and the algae and sessile invertebrates are partially or completely killed. This disturbance frees space for recolonization; its frequency controls the age of a patch of substrate and thus how far succession will proceed. Because small boulders are more likely to be overturned by waves than larger ones, boulder fields are a mosaic of successional stages. The frequency of these disturbances can be easily monitored and experimentally altered, making boulder fields ideal for the investigation of the effect of disturbances on algal community structure. This study documents, with observations and field experiments, the effects of disturbances which are localized in space and time on the composition of this community of sessile organisms. The results suggest that local species diversity is maintained only when disturbances keep the assemblage of species in a nonequilibrium state.

STUDY SITE

Degree of wave exposure

The study site was located at Ellwood Beach, California (latitude 34°25'N, longitude 119°41'W), within the Santa Barbara Channel approximately 9 km west
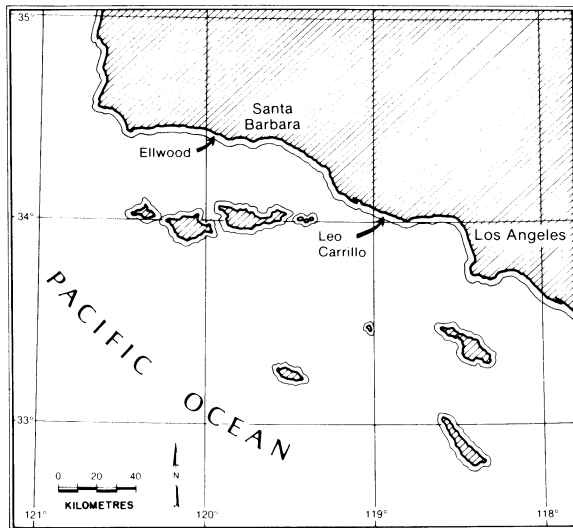
FIG. 1.   Map of the south coast of California from Point Conception to Los Angeles showing the study site at Ellwood. The Channel Islands are also indicated.

FIG. 3.   Average monthly probability of movement for boulders in each 49 N force class.

of the University of California, Santa Barbara (Fig. 1). The boulder field at this site is protected from large summer wave swells by the Channel Islands located 35–40 km offshore. However, winter storms out of the northwest frequently produce midchannel wind waves in excess of 2.5 m in height or swells greater than 1.5 m which overturn many boulders.

Boulders at Ellwood are of hard sandstone and overlie a gently sloping shale platform which extends into the low intertidal zone (from +0.30 m to −0.30 m above mean lower low water, hereafter, MLLW). The
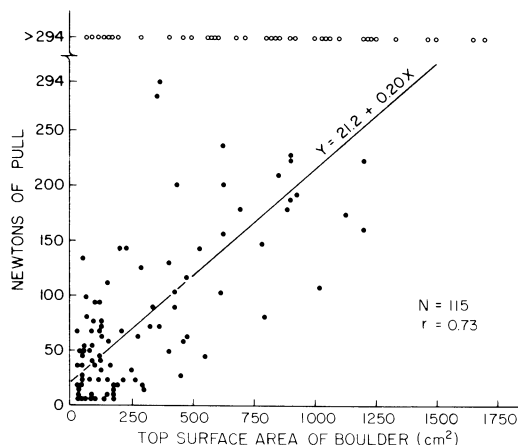

FIG. 2.   Regression of newtons of pull required to move a boulder on the area of the top surface of the boulder. Regression line and correlation coefficient are calculated from data points indicated by solid circles. Open circles indicate boulders >294 N whose actual weights could not be accurately measured.
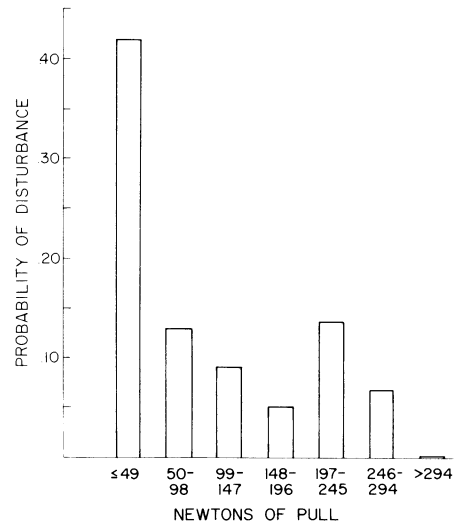
species composition at this site is described in detail elsewhere (Sousa 1977, 1979). Hereafter, all species will be referred to by their generic names, except for the two species of *Gigartina* for which both genus and species names will be used.

Disturbance of boulders by waves

The probability of a boulder of a certain size being overturned by waves was assessed in two ways. I made a relative estimate of this probability for each boulder which was sampled using a spring scale. A chain attached to the scale was placed around the boulder and the scale was pulled towards the shore in a direction perpendicular to the incoming wave front. The force required to move a boulder is an indirect measure of its susceptibility to being moved by waves. While the spring scale employed measured in kilograms, force was being assessed rather than mass. Accordingly, all results are expressed in newtons of pull (=kilograms × 9.80665). The maximum force which could be accurately measured with the scale was 294 newtons. Boulders requiring more force than this were pooled in the analyses described below. Although this measure is correlated with the area of the top surface of a boulder (Fig. 2), it is probably a better indicator of "disturbability" because some rocks which appear small are very stable portions of much larger buried boulders. Conversely, some large boulders which are irregularly shaped move when a relatively small force is applied.

In April 1975 I began making direct observations of boulder movements and from these, estimated the probability of disturbance at Ellwood. I established six permanent 1-m² quadrats in the boulder habitat, marked at the corners by driving lengths of steel rein-

Period of observation		Num-ber of days	Probability of movement		
			Force class (newtons of pull)		
Begin	End		≤49	50–294	>294
30 Apr. 75	6-14-75	46	.30 (69)	.01 (35)	0.0 (40)
15 Jun. 75	11-16-75	155	.04 (58)	0.0 (35)	0.0 (40)
17 Nov. 75	1-18-76	63	.11 (39)	.07 (35)	0.0 (40)
19 Jan. 76	2-17-76	30	.42 (33)	.14 (32)	0.0 (40)
18 Feb. 76	3-18-76	30	.48 (126)	.05 (28)	.02 (40)
19 Mar. 76	4-18-76	31	.62 (114)	.13 (25)	0.0 (41)
19 Apr. 76	5-19-76	31	.50 (63)	.02 (26)	0.0 (41)
20 May 76	6-16-76	28	.35 (45)	.02 (27)	0.0 (41)
17 Jun. 76	7-14-76	28	.21 (56)	0.0 (26)	0.0 (41)
15 Jul. 76	8-27-76	44	.11 (31)	0.0 (26)	0.0 (41)
28 Aug. 76	9-25-76	29	.13 (32)	0.0 (26)	0.0 (41)
26 Sept. 76	10-25-76	30	.35 (60)	.04 (26)	0.0 (41)
26 Oct. 76	11-20-76	25	.58 (62)	.34 (27)	0.0 (41)
21 Nov. 76	12-7-76	17	1.00 (64)	.18 (27)	0.0 (41)
8 Dec. 76	1-17-77	41	.54 (55)	.15 (29)	0.0 (41)
18 Jan. 77	2-16-77	30	.73 (112)	.05 (38)	0.0 (41)
17 Feb. 77	3-19-77	31	.57 (78)	.36 (40)	0.0 (41)
20 Mar. 77	5-19-77	61	.48 (51)	.05 (36)	0.0 (41)
Average probability of movement			.42	.09	.001

forcing bar into the soft shale platform underlying the boulder matrix. Photographs, both Polaroid and 35-mm, were periodically taken of each quadrat from April 1975 to May 1977. From November 1975 to May 1977 photographs were taken at approximately monthly intervals.

To examine the relationship between the newtons of pull required to move a boulder and its probability of being disturbed by waves, I first divided the boulders into 49 N classes. Estimates of the seasonal probability of disturbance for each class were made by dividing the number of rocks which moved in each time period, including those which moved out of the quadrats, by the total number of boulders in the class at the beginning of the interval. For the purpose of comparison, these values were divided by the number of days in the interval and multiplied by 30 to give the average monthly probability of a boulder, in a particular 49 N class, moving during the interval. These probabilities are conservative estimates since boulders which moved two or more times during the interval were only recorded as having moved once. As expected, the average monthly probability of disturbance over all time periods (Fig. 3) decreases with increasing measured force. Some of the variability in the probabilities for intermediate force classes is due to the small number of boulders in each.

To compare statistically the species compositions on boulders subjected to different frequencies of disturbances, I objectively pooled these 49 N classes to form three larger classes of approximately equal size;

those which have a high (≤49 N), intermediate (50–294 N) and low (>294 N) monthly probability of being disturbed. Disturbance probabilities for each of these classes in each sampling period appear in Table 1. Boulders in the 49 N class have over 40% average probability of being disturbed per month, while those >294 N are almost never moved. The average probability of disturbance for boulders in the 50–294 N class is about 9% per month, though this is a bit inflated by the smaller sample sizes.

PATTERNS OF SPECIES COMPOSITION ON BOULDERS OF DIFFERENT SIZE

Methods

If the frequency of disturbance is important in determining the relative abundances of species in intertidal boulder fields, one would expect that the species composition should change in a predictable fashion along a gradient of rock size (or newtons of pull). To determine if this was so, I estimated the percent cover of macro-algae and sessile invertebrates on all rocks within each of the six permanent quadrats established at Ellwood. Estimates of cover were made visually with the aid of a 0.25-m² quadrat subdivided into 25-cm² squares. These estimates differ by less than 5% from those obtained by the conventional projection method (Sousa 1979). The quadrat was also used to visually estimate the top surface area of each boulder. At the same time I counted the number of plants of the middle successional species, Gigartina leptorhynchos, Gelidium and Rhodoglossum (Sousa 1979) on each boulder. I noted for each plant whether it was in a clearing or not.

Sampling was repeated four times, twice at the end of the physically benign summer–fall months (November 1975 and October 1976) when algal growth is most rapid and twice in the early spring (May 1976 and May 1977) following the harsh winter months when space is opened as a result of defoliation and disturbance and when the perennial red algae recruit (Sousa 1979). Though many of the boulders, particularly the very stable ones, were sampled at each date, less stable boulders were moved into and out of the quadrats between censuses by waves. Thus, the censuses conducted on the four dates were not of identical sets of boulders. At each census, the newtons of pull required to move each boulder were measured as described above. Repeated measurements on the same boulders indicated that newtons of pull was consistent between censuses.

The census data were analyzed for differences in species composition and diversity within and between groups of boulders subject to different frequencies of disturbance. Both aspects of diversity were examined: the number of species (i.e., species richness) and their relative abundances. The degree to which the cover on a boulder was dominated was used as an expression

TABLE 2. Seasonal patterns of dominance of boulders in each of the three force classes. Entries are the percentages of the censused boulders (*n*) with a single species or two or more species comprising at least 75% of the living cover. The mean percentage bare space and one standard error (enclosed in parentheses) are presented for each force class. Sessile species which dominated were *Ulva* spp., *Chthamalus fissus* (*C.f.*), *Centroceros clavulatum* (*C.c.*), *Anthopleura elegantissima* (*A.e.*), *Gelidium coulteri* (*Ge.c.*), *Corallina vancouveriensis* (*C.v.*), *Gigartina leptorhynchos* (*G.l.*), *Laurencia pacifica* (*L.p.*), and *Gigartina canaliculata* (*G.c.*).

Census date	Force class (N)	n	Dominating single species									Combination of				Percent bare space
			Ulva	C.f.	C.c.	A.e.	Ge.c.	C.v.	G.l.	L.p.	G.c.	2 spp	3 spp	4 spp	5spp	
November 1975	≤49	27	22.3	40.7	7.4	3.7	0	0	0	0	3.7	14.8	7.4	0	0	78.0 (5.1)
	50–294	31	6.5	6.5	3.2	0	0	0	0	0	12.8	51.6	9.7	3.2	6.5	26.5 (4.1)
	>294	31	0	0	0	0	0	0	0	0	71.0	22.5	6.5	0	0	11.4 (2.1)
May 1976	≤49	44	38.6	25.0	2.3	0	2.3	2.3	0	0	0	20.5	9.0	0	0	66.5 (4.4)
	50–294	17	5.9	0	0	0	0	0	0	0	23.5	35.3	35.3	0	0	35.9 (4.9)
	>294	41	4.9	0	0	0	0	0	0	0	65.9	26.8	2.4	0	0	4.7 (1.0)
October 1976	≤49	40	0	12.5	0	0	2.5	12.5	2.5	10.0	12.5	45.0	2.5	0	0	67.7 (3.4)
	50–294	14	0	0	0	0	0	0	0	0	50.0	42.9	0	7.1	0	32.2 (3.6)
	>294	42	0	0	0	0	0	0	0	0	92.9	7.1	0	0	0	14.5 (1.8)
May 1977	≤49	33	90.9	0	0	0	0	0	0	0	3.0	6.1	0	0	0	49.9 (4.9)
	50–294	23	17.4	0	0	0	0	0	0	0	13.0	56.6	13.0	0	0	34.2 (5.1)
	>294	36	0	0	0	0	0	0	0	0	88.9	11.1	0	0	0	6.1 (1.4)

of the pattern of relative abundance. Dominance was measured by enumerating the minimum number of species which together comprised at least 75% of the living cover on a boulder. The smaller the number of species required, the more dominated the assemblage.

Since the disturbance of a boulder is a probabilistic event, all boulders within a force class will not have been overturned at the same time in the past. As a result, each class has a particular distribution of boulder ages (i.e., length of time since each boulder was last disturbed). I did not, therefore, test the null hypothesis that the force classes had equal mean values of the characteristic in question; rather, I analyzed for differences in the distributions of boulders within the three force classes with respect to both the total number of species on their top surfaces and the minimum number of these species which together comprised at least 75% of the cover.

Many of the rocks ≤25 cm² sampled at Ellwood were entirely bare (except for micro-organisms), pre-

TABLE 3. Statistical comparison of the degree of dominance in each force class of boulders at each census date. All three combinations of frequently (FD, ≤49 N), infrequently (ID, 50–294 N), and rarely (RD, >294 N) disturbed boulders were compared. Among-class differences in the distributions of boulders with respect to the number of dominating species were analyzed with one-tailed Kolmogorov-Smirnov two-sample tests (Siegel 1956). The statistic is chi-square with two degrees of freedom; *P < .05, **P < .01, ***P < .001.

	Census date			
Comparison	November 1975	May 1976	October 1976	May 1977
FD vs. ID	13.75**	8.29*	.29	21.86***
ID vs. RD	10.94**	8.24*	7.73*	19.21***
FD vs. RD	.27	.37	13.38**	.17

sumably because rocks this small are disturbed so frequently that no macro-organism can recruit and survive on their surfaces. A posteriori, I considered these rocks to be in a separate class from those which had some sessile organisms, and they were excluded from the analyses presented here. They were also excluded from calculations of the percent bare space on boulders in the different newton classes.

Patterns at Ellwood

Data from the censuses at Ellwood indicate that the frequency with which a patch of habitat is disturbed has a large effect on its species composition. In three out of the four censuses, a greater percentage of the frequently disturbed boulders (≤49 N) was strongly dominated by a single species than of those boulders disturbed at an intermediate frequency (50–294 N) (Tables 2 and 3). In the November 1975 and October 1976 censuses, some boulders in the latter force class had as many as four or five species comprising 75% of the cover. A greater proportion of rarely disturbed boulders (>294 N) were dominated than 50–294 N boulders in all samples. In three out of four of the censuses small boulders and large boulders were dominated to the same degree.

Most small boulders (≤49 N) were dominated by opportunistic early successional species; the green alga, *Ulva*, and the barnacle, *Chthamalus*. This was not entirely true for the October 1976 census as discussed below. In both censuses conducted in May, more of the unstable boulders were dominated by *Ulva* than in November and October when barnacles dominated a greater percentage of the rocks in this category. In all seasons, population densities on these rocks were low, as indicated by the large amount of bare space. In contrast, large undisturbed boulders (>294 N) were mainly dominated by the late succes-
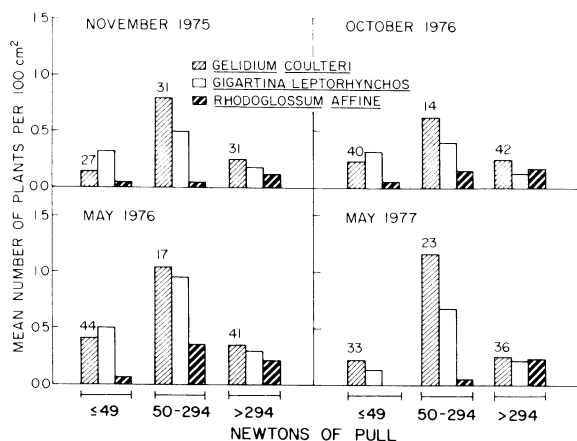
FIG. 4. Mean densities of the middle successional algal species, *Gelidium coulteri*, *Gigartina leptorhynchos*, and *Rhodoglossum affine*, on boulders in different N-of-pull classes. Data are from the four censuses of boulders in permanent quadrats at Ellwood. Sample size for each N-class in a census is indicated above the first bar in each group.

sional red alga, *Gigartina canaliculata*, which covered most of the rock surface, leaving little open space. In the May 1976 census, there were two boulders in this latter category which were dominated by the early successional species, *Ulva*. Analysis of photographs of the quadrats showed that these boulders had been overturned by large waves during the previous winter. Since large boulders are seldom moved, the newly exposed surfaces of these boulders were almost entirely bare when overturned, and rapid colonization by *Ulva* resulted in a dominated early successional community. Boulders subjected to an intermediate frequency of disturbance (50–294 N) had more open space than larger, more stable boulders and a smaller percentage was dominated by a single species. The cover on these boulders was composed of a mixture of early, middle, and late successional species.

The only exception to this pattern of maximum equitability of species abundances with intermediate frequencies of disturbance occurred in the October 1976 census data. On this date, boulders in the <49 N class were no more dominated than those in the 50–294 N class and were less dominated than those which were rarely disturbed (Table 3). This reduced dominance on small boulders is possibly attributable to the combination of reduced wave disturbance during the 4 mo immediately preceding the October 1976 census (Table 1) and coincident changes in the patterns of algal recruitment and growth. *Ulva* and *Chthamalus* were single dominants on over 60% of the small boulders in each of the three other censuses, but dominated 0% and 12.5%, respectively, of the small boulders in October 1976. In addition to this reduced recruitment of species which normally dominate, there was good recruitment and/or growth of a number of species, including *Gelidium*, *Corallina*, *Gigartina leptorhynchos*, and *Laurencia*, which rarely become very abundant on small boulders. In fact, *Corallina* and *Laurencia* were single dominants on 12.5% and 10.0% of these boulders, respectively. More importantly, this enhanced recruitment and growth resulted in a high percentage (45.0%) of the small boulders having two species comprising 75% of the cover. *Corallina* and *Laurencia* contributed to 10 out of these 18 cases of codominance.

Other changes in algal recruitment and growth preceding the October 1976 census contributed to the lack of statistically significant difference in equitability between small and medium-sized boulders. A greater proportion of the boulders in the 50–294 N class were dominated by *Gigartina canaliculata* than in any other census. Apparently, *G. canaliculata* grew vigorously during this period. It also was a single dominant on a relatively large percentage of small boulders, but not enough to compensate for the reduced dominance on others, as discussed above.

TABLE 4. Changes in local populations of middle successional algae on boulders at Ellwood. Data are the percents of boulders on which local populations underwent changes described below during two year-long periods. Boulders were censused in November 1975, May 1976, October 1976 and May 1977.

Percent of boulders on which local populations:	November 1975 to October 1976			May 1976 to May 1977		
	Gelidium coulteri	*Gigartina leptorhynchos*	*Rhodoglossum affine*	*Gelidium coulteri*	*Gigartina leptorhynchos*	*Rhodoglossum affine*
First became established	18.2	30.8	36.3	18.2	27.6	20.0
Increased in density	21.2	7.7	18.2	12.1	10.3	28.0
Remained constant in size	15.2	7.7	13.6	6.1	10.3	24.0
Decreased in density	21.2	7.7	4.6	24.2	27.6	16.0
Went extinct	24.2	46.1	27.3	39.4	24.2	12.0
Mean number of plants per 100 cm² (SD) at:						
Beginning of period	.41 (.41)	.42 (.65)	.23 (.23)	.51 (.49)	.41 (.44)	.31 (.35)
End of period	.41 (.42)	.18 (.29)	.33 (.46)	.39 (.45)	.39 (.43)	.41 (.56)
Total number of boulders	33	26	22	33	29	25

TABLE 5. Seasonal patterns of species richness on boulders in each of the three force classes. Entries are the percentages of the censused boulders (*n*) with a given total number of sessile species. The mean number of species on boulders in each class (s̄) and its standard error (enclosed in parentheses) are also presented.

| Census date | Force class (N) | *n* | Number of species | | | | | | | s̄ |
			1	2	3	4	5	6	7	
November 1975	≤49	27	55.6	18.5	22.2	3.7	0	0	0	1.7 (.18)
	50–294	31	0	32.3	12.9	32.3	6.4	9.7	6.4	3.7 (.28)
	>294	31	25.8	32.3	19.3	9.7	9.7	3.2	0	2.5 (.25)
May 1976	≤49	44	54.5	22.7	9.2	6.8	6.8	0	0	1.9 (.19)
	50–294	17	0	11.8	23.5	11.8	29.4	23.5	0	4.3 (.34)
	>294	40	10.0	25.0	17.5	15.0	17.5	15.0	0	3.5 (.26)
October 1976	≤49	40	40.0	40.0	15.0	5.0	0	0	0	1.9 (.14)
	50–294	14	0	28.6	35.8	21.4	0	7.1	7.1	3.4 (.40)
	>294	42	23.8	47.6	14.3	9.5	2.4	2.4	0	2.3 (.18)
May 1977	≤49	33	78.7	6.1	9.1	6.1	0	0	0	1.4 (.16)
	50–294	23	0	17.4	17.4	52.2	13.0	0	0	3.6 (.20)
	>294	36	5.6	33.3	22.2	16.7	22.2	0	0	3.2 (.21)

In direct contrast, *Ulva* and *Chthamalus* recruited well and *Corallina* and *Laurencia* very poorly during the calm months preceding the November 1975 census. Neither of the latter two species was a single dominant on any small boulder and they only contributed to one out of the six cases in which 75% of the cover on a boulder comprised more than one species. What accounts for these between-year differences is not known, but it is clear that small boulders which have a high percentage of open space are much more affected than boulders which are disturbed less often.

The reduced dominance on most boulders of intermediate size is in part a result of increased densities of the middle successional species, *Gigartina leptorhynchos* and *Gelidium* (Fig. 4). No clear pattern emerges for *Rhodoglossum*, which is relatively rare. While more abundant on boulders of intermediate stability, these species never dominated them (Table 2). Mid-successional species gradually go locally extinct on large undisturbed boulders and cannot reinvade in the presence of *Gigartina canaliculata* (Sousa 1979). Reproduction and recruitment of these species occurs in the late fall and winter. Apparently, the frequency with which small boulders (<49 N) are overturned during this period is too great for these species to become established and grow to maturity despite the greater amount of space open for colonization. As discussed in more detail later, they appear to persist globally by colonizing small openings on the tops of recently disturbed or defoliated medium and large-sized boulders. In the November 1975 census, 86.2% of *Gelidium* (*n* = 116), 83.2% of *Gigartina leptorhynchos* (*n* = 101), and 86.0% of *Rhodoglossum* (*n* = 50) plants were found in or adjacent to clear patches on the tops of boulders. Similar percentages of plants in small openings were observed on the other census dates. The densities of these middle successional species were in a state of flux on most boulders (Table 4). Over the 2 yr of observation, most populations

increased or decreased in density, with a relatively high percentage going extinct or becoming newly established on previously unoccupied boulders.

Species richness is also affected by the frequency of disturbance. Boulders in the 50–294 N class had a significantly greater total number of species than boulders in the ≤49 N class in all four censuses and a greater number than those in the >294 N class in the November 1975 and October 1976 censuses (Tables 5 and 6). In both May censuses, however, undisturbed large boulders had as many species as boulders disturbed at intermediate frequencies and more species than frequently disturbed small boulders. This seasonal increase in the total number of species on large boulders occurs despite continued strong dominance of the cover by *Gigartina canaliculata* (Table 2).

The increased number of species on these boulders in the spring can be attributed to the defoliation of the *G. canaliculata* canopy which occurs each fall and winter coupled with winter recruitment by a number of species including, *Ulva, Chthamalus, Gelidium, Gigartina leptorhynchos,* and *Rhodoglossum* (Sousa 1979). Increased desiccation stress which accompanies the onset of afternoon low tides in the fall and grazing by large numbers of the small snail, *Lacuna unifasciata,* weaken the branches of *G. canaliculata.* Large winter waves remove them, opening small patches of cleared space previously covered by the algal canopy. These small openings are colonized by one or more of the above species. In fact, recruitment of *Gelidium, Gigartina leptorhynchos,* and *Rhodoglossum* occurs only during a 3-mo period in the late fall and early winter, apparently an adaptation which takes advantage of the predictable availability of open space during this period. Seasonal defoliation continues to provide openings for colonization until *Gigartina canaliculata* vegetatively secures 100% of the primary space, which may take a number of years.

During the benign summer months, the *Gigartina*

TABLE 6. Statistical comparison of species richness of each force class of boulders at each census. As in Table 3, all three combinations of force classes were compared. Among-class differences in the distributions of boulders with respect to the total number of sessile species occupying their surfaces were tested with one-tailed Kolmogorov-Smirnov two-sample tests. The statistic is chi-square with 2 degrees of freedom; $*P < .05$, $**P < .01$, $***P < .001$.

	Census date			
Comparison	November 1975	May 1976	October 1976	May 1977
FD vs. ID†	17.84***	20.98***	10.96**	33.58***
ID vs. RD	6.43*	2.57	7.69*	3.88
FD vs. RD	5.13	16.60***	2.15	36.80***

† FD = frequently disturbed; ID = infrequently disturbed; RD = rarely disturbed boulders.

canaliculata canopy regrows and the species richness on large boulders declines. Some of the fall and winter colonists disappear because of direct interference by the *G. canaliculata* canopy which shades or abrades them to death. Others, especially *Gigartina leptorhynchos* and *Gelidium*, are overgrown by epiphytes and removed by waves. Grazers and predatory snails contribute to the disappearance of *Ulva* and barnacles, respectively (Sousa 1979).

The amount of between-boulder variation in species composition also differed with the level of disturbance. Small, frequently disturbed boulders were most variable with respect to the number of different species which occurred as single dominants on their surfaces in the four censuses. Over the course of the study, nine different species occurred as single dominants on boulders ≤49 N as opposed to four species on 50–294 N boulders and only two species on boulders >294 N (Table 2). This observation is somewhat suspect because in three out of the four censuses, many more ≤49 N boulders were censused than 50–294 N boulders. This larger sample size might, in part, account for the greater number of different species which were found dominating small boulders. The pattern is probably real, however, since random samples of ≤49 N boulders from each of the censuses, equal in size to the number of 50–294 N boulders sampled, yield a total of eight different species of single dominants. This is still larger than the number for either of the other two force classes. Certainly, boulders >294 N are less variable in this characteristic since unequal sample size is not a problem.

The three disturbance categories also differ in the level of between-boulder variation in species diversity. Boulders subjected to an intermediate frequency of disturbance (50–294 N) were most variable with regard to species richness and relative abundance as measured by the exponential form of the index, H'. In each of the four censuses, there was significantly greater variation in this measure of species diversity

TABLE 7. Between-boulder variation in species diversity ($e^{H'}$). Null hypotheses of equal variances in different force classes are tested below with one-tailed F tests.

Force class (N)		Census date			
		November 1975	May 1976	October 1976	May 1977
≤49	$\bar{x}$	1.43	1.64	1.65	1.12
	s_1^2	.38	.68	.44	.12
	n	27	44	40	33
50–294	$\bar{x}$	2.63	2.90	2.21	2.32
	s_2^2	1.25	1.21	1.14	.61
	n	31	17	14	23
>294	$\bar{x}$	1.68	1.87	1.45	1.39
	s_3^2	.69	.45	.16	.29
	n	31	41	42	36

Null hypothesis	Census date	F ratios	Significance level
$s_1^2 = s_2^2$	November 1975	3.29	$P < .005$
	May 1976	1.78	$P < .05$
	October 1976	2.59	$P < .025$
	May 1977	5.08	$P < .001$
$s_2^2 = s_3^2$	November 1975	1.81	$P = .05$
	May 1976	2.69	$P < .01$
	October 1977	7.13	$P < .001$
	May 1977	2.10	$P < .05$

among these boulders than among those which were very frequently or very seldom disturbed (Table 7).

EXPERIMENTAL TEST OF THE DISTURBANCE HYPOTHESIS

The patterns described above indicate that the species composition on a boulder, including both species richness and the degree of dominance, changes with the boulder's predicted frequency of disturbance. However, any attempt to relate the species composition on a boulder to the frequency with which it is disturbed is confounded, because this frequency is correlated with the boulder's size (top surface area). It could be argued that the patterns observed are caused by biological, physical, or statistical properties which change with a boulder's size rather than how frequently it is disturbed. For example, the greater number of species on boulders in the 50–294 N class as compared to less stable boulders (≤49 N) could be explained by the difference in boulder size alone. Boulders in the 50–294 N class have a larger top surface area and support a greater cover of sessile species than those in the ≤49 N class. On the basis of greater area (MacArthur and Wilson 1967, Osman 1977) and larger sample size, rare species are more likely to be represented on boulders in the 50–294 N class. These larger boulders would be expected to sample a greater proportion of the pool of available spores and larvae. Experimental stabilization of boulders was necessary to determine clearly whether it is the frequency of disturbance or simply the difference in surface area

which accounts for the observed differences in species composition.

Methods

To test the disturbance hypothesis, I sterilized, with a propane torch, 32 small rocks (mean top surface area = 163.2 cm², SD = 29.9) comparable in size to those in the ≤49 N class (Fig. 2). Sixteen of these rocks were cemented with Sea-Goin Epoxy Putty (Permalite Plastics Corporation, Newport Beach, California 92668) to four 1-m lengths of 10 × 10 cm redwood, four rocks per length. I then haphazardly established these experimental units across the boulder field at the 0.0–0.30 m MLLW tidal level in July 1975. They were set in place by driving a length of steel reinforcing bar through a hole drilled in each end of the redwood beam and into the underlying soft shale platform. A hose clamp was fastened to the top of the reinforcing bar flush with the wood in order to prevent it from riding up on the bars. The remaining 16 rocks were tagged for later identification and several were placed haphazardly within 2 m of each group of stabilized rocks. These loose rocks were subjected to the natural levels of disturbance by waves during the 1½ yr that the experiment was monitored. The tidal heights of the sets of stabilized rocks were adjusted so as to be as close as possible to those of the loose rocks. At each sampling date, all limpets which colonized the rocks were removed to eliminate differences in their density on rocks of different stability as a factor in the experiment. This precaution was not really necessary since earlier experimental manipulations indicated that limpets have little effect on patterns of algal succession (Sousa 1979). Since tidal height and rock size were controlled for, only the frequency of disturbance could account for any differences in the colonization, survival and growth of species which recruited onto the stabilized vs. the unstabilized rocks. I periodically sampled all rocks in the experiment between June 1975 and January 1977. The experiment was terminated in January 1977 because many of the lengths of redwood had been heavily bored by teredinid molluscs. Some disintegrated and a number of the replicate stabilized rocks were lost. It also became difficult to locate the unstabilized rocks. As a result, the January 1977 sample consisted of 10 stable rocks and 7 unstable rocks.

Results

The experimental results show that the frequency with which a rock is disturbed, rather than simply its size, is responsible for the differences in species composition on rocks of differing stability (Fig. 5). Though both stabilized and unstabilized rocks were quickly colonized by *Ulva*, nearly twice as much cover of this plant developed on the stable rocks. The cover of *Ulva* declined on both sets of rocks during the fall of 1975
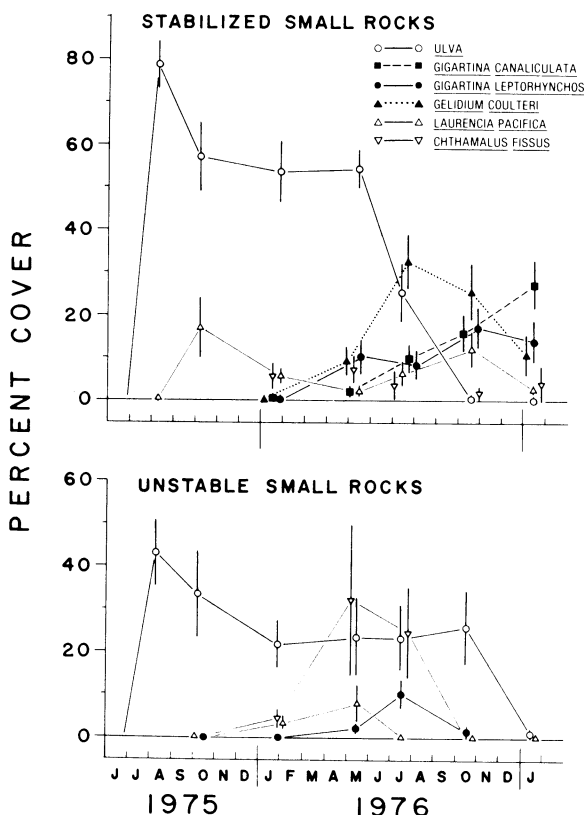

FIG. 5. Effects of stabilizing small rocks on the patterns of recruitment and growth of algae and barnacles. Data are mean percent covers of species which colonized experimentally stabilized rocks and loose control rocks over a 19-mo period between July 1975 and January 1977. Only species which held at least 5% cover on some sampling date over this period are included. Means ± one standard error of the mean are indicated.

presumably due to desiccation and grazing pressure. A low cover of *Ulva* (20%) persisted on the unstable rocks until January 1977 when it declined to near zero, while *Ulva* on the stabilized rocks had disappeared 3 mo before. The important difference between the treatments was that while barnacles and sparse populations of the red algae, *Laurencia* and *Gigartina leptorhynchos*, recruited to the unstable rocks, they persisted only until the fall of 1976. In contrast, four species of red algae including *Gelidium* and *Gigartina canaliculata* in addition to the two mentioned above, recruited to the stable rocks during the fall and winter of 1975–1976 and grew to comprise most of the cover by the fall and winter of 1976–1977. While completely replacing *Ulva*, these red algae also appeared to reduce the recruitment of barnacles to the stable substrates. Barnacles covered an average of slightly over 30% of the surfaces of unstable rocks in May 1976 while covering less than 10% of the surfaces of stable rocks.

By January 1977, when the experiment was termi-

TABLE 8. Species richness and average species diversity ($e^{H'}$) of experimentally stabilized boulders at Ellwood. Entries are percentages of boulders with a given number of species at each sampling date. Parentheses enclose one standard error of the mean. The experiment was started in July 1975. One of the initial 16 boulders disappeared before the first sampling date in August.

| Sampling date | n | Number of species | | | | | | | $e^{H'}$ |
		1	2	3	4	5	6	7	
10 Aug. 75	15	87.7	13.3	0	0	0	0	0	1.05 (.04)
8 Oct. 75	15	20.0	80.0	0	0	0	0	0	1.46 (.10)
29 Jan. 76	15	6.7	6.7	26.6	33.3	20.0	6.7	0	2.00 (.19)
14 May 76	12	0	8.3	16.7	33.3	41.7	0	0	2.48 (.18)
14 Jul. 76	12	0	0	0	16.7	66.7	8.3	8.3	3.26 (.25)
21 Oct. 76	14	0	0	0	14.2	42.9	42.9	0	3.17 (.18)
15 Jan. 77	10	0	0	0	30.0	60.0	0	10.0	3.02 (.27)

nated, the late successional red alga, *Gigartina canaliculata*, was beginning to dominate the cover on stable rocks as the cover of middle successional red algae, *Gigartina leptorhynchos* and *Gelidium*, was declining. At the same time, frequent wave disturbance of small loose rocks ($\leqslant 49$ N), including those involved in the experiment, between November 1976 and January 1977 (Table 1) killed all populations of algae and barnacles on their surfaces setting their successional "age" back to zero. Though not documented, recolonization in the spring of 1977 began a new successional sequence on these rocks. Despite the difference in surface area, stabilized small boulders developed just as high a level of species richness and diversity as the censused 50–294 N boulders which are larger (compare Tables 5 and 7 with Table 8).

DISCUSSION

The results of this study indicate that the frequency of physical disturbance strongly affects intertidal algal species diversity and composition by determining the time interval over which successional species replacements can occur. Frequently disturbed boulders will be available for colonization for only a short time before they are again disturbed, starting the process over. These small substrata are continually in the early stages of colonization with an abundance of open space and are usually dominated by those species settling in the highest abundances at the time of the year sampled. *Ulva* and *Chthamalus* typically dominate small boulders; both produce many propagules which colonize and grow rapidly enough to persist for the short period between disturbances. Though both settle throughout the year, *Ulva*'s peak recruitment occurs in the spring while *Chthamalus* recruits best in the fall and winter. This difference is reflected in the seasonal percentages of small boulders dominated by each. Few species can colonize small boulders and grow to an observable size in the short time between disturbances. As a result, species richness is consistently low. The experimental results indicate that in this system, small area per se does not cause any observable reduction in the number of rare species which colonize

small boulders. Their reduced surface area may contribute to the high degree of dominance observed (Osman 1977). With growth rate independent of surface area, a species could more quickly occupy the majority of the substrate before other species colonize. Most small boulders, however, have an abundance of open space which limits the importance of this effect, but it may occasionally occur. Its influence will be reinforced if, as I have demonstrated experimentally for *Ulva* (Sousa 1979), the species which becomes established first inhibits the recruitment and growth of subsequent colonists.

Species diversity is also low on most large boulders (>294 N). The time between disturbances of these substrata is long, there is little available space for colonization, and succession results in dominance by the red alga, *Gigartina canaliculata* (Sousa 1979). Most large boulders have fewer species than those of intermediate size except during seasons when defoliation, an additional disturbance, temporarily opens space for colonization.

Of the three classes of boulders, those subject to intermediate frequencies of disturbance are most diverse. Most boulders in the 50–294 N class are consistently rich in species irrespective of season and few are strongly dominated. They generally have a greater number of species and are less dominated than boulders in either of the other two classes. As mentioned earlier, some exceptions to this pattern are attributable to simultaneous short-term changes in the regime of disturbance incurred by a particular force class of boulders and in the seasonal patterns of algal recruitment and growth. Others are due to additional kinds of disturbance (e.g., defoliaton), the influence of which is different from that caused by the disturbance of boulders by wave impact.

Two sources of unexplained variance in the census data should be noted. Overturning by waves and defoliation are not the only disturbances which generate space on boulders. All boulders, even those which are stationary, are sometimes hit by other rocks carried by waves. This also produces small clearings in the algal canopy. Colonization of these openings will like-

ly affect the level of species richness on a boulder and even dominance relationships if this form of disturbance occurs often enough. Unfortunately, these events are difficult to observe and probably impossible to quantify. In addition, contrary to the impression which may have been conveyed earlier, the "successional age" of a boulder does not return to zero each time it is overturned by waves. Often, some organisms survive and regrow vegetatively. I have investigated this phenomenon experimentally (Sousa 1977), but it is extremely difficult to predict its effect on the relationship between the frequency of disturbance and species composition. Not only do the species differ in the amount of mortality caused by a particular intensity of disturbance, but also in the rate and extent to which their populations recover. A further complication is that the intensity of disturbance varies directly with boulder size. A large boulder is rarely overturned; when disturbed, all the species occupying what used to be the top surface of the boulder are usually killed before it is righted. Disturbances of smaller boulders are usually less intense because they do not remain overturned for as long a time. Some individuals may survive and regrow.

The relationship between diversity and substratum stability observed in this study has also been documented in communities of algae on subtidal boulders (Reidl 1972, Schwenke 1972) and subtidal shell bottoms (Waern 1958, Sears and Wilce 1975), and in sponge (Rützler 1965) and other epifaunal communities (Osman 1977) on subtidal boulders. One could expect that on a more exposed coast the average size of substrata with maximum diversity would be larger because of the increase in intensity of wave action. This prediction appears to hold true for this algal community. At Leo Carrillo State Beach (latitude 34°06′N, longitude 119°16′W), a more exposed site nearby, boulders >294 N support the most diverse assemblage of algae and strong dominance by *Gigartina canaliculata* develops only on solid rocky bench which is never moved by wave action (Sousa 1977).

The history of disturbance is obviously important in the explanation of patterns of species composition in this system. However, unlike some marine fouling communities (Osman 1977, Sutherland and Karlson 1977, Sutherland 1978), unique histories do not affect which species will dominate if a patch of habitat remains undisturbed for a long period of time. *Gigartina canaliculata* would eventually dominate all patches, regardless of past history or size, if disturbance could be experimentally removed. However, the time a substratum is disturbed does influence the rate at which dominance develops since recruitment of this species and other perennial red algae is highly seasonal (Sousa 1979).

The frequency of disturbance also determines the degree of variation in species composition and diversity between adjacent patches of habitat of similar size. Small boulders are disturbed frequently and the variance in their ages (i.e., time since last disturbed) is small. The time available for colonization is short, so that despite the large amount of open space, the cover which does develop on most small boulders is strongly dominated. However, they are not all dominated by the same species. A greater number of different species occur as single dominants on frequently disturbed boulders than on those which are larger and less often disturbed. This is because small boulders more frequently "sample" the available pool of spores and larvae; the dominants in any particular census reflect seasonal changes in the availability of these propagules for settlement.

Boulders in the least disturbed class are most variable in age, assuming random disturbance of boulders within the class. While many have not been disturbed for relatively long periods of time, a small number are overturned each winter. This large variance in age does not, however, generate large variation in species composition because in 2 to 3 yr time an undisturbed boulder becomes dominated by *Gigartina canaliculata* (Sousa 1979). So, despite the difference in time since the last disturbance, the broad upper tail of the age distribution is composed of rocks all in the same late successional state, reducing between-boulder variation.

Boulders of intermediate size are most variable in diversity because of their intermediate probability of disturbance. Some are strongly dominated by *Ulva* or barnacles if recently overturned or by *G. canaliculata* if undisturbed for long periods. Others which are diverse have remained undisturbed long enough for several species to become established but are disturbed before successional replacements result in dominance. Thus, intermediate frequencies of disturbance not only maintain high levels of diversity within a patch of habitat but enhance variation in species composition between adjacent patches.

Disturbance of boulders by wave action does not maintain diversity in this community by causing proportionately greater mortality of the species which dominates in the absence of such disturbance (Sousa 1977). Compensatory mortality of this sort is not required to maintain diversity in an open nonequilibrium system (Caswell 1978). Instead, local diversity is maintained on boulders of intermediate size because openings in the algal canopy are created often enough to allow recolonization and persistence of early and middle successional species. These species gradually go extinct in undisturbed patches but persist globally because the spores and larvae produced by adults in these patches colonize and grow to maturity in other patches in which space has been recently cleared. These algae do not appear to have extensive refuges outside of the particular zone in which the research was conducted and disturbances are to a large extent responsible for their persistence. The adaptation of

winter settlement in most of these species has probably evolved in response to the predictable availability of space produced by winter storms and defoliation of the algal canopy (Dayton 1975, Sousa 1979).

Do the findings of this and other studies of discretely patchy marine habitats extend to continuous rocky shores where patches cleared by disturbances may not be fixed in size and may even overlap? Not enough data are available at the present time to give a definitive answer to this question. It remains one of the most interesting and challenging areas for future investigation. The limited amount of data available on the spatial patterning of algal communities in continuous rocky habitats appears to support the conclusions of this study. Lubchenco and Menge (1978) examined algal community structure along a gradient of exposure to wave action in New England. They found that the cover of sessile species was least dominated and the spatial distributions of these species most patchy at sites with intermediate exposure to waves. Ongoing studies of the patch dynamics of intertidal mussel beds (Levin and Paine 1974, Paine, *personal communication*) should also yield interesting results relevant to this question.

Community structure: a
nonequilibrium view

The idea that communities and the populations which comprise them are often in a state of local disequilibrium is not a new one. Andrewartha and Birch (1954) provided a graphical model of this situation and argued that environmental heterogeneity reduces the chances of extinction. While some local populations are increasing in size, others are declining towards extinction, and still others may remain relatively stable. Differences in the densities of local populations reflect differences in the chance of each area being colonized as well as local differences in the environment (both biological and physical). Each local population is likely to go extinct in time but in the absence of any large environmental changes, surviving populations serve as sources of propagules for recolonization of the vacated favorable sites. Fluctuations in local populations are often asynchronous because most disturbances which renew space and thus allow recolonization, are heterogeneous in space, time and the intensity of destruction they cause.

Species with similar resource requirements coexist locally not because of evolved differences in their use of resources but as a consequence of disequilibrium conditions and renewed space generated by disturbances. The length of time that these species coexist depends upon the frequency and intensity with which disturbances occur in the particular area, the relative rates of recruitment of the species in question, and relative susceptibility of the species to various sources of mortality. If the time between disturbances is long, a single species may dominate and others will go extinct locally. The latter species persist globally (i.e., in the system of patches) by colonizing other patches in which conditions are more open.

Until recently, many workers in community ecology have accepted the equilibrium view of early population ecologists. There is a great intellectual appeal in the resource utilization theories of MacArthur (1972) and others (see Pianka 1976 for a recent review). Acceptance of this view is reinforced by the tractable nature of deterministic models of population and community dynamics. Unfortunately, an equally well developed theoretical construct which takes into account patchiness and local disequilibrium does not exist. Hutchinson's (1951) concept of fugitive species was an early presentation of this idea. Subsequent attempts to incorporate patchiness and migration into models of community structure (Skellam 1951, MacArthur and Levins 1964, Cohen 1970, Levins and Culver 1971, Horn and MacArthur 1972, Levin 1974, Levin and Paine 1974, Roff 1974, Slatkin 1974, Steele 1974, Armstrong 1976, Caswell 1978 and others) have been especially important for their heuristic value.

Despite the difficulties of developing models which describe natural stochastic processes, evidence from certain field studies supports the nonequilibrium view, particularly for communities of sessile organisms. Studies in the rocky intertidal (Paine 1966, 1974, Dayton 1971, 1973, 1975, Harger and Landenberger 1971, Levin and Paine 1974, this study) and on coral reefs (Connell 1973, 1976, 1978, Glynn 1976, Loya 1976) clearly demonstrate that while species are outcompeted locally, inevitable local disturbances substantially alter community structure and maintain diversity. The work of Eggeling (1947), Jones (1956), Connell (1978), and Hubbell (1979) in tropical forests in Uganda, Nigeria, Australia, and Costa Rica, respectively, suggests that even in the community which has been viewed for decades as the epitome of stability, canopy trees often do not replace themselves locally, and disturbances seem to account, in large part, for the maintenance of the present diversity of these forests. It is also likely that when the dynamics of local populations of motile organisms are studied in more detail many will be found to exist in a nonequilibrium state (Davidson and Andrewartha 1948a, b, Huffaker 1958; Dodd 1959, Huffaker et al. 1963, Pearson 1963, Ehrlich and Birch 1967, Birch 1970, Richerson et al. 1970; Ehrlich et al. 1972; Spight 1974, Willis 1974, Ehrlich et al. 1975, Sale 1977, 1978, Wiens 1977, Talbot et al. 1978, and others).

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