The Responses of a Community to Disturbance: The Importance of Successional Age and Species' Life Histories

Wayne P. Sousa*

Department of Biological Sciences, University of California, Santa Barbara, California 93106, USA

Summary. The responses of different successional stages of a temperate intertidal algal community to disturbance were investigated with a field experiment. The experiment was conducted in a low intertidal boulder field in southern California. In this habitat, the top surfaces of boulders are covered with algae. The composition of the assemblage on any particular boulder depends on the length of time since it was last overturned by wave action. When a boulder is overturned, the algae on what was formerly the top surface, are killed in whole or part by a combination of sea urchin grazing, anoxia, light levels below compensation intensity, and mechanical damage caused by crushing or abrasion. The length of time that a boulder remains overturned and the local abundance of sea urchins determines the intensity of the disturbance. When the boulder is righted, recolonization begins either by vegetative regrowth of survivors and/or by spores from outside.

Using a three-factorial design, this natural form of disturbance was experimentally mimicked and the responses of three different successional stages of the algal community monitored. Boulders in each successional category were overturned for periods of 17, 27 and 54 days in areas with and without sea urchins, then righted. Two aspects of community response to perturbation were evaluated. These were (1) the assemblage's ability to resist change and (2) its ability, if altered, to adjust to some semblance of its original state. The resistance of each assemblage and of its component species to change was measured by the percent decrease in algal cover and by the decline in percent similarity of the community to its original composition. The recovery rate of each assemblage and of the cover lost by each species during the first 35 days following a disturbance was measured by the rate of increase in percent similarity to the original composition and the percent reestablishment of lost cover.

The experimental evidence demonstrates that the successional stages of the producer level of an intertidal algal community differ significantly in their responses to disturbance. Early successional communities suffer more damage from a given level of perturbation but recover more quickly than either middle or late successional communities. Damage to any particular assemblage of algae, irrespective of successional age, is more extensive and recovery slower, the longer the boulder is overturned and/or sea urchins are present. Several thresholds in these responses were also identified.

Differences in community responses and non-linearities in these responses were attributable to the life history characteristics of

the component species rather than emergent properties of the assemblage. These characteristics have evolved in response to a variety of recurrent natural disturbances. This interpretation is in agreement with recent critical reevaluations of the trends and mechanisms of successional change in natural communities.

Introduction

Recent critical reviews of the literature on the trends and mechanisms of ecological succession (Connell, 1972; Drury and Nisbet, 1973; Colinvaux, 1973; Horn, 1974 and 1975; Connell and Slatyer, 1977) have revealed a number of flaws in what has become the classical theory of the process (Clements, 1916; Margelef, 1968; Odum, 1969). Most importantly, the processes of recolonization and species replacement following a disturbance which opens space are better explained by the life-history characteristics of individual species than by any emergent properties (Salt, 1979) of the whole community. Such characteristics include a species' pattern of reproduction with special regard to the quantity and seasonality of propagule production, how far propagules are dispersed, and their subsequent rates of growth. Also critical are the species' vulnerability to death or injury from natural enemies and physical disturbances, and its ability to recruit from dormant propagules or to vegetatively regrow from damaged tissues.

There is little evidence from marine rocky intertidal algal communities to support long-standing generalizations concerning successional patterns (Odum, 1969). Relay floristics (Egler, 1954) are not characteristic of secondary succession in this system. Early colonists rapidly fill openings and inhibit rather than facilitate subsequent invasion (Paine, 1977; Lubchenco and Menge, 1978; Sousa, 1979). Predictable sequences occur because species differ in the number and vagility of propagules they produce and in their vulnerability as adults to sources of mortality such as grazing, physical disturbance, and overgrowth by epiphytes (Luchenco and Menge, 1978; Sousa, 1979). Diversity at the producer level does not increase monotonically with time; rather it peaks in the middle of recolonization and declines later as one or a few species dominate (Paine and Vadas, 1969; Dayton, 1975; Lubchenco, 1978; Lubchenco and Menge, 1978; Sousa, 1979 and 1979a).

One generalization which does not seem to have been tested experimentally in marine intertidal communities is the idea that late successional stages are more stable than younger ones. Much ambiguity and tautological thinking (Frank, 1968) has been associated with the use of the term "stability". Ideally, an assemblage of species within a defined area should only be judged stable

* *Present address:* Department of Zoology, University of California, Berkeley, California 94720, USA

if the characteristic of interest (e.g., relative abundance of species, diversity, productivity, etc.) remains relatively unchanged for at least the time required for one turnover of the population of the longest-lived species (Connell and Slatyer, 1977). Since turnover of perennial algal populations may take many years, this paper considers two aspects of community response to perturbation which, while not synonymous with the above criteria for stability, certainly indicate the likelihood that an assemblage will persist with little change. These are (1) the assemblage's ability to resist change and (2) its ability, if altered, to adjust to some semblance of its original state. These aspects of a community's response to perturbation have been discussed by a number of authors (Margalef, 1969; Holling, 1973; Horn, 1974; Orians, 1974; Connell and Slatyer, 1977; Harrison, 1979).

The experimental data presented in this report were gathered to answer two questions. First, how does the resistance and adjustment characteristics at the producer level of a marine benthic macro-algal community change with successional age and intensity of disturbance? Second, are the responses of differently-aged assemblages to perturbation attributable to the life history characteristics of their component species without reference to emergent properties? Following Salt's (1979) operational definition, an "emergent property of an ecological unit is one which is wholly unpredictable from observation of the components of that unit." The operation of plant defense guilds (Atsatt and O'Dowd, 1976) serves as an example. The defensive nature of these guilds results from the property that the probability of an individual plant being fed upon depends not only on its inherent quality or quantity, but on the chemistry, morphology, distribution and abundance of alternate food plants and non-food plants as well. In addition, the development of a coevolutionary relationship between a food plant and a grazer may well be modified as a result of membership in such a guild. This group property could not be inferred from a study of the interaction between each plant species and the grazer alone. Salt (1979) discussed several other examples of emergent properties of populations and communities.

Study Area and Organisms

The study area, described in detail elsewhere (Sousa, 1979), was a low intertidal boulder field at Ellwood Beach, California (34°25'N, 119°41'W). This type of habitat comprises much of the rocky shore of southern California. The top surfaces of boulders between 0.0 and +0.30 m MLLW (mean lower low water) are covered with algae and barnacles. The composition on any particular boulder depends on the length of time since it was last overturned by wave action (Sousa, 1979a). Large winter waves generated by storms in the Pacific northwest overturn many boulders. When this happens, the algae and sessile invertebrates on what was formerly the top surface of an overturned boulder, are killed in whole or part by a combination of sea urchin grazing, anoxia, light levels below compensation intensity, and mechanical damage caused by crushing or abrasion. The length of time that a boulder remains overturned and the local abundance of sea urchins determines the intensity of the disturbance. If this time is relatively short and/or urchins are rare, the attached organisms may simply be damaged and open space on the boulder recolonized primarily by vegetative regrowth of surviving individuals. At the opposite extreme, if boulders are overturned a long time and/or if urchins are abundant, all the organisms may be killed and recolonization accomplished completely by propagules from the outside.

When a boulder surface is cleared, it is first colonized by the green alga, Ulva, and the barnacle Chthamalus fissus (Sousa, 1979).

In the fall and winter of the first year after clearing, several species of perennial red algae, Gelidium coulteri, Gigartina leptorhynchos, Rhodoglossum affine, and Gigartina canaliculata colonize the surface. If there is no intervening disturbance, Gigartina canaliculata gradually dominates. During succession, diversity increases initially as species colonize the bare surface of a boulder but declines later as one species monopolizes the space.

Methods

Community-Level Responses to Perturbation

Boulders of approximately equal size ($\bar{x} = 1,230$ cm^2; S.D. = 178) occupied by algal communities of different successional ages were experimentally overturned to determine the amount of damage suffered by each assemblage, this being a measure of its resistance to perturbation. The recovery of each assemblage towards its original composition was then monitored. The rate and fidelity of this recovery is a measure of an assemblage's ability to adjust to change caused by a perturbation. A multifactorial experimental design allowed examination of the effects of sea urchin grazing and different intensities of disturbance (i.e., duration of overturning) on the resistance and adjustment properties of each assemblage.

Three groups of 30 boulders with species compositions representative of early, middle, and late successional stages were chosen for use in the experiment (Tables 1 and 2). Boulders in the early successional category were dominated by a cover of Ulva with some barnacles and occasional red algal sporelings. Middle successional boulder communities were more diverse, with a mixture of Ulva, Gigartina canaliculata, Gigartina leptorhynchos, Gelidium, and the rare Rhodoglossum plant. Late successional stages were defined to be those which were dominated by Gigartina canaliculata. Groups of 8 boulders at each successional stage were overturned for 54, 27 and 17 days, with and without sea urchins, and then righted. The experiment was conducted during the winter when boulders are naturally most likely to be disturbed. The initial overturnings were staggered so the recovery phase would begin simultaneously for all boulders. One early successional boulder in the 17-day treatment was disturbed by waves before being righted and was not included in the analysis.

Replication with regard to the presence or absence of sea urchins was difficult to control. In some instances, sea urchins moved away from areas which had been disturbed by the overturning of a boulder while in others urchins moved into areas from which they had originally been removed. Because of this, some boulders had to be reassigned a posteriori to either the "with urchin" or the "without urchin" treatments, thus the number of replicates in each treatment was not equal.

The percentage covers of the species on each boulder was sampled before being overturned (2–16, 3–16, 3–26–76), immediately after being righted (4–11–76) and again 35 (5–16–76) and 64 days (6–14–76) later. The percentage cover of species was monitored on 18 unmanipulated control boulders, 6 of each successional stage, between 2–16–76 and 6–14–76. Cover estimates were made in the field with the aid of a 0.25 m^2 sheet of plexiglass on which 100 random points were plotted. These values are for the canopy layer only.

Two measures of the effects of disturbance on the algal communities were calculated from the cover data. I assessed the total damage caused by calculating the percent decrease in the total cover of algae for each boulder. Differences in this measure were

Table 1. Initial species composition of early, middle, and late successional communities on boulders used in overturning experiment. Data are mean percent covers of species on 30 boulders of each successional age. Variance is expressed as one standard deviation of the mean and is enclosed in parentheses

Successional age	% Bare	Species with greater than 1% cover						Species with less than 1% cover
		Ulva spp.	*Chthamalus fissus*					*Gigartina leptorhynchos* *Gelidium coulteri* *Gigartina canaliculata* *Centroceros clavulatum*
Early	5.4 (4.8)	73.1 (15.6)	18.1 (14.7)					
		Ulva spp.	*Chthamalus fissus*	*Gigartina leptorhynchos*	*Gelidium coulteri*	*Centroceros clavulatum*	*Gigartina canaliculata*	*Anthopleura elegantissima* *Corallina vancouveriensis* *Gastroclonium coulteri* *Laurencia pacifica* *Porphyra perforata* *Rhodoglossum affine*
Middle	9.7 (6.9)	10.8 (8.4)	4.3 (7.3)	15.8 (10.4)	4.9 (5.7)	3.7 (6.2)	47.1 (19.0)	
				Gigartina leptorhynchos	*Gelidium coulteri*		*Gigartina canaliculata*	*Anthopleura elegantissima* *Chthamalus fissus* *Corallina vancouveriensis* *Centroceros clavulatum* *Gastroclonium coulteri* *Rhodoglossum affine* *Ulva* spp.
Late	1.9 (2.8)			3.5 (5.6)	2.4 (4.8)		91.8 (6.2)	

Table 2. Species richness and diversity ($e^{H'}$) of differently-aged communities on experimental boulders. Data are means of 30 boulders in each successional category. Parentheses enclose one standard deviation of the mean

Successional age	Number of species	$e^{H'}$
Early	2.5 (1.1)	1.6 (0.5)
Middle	6.3 (1.9)	4.1 (1.3)
Late	3.5 (1.3)	1.5 (0.3)

tested with a three-way analysis of covariance with successional age of the community, presence or absence of sea urchins and length of time that a boulder was overturned as the independent variables and with initial percent cover as a covariate. As a measure of the change in composition of the community I calculated the percent similarity of the community to its original composition prior to the disturbance. The measure of similarity used was that of Whittaker (1975, page 118) and is calculated as: Percentage similarity $= 2 \Sigma$ min (n_a or n_b)/($N_a + N_b$), where n_a and n_b are the percent covers of a given species in samples A and B, and N_a and N_b are the totaled percent covers of all species in samples A and B. The sum is over all species present. Analysis of variance was used to test for differences in the mean percent similarity of the three types of communities caused by the different levels of disturbance (i.e., all levels of urchin and time factors).

Data on recovery from disturbance were evaluated over the 35-day period from 4–11–76 to 5–16–76 as opposed to the longer 64-day sampling period (4–11–76 to 6–14–76) because the shorter period was more likely to reflect true differences in regenerative powers rather than seasonal changes in species-specific growth rates. Such seasonal changes in composition began to appear on control boulders between 5–16–76 and 6–14–76. It is impossible to determine the actual rates of recovery, or compare them statisti-cally since I do not know how quickly the algae regrew in the first 35 days after a boulder was righted. However, the rates of increase in percent similarity over this period are probably indica-tive of the relative rates of recovery of the different assemblages particularly since none reached an average of 100% similarity after 35 days.

Responses of Individual Species to Perturbation

The experiment described above also provided detailed informa-tion on the amount of cover lost by each of four species of algae when subjected to the different intensities of disturbance and the percentage of this lost cover which was regenerated within the first 35 days after the disturbance. The species which were abun-dant enough for meaningful use in statistical analyses included *Ulva, Gigartina leptorhynchos, Gelidium* and *Gigartina canaliculata*.

I tested for differences in the percent decrease in cover of each algal species using a three-way analysis of covariance with presence or absence of urchins, length of time that a boulder was overturned, and species of algae as the independent variables. The initial cover of each species of algae on a boulder was entered into the analysis as a covariate, since it was conceivable that

such disturbances might cause density-dependent mortality particularly in the presence of sea urchins.

As a measure of the powers of recovery of each species, I calculated the percent reestablishment of lost cover by each alga. Differences in this measure were tested using an identical three-way analysis of covariance but with the initial percent loss of cover due to the disturbance as a covariate.

A caveat is warranted. Because of the large amount of effort and space required to run this experiment, the same data are used repeatedly in the analyses described above. This violates assumptions concerning statistical independence and should be kept in mind when interpreting the results. All percentages are normalized with an arcsine transformation prior to their use in statistical analyses (Sokal and Rohlf, 1969). Changes of less than 5% cover were considered to be no change. This is the approximate level of error inherent in the method of cover estimation (Sousa, 1979).

Results

Community-Level Responses to Perturbation

The extent to which a community is changed by a perturbation depends in part on the intensity of disturbance. The presence or absence of sea urchins and the length of time a boulder was overturned determined this intensity. There were significant effects of both sea urchins and period of overturning on both the percent loss of total algal cover (Tables 3 and 4) and on the percent similarity of the community to its original composition (Fig. 1, Tables 4 and 5). Boulders of all three successional ages overturned in the presence of urchins lost a greater percentage of their algal cover and were less similar to their original composition when righted, than those overturned in areas without urchins.

The length of time a boulder was overturned had a similar effect. The cover and percentage similarity of the algae declined with time. This trend seemed to have a threshold value at 27 days: the most rapid change occurred during this early period followed by a more gradual decline in cover and percent similarity. This general pattern held for all three assemblages.

Differently-aged communities did differ significantly in their absolute responses to the same level of a potentially perturbing disturbance (Fig. 1, Tables 3, 4, and 5). Early successional algal communities suffered the greatest loss of cover and were the least similar to their original composition as a result of being overturned. Middle successional communities did not lose as much cover and underwent less change in community composition. Late successional communities were least affected in both respects.

The rate of recovery of the differently aged communities followed almost the opposite pattern. Early successional communities recovered much more rapidly than either middle or late succes-

Table 3. The effects of stage of succession, sea urchin grazing, and length of time a boulder is overturned, on the percent decrease in total algal cover on a boulder's top surface. Test is a three-way analysis of covariance (fixed model) with initial total percent cover algae entered as a covariate. Because the design is not orthogonal, the sums of squares of the main effects and two-way interactions do not sum to the corresponding sub-totals for each category (Nie et al., 1975)

Source of variation	Sum of squares	df	Mean square	F	Probability
Covariates	9,294.88	1	9,294.88	67.77	0.001
Initial cover	9,294.88	1	9,294.88	67.77	0.001
Main effects	15,694.50	5	3,138.90	22.89	0.001
Stage of succession	3,572.46	2	1,786.23	13.02	0.001
Urchin grazing	2,692.11	1	2,692.11	19.63	0.001
Time overturned	4,625.09	2	2,312.54	16.86	0.001
Two-way interactions	3,699.78	8	462.47	3.37	0.004
Stage-Urchin	839.74	2	419.87	3.06	0.054
Stage-Time	973.21	4	243.30	1.77	0.147
Urchin-Time	649.40	2	324.70	2.37	0.102
Three-way interactions	984.09	4	246.02	1.79	0.143
Stage-Urchin-Time	984.09	4	246.02	1.79	0.143
Explained	29,673.24	18	1,648.51	12.02	0.001
Residual	7,132.03	52	137.15		
Total	36,805.27	70	525.79		

Table 4. Responses of algal communities of different successional stages to various intensities of disturbance. Data are mean values of the dependent variable for all levels of significant factors in the analyses of (co) variance presented in Tables 3 and 5. Means are unadjusted for covariates.

Significant factor	Percent decrease in total algal cover			Significant factor	Percent similarity of the algal community to its original composition		
	Level	N	Unadjusted mean		Level	N	Unadjusted mean
Stage of succession	Early	23	82.1	Stage of succession	Early	23	27.1
	Middle	24	42.2		Middle	24	77.9
	Late	24	37.1		Late	24	84.3
Length of time boulder was overturned (days)	17	23	24.1	Length of time boulder was overturned (days)	17	23	94.1
	27	24	66.7		27	24	52.0
	54	24	70.9		54	24	40.9
Urchin grazing	With	33	75.7	Urchin grazing	With	33	34.8
	Without	38	33.1		Without	38	86.9
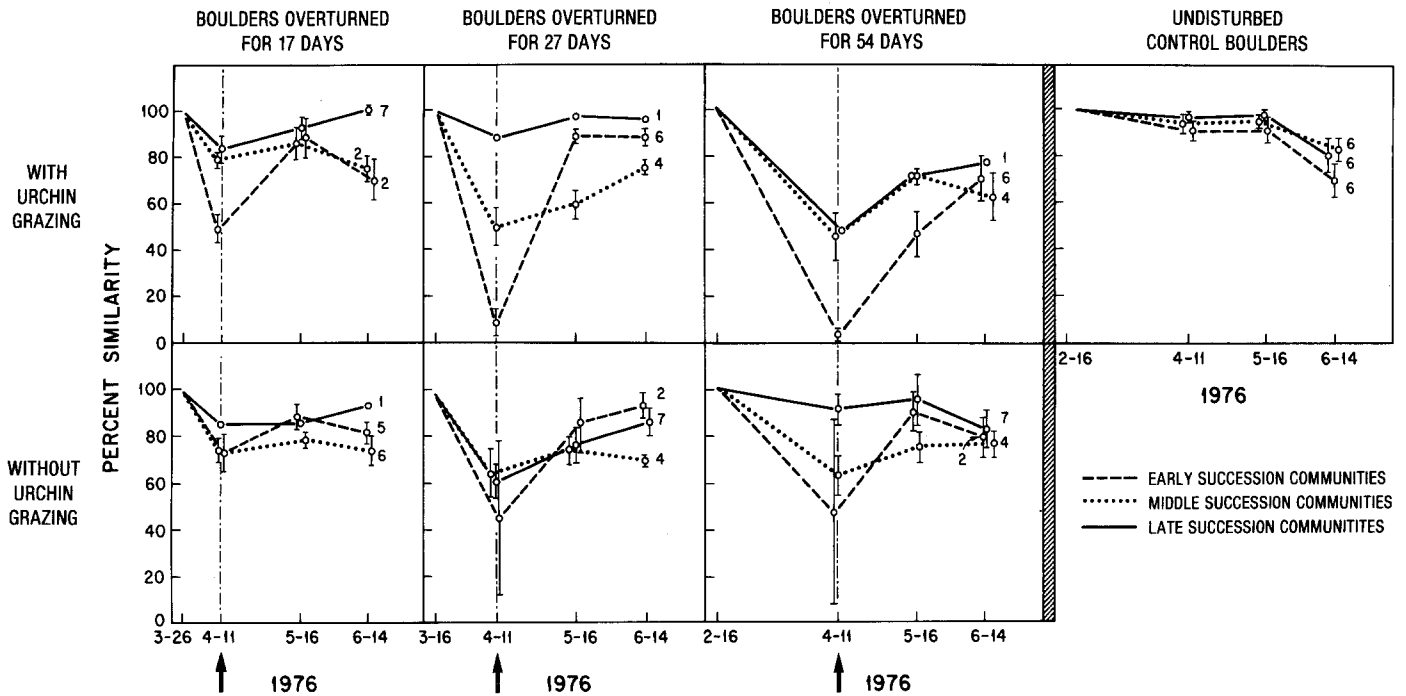
Fig. 1. Mean percent similarity of boulders with early, middle and late successional algal communities to their original composition after being overturned in areas with and without sea urchins for 17, 27, or 54 days, then righted. Sets of boulders were overturned on 2-16-76, 3-16-76, and 3-26-76 and all were righted on 4-11-76 as indicated by arrows. Control boulders of each successional stage were monitored for the duration of the experiment. Numbers of replicate boulders in each treatment are indicated to the right of the data points plotted for 6-14-76. Percent covers of the species on each boulder were estimated on the date boulders were overturned and on 4-11-76, 5-16-76, and 6-14-76. Variance is presented as ± one standard error of the mean

Table 5. The effects of stage of succession, sea urchin grazing, and length of time a boulder was overturned on the percent similarity of the community on the boulder to its original composition, immediately after being righted. Test is a three-way analysis of variance (fixed model). Because the design is not orthogonal, the sums of squares of the main effects and two-way interactions do not sum to the corresponding sub-totals for each category (Nie et al., 1975)

Source of variation	Sum of squares	df	Mean square	F	Probability
Main effects	19,684.94	5	3,936.99	25.60	0.001
Stage of succession	5,962.27	2	2,981.13	19.38	0.001
Urchin grazing	2,492.44	1	2,492.44	16.21	0.001
Time overturned	4,761.34	2	2,380.67	15.48	0.001
Two-way interactions	2,484.38	8	310.55	2.02	0.061
Stage-Urchin	596.73	2	298.37	1.94	0.150
Stage-Time	212.94	4	53.23	0.35	0.999
Urchin-Time	594.98	2	297.49	1.93	0.152
Three-way interactions	977.66	4	244.42	1.59	0.190
Stage-Urchin-Time	977.66	4	244.42	1.59	0.190
Explained	23,146.99	17	1,361.59	8.85	0.001
Residual	8,150.65	53	153.79		
Total	31,297.64	70	447.11		

Table 6. The effects of sea urchin grazing, length of time a boulder is overturned, and species of algae on the percent decrease in cover of individual species of algae on the tops of boulders. Test is a three-way analysis of covariance (fixed model) with initial percent cover entered as a covariate. Because the design is not orthogonal, the sums of squares of the main effects and two-way interactions do not sum to the corresponding sub-totals for each category (Nie et al., 1975)

Source of variation	Sum of squares	df	Mean square	F	Probability
Covariates	82.99	1	82.99	0.16	0.999
Initial cover	82.99	1	82.99	0.16	0.999
Main effects	58,345.62	6	9,724.27	18.54	0.001
Urchin grazing	4,412.40	1	4,412.40	8.41	0.005
Time overturned	19,311.16	2	9,655.58	18.41	0.001
Species of algae	18,562.92	3	6,187.64	11.80	0.001
Two-way interactions	5,479.34	10	547.93	1.04	0.412
Urchin-Time	1,283.68	2	641.84	1.22	0.298
Urchin-Species	1,349.19	3	449.73	0.86	0.999
Time-Species	1,976.40	5	395.28	0.75	0.999
Three-way interactions	3,904.68	5	780.94	1.49	0.199
Urchin-Time-Species	3,904.70	5	780.94	1.49	0.199
Explained	67,812.63	22	3,082.39	5.88	0.001
Residual	54,535.12	104	524.38		
Total	122,347.75	126	971.01		

Table 7. Responses of different species of algae to various intensities of disturbance. Data are mean values of the dependent variable for all levels of significant factors in the analyses of covariance presented in Tables 6 and 8. Means are unadjusted for covariates. Species of algae are *Ulva* spp., *Gigartina canaliculata* (G. c.), *Gigartina leptorhynchos* (G. l.), and *Gelidium coulteri* (Ge. c.).

Dependent variable:	Percent decrease in cover of individual species of algae			Percent reestablishment of cover lost due to overturning			
Significant factor	Level	N	Unadjusted mean	Significant factor	Level	N	Unadjusted mean
Urchin grazing	With	60	76.9	Species of algae	Ulva	33	77.1
	Without	67	34.4		G.c.	38	54.7
					G.l.	24	32.6
Length of time boulder	17	43	19.0		Ge.c.	5	24.9
was overturned (days)	27	37	65.7				
	54	47	79.5				
Species of algae	Ulva	33	59.7				
	G.c.	38	25.2				
	G.l.	24	86.1				
	Ge.c.	5	33.7				

Table 8. The effects of sea urchin grazing, length of time a boulder is overturned, and species of algae on the percent reestablishment by individual species of algae, of cover lost due to experimentally-applied disturbance. Test is a three-way analysis of covariance (fixed model) with initial percent cover loss entered as a covariate. Because the design is not orthogonal, the sums of squares of the main effects and two-way interactions do not sum to the corresponding sub-totals for each category (Nie et al., 1975)

Source of variation	Sum of squares	df	Mean square	F	Probability
Covariates	615.42	1	615.42	1.07	0.304
Initial cover loss	615.42	1	615.42	1.07	0.304
Main effects	26,923.49	6	4,487.25	7.82	0.001
Urchin grazing	54.84	1	54.84	0.10	0.999
Time overturned	1,512.24	2	756.12	1.32	0.273
Species of algae	24,417.58	3	8,139.19	14.18	0.001
Two-way interactions	20,226.54	9	2,247.39	3.91	0.001
Urchin-Time	1,312.48	2	656.24	1.14	0.325
Urchin-Species	11,877.43	3	3,959.14	6.90	0.001
Time-Species	9,411.32	4	2,352.83	4.10	0.005
Three-way interactions	2,839.37	4	709.84	1.24	0.302
Urchin-Time-Species	2,839.37	4	709.84	1.24	0.302
Explained	50,604.82	20	2,530.24	4.41	0.001
Residual	45,356.05	79	574.13		
Total	95,960.87	99	969.30		

Table 9. Effect of sea urchins on the percent reestablishment of cover lost by individual species of algae in the first 35 days following the disturbance. Data are means unadjusted for covariates. Parentheses enclose one standard deviation of the mean

Species of algae	Percent reestablishment after being overturned			
	With urchins		Without urchins	
	N	%	N	%
Ulva spp.	19	76.3 (32.8)	14	78.1 (34.0)
Gigartina canaliculata	18	58.3 (35.8)	20	51.5 (30.7)
Gigartina leptorhynchos	13	18.3 (26.4)	11	49.6 (40.3)
Gelidium coulteri	4	6.1 (7.2)	1	100.0

Responses of Individual Species to Perturbation

Sea urchin grazing and increased periods of overturning strongly affected the loss of cover of individual algal species (Tables 6 and 7). All four algal species suffered a greater loss of cover in the presence of sea urchins. The lack of a significant urchin-algal species interaction term in the analysis indicates that the effect of sea urchin grazing was not species-specific; that is, no species was more heavily fed upon than another. This result was not unexpected since urchins did not demonstrate any strong preference when simultaneously offered all four species in equal quantities in the lab (Sousa, 1977). The loss of cover by all four species was also greater the longer a boulder was overturned. As with sea urchin grazing, this effect was not species-specific (i.e., there is no significant time-species interaction term in Table 6).

sional communities as is reflected in the slopes of the percent similarity between 4-11-76 and 5-16-76 (Fig. 1). Early communities have a steeper ascending slope in all cells of the design except when boulders were subjected to urchin grazing for 54 days. There was essentially no difference between the rates of recovery of middle and late successional communities.

Table 10. Effect of length of time that a boulder is overturned on the percent reestablishment of cover lost by individual species of algae in the first 35 days following the disturbance. Data are means for the three experimental time periods, unadjusted for covariates. Parentheses enclose one standard deviation of the mean

| Species of algae | Percent reestablishment after being overturned for |
| | 17 days | | 27 days | | 54 days | |
	N	%	N	%	N	%
Ulva spp.	1	100.0	9	91.8 (15.6)	16	57.2 (36.4)
Gigartina canaliculata	9	51.7 (35.8)	24	69.7 (31.7)	14	54.7 (34.8)
Gigartina leptorhynchos	7	25.9 (38.1)	8	32.3 (37.9)	9	38.2 (37.3)
Gelidium coulteri	no data		no data		5	24.9 (42.5)

In addition to the expected urchin and time effects, there was a significant difference in the susceptibility of the four species of algae to damage by boulder overturning. The middle successional species *G. leptorhynchos* suffered the greatest loss of cover (Table 7). The early species, *Ulva*, suffered somewhat less. The least damage was done to the middle successional *Gelidium* and the late successional *G. canaliculata*, both having approximately equal mean losses of percent cover.

The relative ranking of the species in terms of percent recovery was somewhat different. There was a significant difference in the mean percent recovery of lost cover by the 4 species (Table 8). Within the first 35 days after being disturbed, *Ulva* regenerated

77.1% of its lost cover either by regrowth of damaged individuals or recruitment of new plants (Table 7). The late successional species, *G. canaliculata*, vegetatively replaced nearly 55% of its lost cover while the two middle successional species, *Gelidium* and *G. leptorhynchos*, vegetatively regenerated about half as much. All three species of perennial red algae regrew vegetatively from surviving holdfasts or possibly from dormant spores since they were not settling during this period (Sousa, 1979). Their holdfasts are very persistent. Even if all the branches on a plant are lost, the holdfast remains viable and can regrow lost branches for a long period of time. Plants frequently regrow even after the branches are burned off with a propane torch.

The effects of urchin grazing and increased period of overturning on the regrowth of lost cover were species-specific (Table 8). Urchin grazing reduced the percent reestablishment of the middle successional species, *G. leptorhynchos* and *Gelidium*, while having no effect on the recovery of *Ulva* or *G. canaliculata* (Table 9). Apparently, the holdfasts of the former two species are more severely damaged by urchin grazing than are those of the latter two. The length of time that a boulder was overturned had no effect on the percent reestablishment of the perennial red algae, *G. leptorhynchos* or *G. canaliculata* but the percent recovery of *Ulva* declined as the length of time a boulder was overturned was increased (Table 10). A 54-day period appears to be sufficiently long to cause mortality of whole plants of this species. Shorter periods cause tissue damage, but plants survive and quickly regenerate. Data for *Gelidium* were too scanty to determine whether the different durations of disturbance influenced its ability to regenerate.

There were sufficient data for two of the species to compare their individual responses as members of differently-aged assemblages (Table 11). *Ulva* lost proportionately less cover as a member of a middle successional assemblage when subjected to a 17- or 27-day perturbation. However, the composition of the surrounding vegetation had no effect on its loss of cover due to a more extreme 54-day disturbance. The successional stage of the assemblage had no influence on the rate of *Ulva's* recovery from a disturbance

Table 11. Responses of *Ulva* and *Gigartina canaliculata* to disturbance as members of different successional stages. Data are the mean values of the indicated response. One standard deviation of the mean is enclosed in parentheses. A dash indicates insufficient data

| Species of algae | Response | Days over-turned | \multicolumn{3}{c}{Successional stage} | | Exact Mann-Whitney U probability |
			Early	Middle	Late	
Ulva	A. Percent decrease in cover	54	88.5 (26.4)	79.7 (18.8)	—	0.097
		27	87.6 (22.2)	42.2 (42.2)	—	0.047
		17	46.0 (24.2)	15.5 (19.2)	—	0.027
	B. Percent reestablishment of lost cover in first 35 days after disturbance	54	47.0 (31.6)	67.4 (40.1)	—	0.164
		27	90.8 (16.4)	66.6 (47.2)	—	0.362
		17	100.0 (0.0)	100.0 (0.0)	—	0.538
Gigartina canaliculata	A. Percent decrease in cover	54	—	57.0 (41.0)	58.6 (28.0)	0.221
		27	—	52.4 (25.5)	48.4 (22.0)	0.221
		17	—	15.7 (20.4)	20.4 (18.1)	0.323
	B. Percent reestablishment of lost cover in first 35 days after disturbance	54	—	44.8 (29.7)	64.7 (38.8)	0.267
		27	—	48.4 (22.0)	69.3 (24.1)	0.095
		17	—	82.7 (32.2)	38.5 (36.0)	0.026

of any intensity. *Gigartina canaliculata* suffered the same percent loss of cover regardless of the successional stage of which it was a part. The same was true for its rate of recovery except following 17 days of overturning in which case its cover in a middle successional assemblage was reestablished more quickly than that in a late successional assemblage.

Discussion

The experimental evidence demonstrates that the successional stages of the producer level of an intertidal algal community differ significantly in their responses to disturbance. Early successional communities suffer more damage for a given level of perturbation but recover more quickly than either middle or late successional communities. Damage to any particular assemblage of algae, irrespective of successional age, is more extensive and recovery slower, the more intense the disturbance, that is, the longer a boulder is overturned and/or is in the presence of urchins which graze or abrade algae off the rock surface.

Over the range of disturbance intensities studied, all three assemblages recovered fairly completely due either to rapid colonization and growth of new plants from spores or regeneration from surviving portions of holdfasts. However, an important threshold in the response of an assemblage to disturbance, not identified quantitatively by this experiment, occurs when a boulder remains overturned for a period long enough (i.e., considerably longer than 2 months) that all individuals are killed, precluding vegetative regrowth. When this happens recovery may take a long time. Recruitment and growth of plants entirely from spores on bare surfaces set out for colonization in winter, leads to development of an early successional assemblage equivalent to the experimental one in approximately 5 months, an equivalent middle successional assemblage in about $2^{1}/_{2}$ years, and the equivalent late successional stage in a minimum of 4 years (Sousa, 1979).

In answer to the second question posed in the introduction, this study did not reveal any emergent properties of the assemblages which accounted for their responses to perturbation. The amount of damage suffered by the different successional stages and their rates of recovery seem entirely predictable from a knowledge of the responses of individual species. A rigorous test of this idea would require careful study of the responses of individual species to disturbance both in isolation and as members of different assemblages. The former information is difficult to obtain in a field study and is lacking for the species discussed here. However, even in instances where the response of a species was different when a member of different successional stages, emergent properties need not be invoked. *Ulva's* better survival on middle successional boulders overturned for 17 and 27 days is probably explained by its rarity in such communities as compared to early successional stages which it dominates (Table 1). Because of irregularities in the surface of boulders (e.g., pits, bumps, etc.) small patches of *Ulva* in middle successional stages may be proportionately less likely to come in contact with patches of anoxic sand, underlying rocks, or sea urchin spines when a boulder is overturned than is the extensive cover of *Ulva* on overturned early successional boulders. Consequently, if the intensity of the disturbance is low (i.e., 17 or 27 days) *Ulva* may suffer proportionately less loss of cover in middle successional communities. However, even small isolated patches of *Ulva* may not escape damage from an extreme disturbance. This may account for the lack of any statistically significant difference in the percent loss of cover by the

alga in different assemblages after 54 days of overturning. The cover of *Gigartina canaliculata* recovered more quickly from a 17 day disturbance in middle successional communities than in late successional communities. Again, this can be explained by the response of the individual species. If intraspecific competition for resources, particularly light, is more intense than interspecific, the regrowth of surviving *Gigartina canaliculata* branches may have been more inhibited by a surrounding late successional canopy composed predominantly of its own species (Table 1) than by the mixed species canopy of a middle successional assemblage. If the disturbance is intense enough (i.e., greater than 27 days) enough of its own canopy might be lost to eliminate any substantial difference in the recovery rates in different assemblages during the 35 days over which recovery was monitored.

If emergent properties are important in the successional processes documented for this community it seems surprising that the responses of individual species are not more strongly influenced by the successional stage of the community. Neither the recovery rate of *Ulva* nor the percent loss of *Gigartina canaliculata* canopy was affected by successional stage. Instead, the magnitudes of these responses seem almost entirely due to the evolved adaptations of the individual species to periodic damage caused by overturning of the substratum to which they are attached, sea urchin grazing, or qualitatively similar disturbances such as sand burial which is also common in parts of this habitat (Sousa, personal observation). Clearly, the ability of a species to regrow vegetatively from damaged tissues makes a tremendous difference to the rate at which lost cover is reestablished. The same is true for perennial red algae in the New England intertidal zone (Lubchenco and Menge, 1978; Lubchenco, 1979). The quantity and seasonality of spore production is also critical. *Ulva* recruits year-round and grows more rapidly than perennial red algae (Sousa, 1979; unpublished data) thus accounting for the more rapid recovery of early successional communities. Production of spores by red algae is much more seasonal. If all individuals are killed recovery takes a relatively long time.

Non-linearities or thresholds in the responses of communities to perturbations also seem attributable to thresholds in the resistance of their component species to damage caused by grazing or physical disturbance. This study has identified several such thresholds. Sea urchin grazing, when added to the disturbance of overturning, strongly reduces the recovery of lost cover by *Gigartina leptorhynchos* and *Gelidium coulteri*. Apparently this grazing and abrasion removes their holdfasts more completely than those of *Gigartina canaliculata* which recovers equally well with or without urchins. Similarly, long periods of overturning (i.e., 54 or more days) reduces the extent of recovery by *Ulva*. Presumably, this intensity of disturbance kills the entire plant preventing vegetative regrowth from surviving basal portions. A detailed study of the anatomy and physiology of the holdfasts of these plants might suggest the reasons for these differences in responses to urchin grazing and long periods of overturning.

This study has considered only two types of perturbation – sea urchin grazing and movement of the substratum to which plants are attached. These perturbations occur intermittently and more frequently in the winter. At other times algal assemblages must contend with other potential sources of change, particularly the invasion and growth of new species. Early successional communities are least resistant to invasion and late successional stages most resistant. This is because early successional species are more susceptible to mortality by grazers other than urchins and to physical stress (Sousa, 1979). As they are killed, individuals of longer-lived species invade and replace them.

In summary, early successional comunities dominated by green algae are least resistant to change because their component species are more susceptible than are the perennial red algae of later successional stages to damage caused by the particular perturbation examined in this study. Early successional species are also more susceptible to mortality caused by grazes other than sea urchins and to desiccation stress and therefore are replaced by the latter species in a successional sequence. However, populations of early successional species recover very rapidly from large disturbances because they produce many propagules, disperse them widely, and grow rapidly in open areas. Communities in a later stage of succession are composed of perennial species with persistent holdfasts which resist grazing and slight disturbances better than those of early species, but if a disturbance is very extreme, and kills all individuals, recovery is slow. The recovery of late successional communities is enhanced by grazing molluscs and crabs which prefer early successional species and by removing them accelerate the reestablishment of late successional species (Lubchenco and Menge, 1978; Sousa, 1979).

Similar conclusions regarding the individualistic nature of plant succession have been drawn by some early terrestrial plant ecologists (Gleason, 1926; Egler, 1954; Keever, 1950). Marks' (1974) more recent study of pin cherry population dynamics in northern hardwood forests also supports this view. However, some investigators continue to interpret successional change as an emergent property of the community. These divergent views are explained, in part, by differences in the focus of the studies of succession from which the views emerged. For example, the well-known Hubbard Brook study of hardwood forest succession has been investigating the mechanisms which act to reestablish steady-state nutrient cycling following deforestation (Bormann et al., 1974). This study has shown that the recovery of steady-state nutrient cycling is an emergent property of a suite of interdependent biotic and abiotic factors affecting the erodibility of the ecosystem and nutrient flux. However, the answer to the question of whether the recovery of the original species composition and relative abundance of species in the same forest is an emergent property of the assemblage seems to be different. As was shown for the algal community discussed in this paper, Marks' (1974) sketch of the temporal sequence of species replacements in northern hardwood forests, including the Hubbard Brook site, emphasizes the importance of the life history characteristics of individual species to successional change rather than emergent properties. Such characteristics include seed dormancy, seed dispersal, stump sprouting, and the ability of seedlings to withstand long periods of suppression in the understory. Of course, changes in species composition and ecosystem-level processes such as nutrient flow are not independent. Changes in the former can directly influence the latter and vice versa. The important point to be made is that the answer to the question of whether or not successional change is an emergent property depends on the characteristic under study.

References

Atsatt, P.R., O'Dowd, P.J.: Plant defense guilds. Science **193**, 24–29 (1976)

Bormann, F.H., Likens, G.E., Siccama, T.G., Pierce, R.S., Eaton, J.S.: The export of nutrients and recovery of stable conditions following deforestation at Hubbard Brook. Ecol. Monogr. **44**, 255–277 (1974)

Clements, F.E.: Plant succession: An analysis of the development of vegetation. Carnegie Inst. Washington. Publ. 142 (1916)

Colinvaux, P.A.: Introduction to ecology. New York: Wiley 1973

Connell, J.H.: Community interactions on marine rocky intertidal shores. Ann. Rev. Ecol. Syst. **3**, 169–192 (1972)

Connell, J.H., Slatyer, R.O.: Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. **111**, 1119–1144 (1977)

Dayton, P.K.: Experimental evaluation of ecological dominance in a rocky intertidal algal community. Ecol. Monogr. **45**, 137–159 (1975)

Drury, W.B., Nisbet, I.C.T.: Succession. J. Arnold Arboretum **54**, 331–368 (1973)

Egler, F.E.: Vegetation science concepts. I. Initial floristic composition – a factor in old-field vegetation development. Vegetatio **4**, 412–417 (1954)

Frank, P.W.: Life histories and community stability. Ecology **49**, 355–357 (1968)

Gleason, H.A.: The individualistic concept of the plant association. Bull. Torrey Bot. Club **53**, 7–26 (1926)

Harrison, G.W.: Stability under environmental stress: resistance, resilience, persistence, and variability. Am. Nat. **113**, 659–669 (1979)

Holling, C.S.: Resilience and stability of ecological systems. Ann. Rev. Ecol. Syst. **4**, 1–23 (1973)

Horn, H.S.: The ecology of secondary succession. Ann. Rev. Ecol. Syst. **5**, 25–37 (1974)

Horn, H.S.: Succession. In: Theoretical ecology (R.M. May, ed.), pp. 187–204. Philadelphia: W.B. Saunders 1975

Keever, C.: Causes of succession in old fields of the Piedmont, North Carolina. Ecol. Monogr. **20**, 229–250 (1950)

Lubchenco, J.: Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. Am. Nat. **112**, 23–39 (1978)

Lubchenco, J.: Algal zonation in the New England rocky intertidal community: an experimental analysis. Submitted to Ecology (1979)

Lubchenco, J., Menge, B.A.: Community development and persistence in a low rocky intertidal zone. Ecol. Monogr. **59**, 67–94 (1978)

Margalef, R.: Perspectives in ecological theory. Chicago: Univ. of Chicago Press 1968

Margalef, R.: Diversity and stability: a practical proposal and a model of interdependence. In: Diversity and stability in ecological systems, pp. 25–37. Brookhaven Symp. Biol. no. 22 (1969)

Marks, P.L.: The role of the pin cherry (*Prunus pensylvanica* L.) in the maintenance of stability in northern hardwood ecosystems. Ecol. Monogr. **44**, 73–88 (1974)

Nie, N.H., Hull, C.H., Jenkins, J.G., Steinbrenner, K., Bent,

D.H.: Statistical package for the social sciences, 2nd edition. New York: McGraw-Hill 1975

Odum, E.P.: The strategy of ecosystem development. Science **164**, 262–270 (1975)

Orians, G.H.: Diversity, stability and maturity in natural ecosystems. In: Unifying concepts in ecology (W.H. van Dobben and R.H. Lowe-McConnell, eds.), pp. 139–150. The Hague (Netherlands): Junk 1974

Paine, R.T.: Controlled manipulations in the marine intertidal zone, and their contributions to ecological theory. In: The changing scenes in natural sciences, 1776–1976. Acad. Natural Sci. Special publ. **12**, 245–270 (1977)

Paine, R.T., Vadas, R.L.: The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. Limnol. Oceanogr. **14**, 710–719 (1969)

Salt, G.W.: A comment on the use of the term emergent properties. Am. Nat. **113**, 145–148 (1979)

Sokal, R.R., Rohlf, F.J.: Biometry. San Francisco: W.H. Freeman and Co. 1969

Sousa, W.P.: Disturbance and ecological succession in marine intertidal boulder fields. Ph.D. Thesis, Univ. California, Santa Barbara 1977

Sousa, W.P.: Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecol. Monogr. (in press, 1979)

Sousa, W.P.: Disturbance in marine intertidal boulder fields: the non-equilibrium maintenance of species diversity. Ecology (in press, 1979a)

Whittaker, R.H.: Communities and ecosystems, 2nd edition. New York: MacMillan Publ. 1975