

# Disturbance and organisms on boulders

## II. Causes of patterns in diversity and abundance

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**Summary.** The tops of intertidal boulders on the east coast of Australia may carry a half-dozen algae, while the undersides may support a dozen or more species of sessile animals; mobile forms such as molluscs, crustaceans, and echinoderms are also common. These organisms are disturbed when boulders are moved by waves or buried in sand. Experiments were done to test the hypothesis that these disturbances are responsible for the reduced diversity and abundance of the assemblages on the undersides of small boulders. Boulders on one shore were bolted to the substratum to prevent movement by waves. In two separate experiments on another shore, boulders with and without attached organisms were buried in a few centimetres of sand. All experiments included relevant controls and were done high and low on the shore using rocks of several sizes.

The assemblages of algae developing on the tops of all stabilised boulders, regardless of size, were similar to those on boulders free to roll indicating that, in contrast to results elsewhere, disturbance by waves was too infrequent or slight to affect these species. The tops of rocks were also rarely buried in sand and the main influences on the community in this situation were apparently exposure at low-tide and grazing gastropods.

More species, however, did settle or survive on the undersides of rocks which were free of sand or could not be moved by waves; thus disturbances were important in this situation. In the absence of disturbance low on the shore, much or all space was occupied and sessile species such as sponges and ascidians overgrew other forms and reduced diversity. This did not happen higher on the shore and here diversity was simply an increasing function of rock-size. Overall disturbance played a similar role in all places – it killed organisms and created free space – but the final effects on the community varied depending upon the species present and the actions of other factors.

**Key words:** Intertidal communities on rocks – Disturbance – Community structure – Species richness

such as grazing and competition (Sousa 1979a; Littler and Littler 1981; Lieberman et al. 1984). Earlier workers only discussed the disturbance caused by waves moving the rock or by other wave-borne objects (Osman 1977; Sousa 1979a; Littler and Littler 1981, 1984; Lieberman et al. 1984). Another disturbance is common in rocky intertidal areas – sand – which may abrade or bury rocks (Taylor and Littler 1982; Turner 1983; McGuinness 1987), though this has been studied less frequently. The general conclusion of these studies is that these disturbances kill organisms and create free space for other organisms to occupy. However, moderate “intermediate” amounts of disturbance are often thought to increase the diversity of the community by preventing one or a few species from dominating resources (Connell 1978; Sousa 1979a, 1984).

In any case, despite the conclusions which have been drawn about particular disturbances, and about disturbance in general, few field tests of hypotheses have been made. Sousa (1979a) experimentally stabilised small boulders and did show that the assemblage which resulted was similar to that on less frequently disturbed, but unstabilised, large boulders. There has been little work beyond this other than a few laboratory tests of the effects of burial in sand (e.g. Brenchley 1981; Taylor and Littler 1982); other conclusions about disturbance in marine communities are based only on observational studies. There are now so many of these studies that the importance of disturbance as a process in marine communities is well known (Connell and Keough 1984; Dayton 1984; Sousa 1984). What is less clear is whether disturbance is always important, and whether it always interacts similarly in different places with the other factors affecting the community. The answers to these questions will determine the extent to which those models of community ecology including disturbance can be considered “general” explanations for community structure.

As Sousa (1979a) noted, the communities of organisms on intertidal boulders offer ideal opportunities for examining questions of this nature. The habitat can be unambiguously identified as the boulder. The structure of this habitat is probably less variable and more easily quantified than that of most others. In fact, since boulders are discrete and portable, the effects of differences in habitat structure, and their role in causing differences among places, can themselves be experimentally determined (McGuinness and Underwood 1986). Further, the potential importance of disturbance in this system is well established (Riedl 1964; Rutzler 1965; Osman 1977; Sousa 1979a, b, 1980; Littler

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Physical disturbance is now considered to be an important factor structuring many marine communities (Connell 1978; Paine and Levin 1981; Pickett and White 1984; Sousa 1984; Dayton 1984; Connell and Keough 1984). Indeed, it is usually thought to be the single most important process influencing the abundance and diversity of sessile organisms on intertidal boulders, overriding the effects of other factors

and Littler 1981, 1984; Lieberman et al. 1984), though patterns in the communities studied here suggest that it will only affect species on the undersides of boulders (McGuinness 1984a, 1987). Finally, many of the models of ecology, particularly those dealing with disturbance, are relevant to these communities (McGuinness 1984a, b, 1987) and have been applied to organisms on rocky shores (e.g. Connell 1972, 1975, 1978; Paine 1974; Menge and Sutherland 1976; Huston 1979; Sousa 1979a).

In summary, the aim of this work was to determine the effects of the two types of disturbance in a number of different situations (that is, on the tops and bottoms of boulders at different heights on different shores). The subsequent aim was to use these results to test existing models for the effects of disturbance and their validity as explanations for the structure of these communities. A final aim was to combine the conclusions of this work with those of other studies of communities on local shores (references cited later) to evaluate some of the so-called "general" models of ecology.

### Materials and methods

*Location and description of study sites.* Boulder fields low (0.2–0.3 m above Mean Low Water; the "low-shore" area) and high (0.6–0.9 m above MLW; the "high-shore" area) on the shore on two rock platforms near Sydney – Cape Banks and Long Reef – were studied (see also McGuinness 1984a, 1987; McGuinness and Underwood 1986). Boulders high on the shore were typically disturbed by waves more than those low on the shore, and boulders at Long Reef were disturbed by sand more than those at Cape Banks (McGuinness 1986a): this influenced the placement of experiments. Some experiments were done at two different sites within each area on a shore. These sites were patches of boulders five to ten m<sup>2</sup> in extent selected by haphazardly casting a marker into the boulder field (the "random sites" of McGuinness 1987). The bare, unoccupied boulders needed for some experiments were taken from above the high-water mark on each shore.

*Sampling of organisms on boulders.* The upper and lower sides of boulders were photographed with colour transparency film. The slides were examined under a binocular microscope for: (1) the identity of all macroscopic species (accurate identification of amphipods and spirorbids was not possible from slides and these were recorded as single species); (2) the percentage cover of sessile species; and (3) the density of each mobile species (except amphipods) and solitary sessile species (e.g. barnacles, spirorbids). Fifty random points superimposed on the slide were used to estimate percentage covers. Densities were estimated by a total count of all individuals on the rock, or by using five 4 × 4 cm or 2 × 2 cm quadrats (depending upon the abundance of the species). The surface-area of each rock was obtained from regressions of surface-area on the length and breadth of the rock (McGuinness 1984b). The surface-areas given here are only for one surface of the rock (upper or lower). See McGuinness (1984b, 1987) for further details of sampling methods.

*Experimental design and statistical analyses.* I used two different experimental designs. In one, there was only one rock of each size in each treatment, but abundances and diversity

covaried linearly with log of rock-size, and data were analysed by Analysis of Covariance (ANCOVA; see Huitema 1980; Winer 1971). The second design used equal numbers of replicate rocks of each size in each treatment; size of rock was explicitly included as a factor in the design, and data were analysed by Analysis of Variance (ANOVA; see Underwood 1981; Winer 1971). The first design had the advantage of allowing more sizes of rock to be included in an experiment for a given effort (that is, number of rocks), since replicates of each size were not needed. The major disadvantage of this design was ANCOVA's assumption of homogeneity of regression slopes. This assumption was violated by any difference among treatments (e.g. sides of the rock, areas or sites) in the slope of the relationship between abundance and rock-size, invalidating the analysis (Huitema 1980; Winer 1971). When this happened I used the rocks of each size from the two sites within each area as replicates in an ANOVA, though this meant that variation among sites could not be assessed. I transformed abundances or diversities (almost always as log) only if Cochran's test (Underwood 1981; Winer 1971) indicated that variances were heterogeneous.

If an ANOVA indicated significant treatment effects then means were compared using Student-Newman-Keuls (SNK) tests (Underwood 1981; Winer 1971). Similarly, Bryant-Paulson-Tukey (BPT) tests were used to compare adjusted means following ANCOVA. An adjusted treatment mean was just the mean abundance or diversity in the treatment, adjusted by the covariance relationship to the overall mean rock-size. This simply compensated for small differences among treatments in mean rock-size. These analyses are too numerous to report here in full but examples are given (Tables 4 and 5).

*Disturbance by sand.* The effects of sand on existing communities, and on communities developing from bare space, were examined in two separate experiments. The length of burial could be important for existing communities, with longer burials causing greater disturbance. This could, of course, also be true for developing communities. In addition the depth of burial might influence both the type of organisms arriving and the rate at which these accumulated. The two experiments were designed to investigate these different aspects of the disturbance. They were both done at Long Reef because there was consistently more sand on this shore. Sampling was kept to a minimum in these experiments in order to reduce the disturbance, to the rocks and the surrounding area, caused by digging.

*Experiment 1: Existing communities.* Three sets of five rocks were tagged in each of two sites in the high and low-shore areas at Long Reef. The rocks in each set, haphazardly selected from those in the site, included one replicate 20, 79, 177, 314 and 491 cm<sup>2</sup> in surface-area (representing 5, 10, 15, 20 and 25 cm in diameter: I used wire frames to find rocks of the required size). The three sets of rocks in the site were sampled, then two of the sets were buried about 1–3 cm in the sand; the remaining set was left on the sand as a control. Analyses showed that there were no significant differences at the start of this experiment among the three treatments in the mean number of algal, sessile animal or grazing species (Table 1).

The experiment was started on 26th March 1982 and first sampled after 13 days (8/vi/82). All buried rocks were

**Table 1.** Results of four-factor ANCOVA's on the number of species of grazers, algae and sessile animals on the tops and bottoms of boulders in two sites high and low on the shore; rocks were either unburied (control), buried for 132 days (short-burial) or buried for 236 days (long-burial)

Time (days)	Grazers				Algae				Sessile Animals			
	0	13	132	236	0	13	132	236	0	13	132	236
Source of Variation												
Treatment (T)	—	*	*	—	—	—	—	—	—	—	—	—
Area (A)	—	—	—	—	*	*	*	*	*	*	*	*
Side (Sd)	*	*	—	*	*	*	—	—	*	*	*	*
Site (St)	—	*	—	—	*	—	*	—	—	*	—	—
T × A	—	—	—	—	—	—	*	—	—	—	—	—
T × Sd	—	*	—	—	—	—	—	—	—	—	—	—
T × St	—	—	—	—	—	—	*	—	—	—	—	—
A × Sd	—	—	—	—	—	*	—	—	*	*	—	*
Sd × St	—	—	*	—	—	—	*	—	—	—	—	—
T × A × St	—	—	—	—	—	—	*	—	—	—	—	*
T × Sd × St	—	—	*	—	—	—	*	—	—	—	—	—

\* indicates that the factor or interaction was significant (at  $P < 0.05$ )

— indicates that it was not (sources of variation that were not significant are not listed)

dug up at this time but only one of the sets in each site and area was reburied ("long-burial" treatment). The other set was left on the sand to recover from the disturbance ("short-burial" treatment). The rocks were sampled again after a further 119 days (5/viii/82), but none was reburied; all were left to recover. Further samples were taken after 104 days (17/xi/82) and 370 days (10/vii/83). Very few of the rocks were found at the last time.

*Experiment 2: Developing communities.* Two sites in each area were again selected. Since the experiment was to test the hypothesis that sand affected the rate and type of organisms arriving, I tagged bare rocks (from above the high-water mark) and moved them into the sites. In anticipation of losses I used additional replicates of the smaller rocks. Thus, there were eight rocks in each treatment: three 20 cm<sup>2</sup>, two 79 cm<sup>2</sup>, and one each of 177, 314 and 491 cm<sup>2</sup>. The treatments were:

1. Fully-buried – rocks buried 1–3 cm below the sand (as in Experiment 1);
2. Half-buried – rocks with the undersurface completely buried but the uppersurface free of sand; and
3. Unburied – control rocks lying on the sand.

The experiment was set up on the 3rd September 1982 and sampled after 75 days (17/vi/82) and an additional 266 days (10/viii/83). Rocks were returned to their original position (that is, fully-buried, half-buried or unburied) after sampling.

*Disturbance by waves.* The sand at Long Reef made it difficult to secure rocks in place so the effects of movement of rocks by waves were examined high and low on the shore at Cape Banks. Bare rocks of three sizes were used: small (mean size = 127 cm<sup>2</sup>, 95% Confidence Limits = 16 cm<sup>2</sup>), medium (mean size = 314 cm<sup>2</sup>, 95% CL = 80 cm<sup>2</sup>) and large (mean size = 789 cm<sup>2</sup>, 95% CL = 95 cm<sup>2</sup>). Four replicate rocks of each size were used in each of three treatments:

1. Fixed – a 10 mm hole was drilled through the centre of the rock and a 6 mm diameter bolt was passed through this hole and into a "Ramset" nut secured in the platform;

2. Bolt – the rock was treated as above but the bolt was simply fastened with a nut and the rock left free to move (this controlled for effects due to the hole and/or the bolt); and

3. Free – the rock was not manipulated.

All rocks were tagged on the top and bottom, with four replicates of each treatment in the high and low shore areas. The experiment was started on the 28th January 1983 but two days later a storm caused much damage and I was forced to add extra replicates to each treatment. I had planned to sample the rocks every three months but found it impossible to raise the fixed rocks (to view the underside) without the risk of either breaking the rock or being unable to secure it in place again. Accordingly, the experiment was sampled only once – after 223 days (8/ix/83) – and this was delayed as long as possible (severe storms were predicted shortly thereafter).

## Results

### *Effects of disturbance by sand*

*Experiment 1: Existing communities.* The number of grazing species on the rock was affected by burial after only 13 days (Table 1): more species were present on the bottoms of unburied rocks than in any other situation (Table 2). After 132 days there were few grazers present on any of the long-buried rocks (Table 2). The unburied (control) rocks tended to have most species, but there was often a similar number present on short-burial rocks (Table 2). Short-burial rocks were like unburied rocks at some sites but like long-buried rocks at others.

Algae were not affected until 132 days (Table 1). Overall, unburied and short-burial rocks had more species than long-burial rocks, though the difference was not always significant (by BPT tests). This difference did vary between the sides of the rock and the two sites within each area (Table 2). Low on the shore, short-burial rocks had the same number of species as unburied rocks at one site, but at the other short-burial rocks were similar to long-burial

**Table 2.** Results of BPT-tests on significant effects of treatments on number of species on boulders: U=unburied (control); S=short-burial; L=long-burial. The values given are untransformed, adjusted mean numbers of species on boulders about 250 cm<sup>2</sup>

	Top			Bottom		
	U	S	L	U	S	L
<b>Grazers</b>						
0 High	0.1	0.2	0.4	0.3	0.4	0.2
Low	1.2	1.1	1.6	1.3	1.8	1.8
13 High and Low	0.2	0.5	0.3	2.0	0.4	0.4
132 High site 1	1.6	0.3	0.3	0.3	0.6	0.0
site 2	0.0	0.3	0.0	1.9	0.6	0.0
Low site 1	0.8	0.8	0.0	0.6	0.3	0.0
site 2	0.6	0.4	0.0	1.3	0.6	0.3
<b>Algae</b>						
0 High	0.9	1.5	1.1	0.6	0.7	0.4
Low	1.9	2.4	2.1	1.2	0.6	0.8
132 High site 1	1.4	2.4	0.3	0.9	1.7	0.0
site 2	0.9	1.3	1.5	0.5	0.3	0.0
Low site 1	5.4	4.8	2.5	2.9	1.1	0.5
site 2	5.6	0.3	0.0	2.1	3.4	0.9
<b>Sessile Animals</b>						
0 High	0.4	0.3	0.6	1.3	0.9	1.4
Low	0.1	0.3	0.3	4.0	4.8	3.5
236 High	0.3	0.2	0.0	1.5	0.0	0.7
Low	1.2	0.5	0.4	3.4	4.8	3.6

Means connected by a line were not significantly different (at  $P=0.05$ ). Note that there were no significant differences among treatments at time 0; these values are included only for comparison

rocks. These differences among treatments disappeared by 236 days (Table 1).

Two foliose algae, *Ulva lactuca* and *Polysiphonia sp.*, were common low on the shore. There was no relationship between the abundance of either alga and the size of the

rock but both were affected by burial (Table 3). After 13 days the cover of *Polysiphonia* was much greater on unburied rocks (mean=25%) than on rocks in the other treatments (means=5% and 1%), but it subsequently declined in abundance at one site and became rare on rocks in all treatments. *Ulva* was affected after 132 days: it was equally abundant on unburied and short-burial rocks (both means=16%) but sparse on long-buried rocks (mean=1%). After 236 days it was equally abundant on unburied and short-burial rocks at both sites, but less abundant on long-buried rocks at one site, and most abundant on rocks in this treatment at the other site – this latter result simply indicates that the effects of burial were not permanent.

The number of species of sessile animals on boulders was not affected until 236 days, by which time short-burial rocks had been recovering for 223 days and long-burial rocks for 104 days (Table 1). The tops and bottoms of unburied rocks high on the shore, and the tops of unburied rocks low on the shore, had more species than rocks in other treatments, but these differences were not detected as significant (by BPT tests; Table 2).

*Experiment 2: Developing communities.* Few algae and sessile animals settled onto these rocks and so these organisms were grouped together for analyses as “sessile species”. The number of sessile species on rocks in the treatments was related to the size of the rock at both 75 days (combined  $r$  from ANCOVA=0.43,  $df=96$ ,  $P<0.01$ ) and 341 days (combined  $r$  from ANCOVA=0.46,  $df=72$ ,  $P<0.01$ ) but the slopes of the regressions were not the same at either time ( $F$  at 75 days=3.72,  $df=23$  and 96,  $P<0.001$ ,  $F$  at 341 days=2.06,  $df=23$  and 72,  $P<0.025$ ). Thus, simple interpretations of the adjusted means were not possible. Instead, rocks of each size from the two sites within each area were used as replicates in an ANOVA including “size of rock” as a factor.

There were highly significant effects of the treatments after 75 days which persisted through to 341 days (Fig. 1; Table 4). At 75 days fully-buried rocks had fewest sessile species and unburied rocks had most. As usual, the number of species was influenced by area on the shore and size of rock. The effects of area on the shore were straightforward: there were simply more species low on the shore. Interactions with rock-size were more complex. Few species settled or survived on any small rocks and only at the larger sizes ( $>=177$  cm<sup>2</sup>) did treatments differ (see also Fig. 1). This was generally the case in this experiment and was the reason for the significant differences in the slopes of regressions observed above. Results at 341 days were similar but the differences among treatments were much greater low on the shore, with means ranging from 0 to 7.5, than high on the shore where the range was only 0 to 1.5 (Fig. 1).

**Table 3.** Two-factor analyses of variance on percentage cover of three species of algae on the tops of boulders low on the shore. Notation as in Table 1

Time	<i>Ulva</i>				<i>Polysiphonia</i>				<i>Ralfsia</i>			
	0	13	132	236	0	13	132	236	0	13	132	236
Treatment	—	—	*	—	—	*	*	*	—	—	—	—
Site	—	—	—	—	—	—	*	*	—	—	*	—
T × St	—	—	—	*	—	—	*	—	—	—	—	—

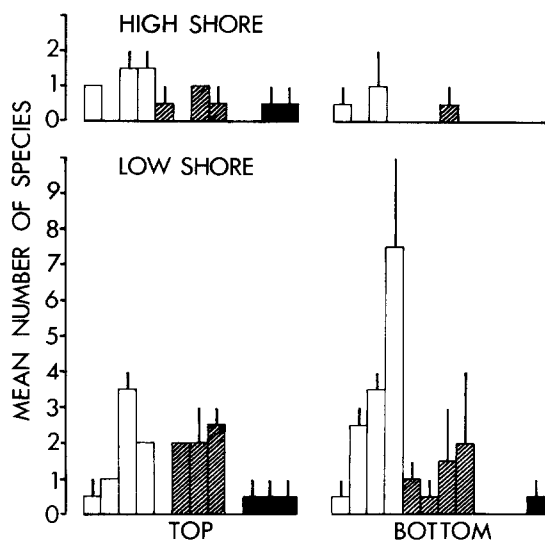


Fig. 1. Mean number of species recruiting to control (open bars), half-buried (hatched bars) and fully-buried (filled bars) rocks of four sizes (20, 79, 314 and 491 cm<sup>2</sup>, left to right) after 341 days. The lines above each bar give one standard error

Only three sessile species became very abundant – *Ulva*, *Galeolaria* and the spirorbids. The percentage cover of *Ulva* on the tops of rocks was influenced at 75 and 341 days by sand (Table 5). Fully-buried rocks high and low on the shore had, as might be expected, no cover of algae but a similar cover developed on rocks in the other two treatments (mean = 23%). Overall there was much greater cover low on the shore. A similar pattern was seen after 341 days but by this time all three treatments differed, with fully-buried rocks again having little cover (0.3%), half-buried somewhat more (23%) and unburied most (35%). These differences were again more pronounced low on the shore.

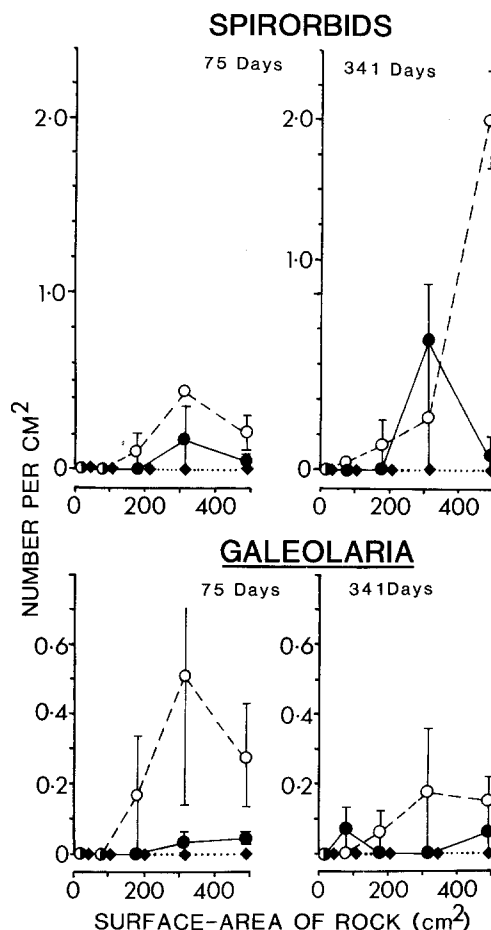


Fig. 2. The density of *Galeolaria* and the spirorbids on the undersides of control (open circles), half-buried (closed circles) and fully-buried rocks (diamond) after 75 and 341 days. The bars give plus and minus one standard error

Table 4. Four-factor ANOVA's on the numbers of sessile species (animals and algae) settling onto the tops and bottoms of unburied, half-buried and fully-buried rocks of five sizes high and low on the shore

	Sums of Squares		DF		F-Ratio	
	75	341	75	341	75	341
Treatment	7.47	6.41	2	2	27.79***	26.14***
Area	3.11	4.33	1	1	31.64***	35.37***
Side	0.21	0.49	1	1	2.16	3.98
Size	4.27	3.91	4	3	10.84***	10.63***
T × A	0.72	1.49	2	2	3.72	6.08**
T × Sd	0.58	0.25	2	2	2.98	1.02
T × Sz	2.10	0.86	8	6	2.66*	1.17
A × Sd	0.01	0.43	1	1	0.11	3.52
A × Sz	0.76	2.33	4	3	1.93	6.34***
Sd × Sz	0.52	0.19	4	3	1.31	0.51
T × A × Sd	0.01	0.80	2	2	0.03	1.28
T × A × Sz	1.61	0.89	8	6	2.05	1.21
T × Sd × Sz	1.04	0.39	8	6	1.32	0.52
A × Sd × Sz	1.03	0.77	8	6	5.22**	2.08
T × A × Sd × Sz	1.64	0.72	8	6	2.08	0.98
Residual	5.91	5.89	60	48		
Total	30.99	30.15	119	95		

Note variances non-homogeneous at 75 days (Cochran's value:  $0.05 > P > 0.01$ ); degrees of freedom reduced at 341 days because data for one size of rock were not available

**Table 5.** Analyses of percentage cover of *Ulva* on the tops (high and low on the shore), and density of *Galeolaria* and the spirorbids on the bottoms (low on the shore), of unburied, half-buried or fully-buried rocks after 75 and 341 days. The values given are sums of squares and degrees of freedom; the latter are reduced at 341 days because replicates of one size of rock were not available. The data for *Ulva* at 341 days were arc-sin transformed

Time (days)	Top				Bottom					
	75		341		75			341		
	<i>Ulva</i>				spirorbids <i>Galeolaria</i>			spirorbids <i>Galeolaria</i>		
Treatment	7,449*	2	47*	2	0.09*	0.0021*	2	0.77*	0.0026	2
Area	2,621*	1	26*	1						
Size	3,287*	4	19*	3	0.13*	0.0013*	4	0.68	0.0018	3
T × A	1,358*	2	11*	2						
T × S	2,503*	8	11	6	0.10	0.0021*	8	1.02	0.0041	6
A × S	624	4	6	3						
T × A × S	940	8	5	6						
Residual	3,671	30	26	24	0.08	0.0036	15	0.21	0.0084	12
Total	22,453	59	151	47	0.40	0.0091	29	2.68	0.0169	23

\* =  $P < 0.05$

**Table 6.** Results of four-factor ANOVA's on the numbers of species of grazers on the tops and bottoms of unburied, half-buried and fully-buried rocks high and low on the shore after 75 and 341 days. The values in the left-hand columns are the percentage of the variation (given in parentheses at the bottom of the table) due to each factor

	Sums of Squares		DOF		F-Ratio	
	75	341			75	341
	Treatment	14.2			7.4	2
Area	0.4	11.0	1	1.01	26.27*	
Side	1.4	1.0	1	3.71	2.27	
Size	16.0	26.5	4	10.92*	5.18*	
T × A	2.1	5.6	2	2.87	6.64*	
T × Sd	2.9	5.1	2	3.91	16.09*	
T × Sz	26.9	3.9	8	9.12*	1.55	
A × Sd	0.0	0.4	1	0.00	0.82	
A × Sz	1.9	7.5	4	1.27	5.91*	
Sd × Sz	0.7	1.0	4	0.49	0.82	
T × A × Sd	1.1	3.0	2	1.52	3.55*	
T × A × Sz	2.4	5.7	8	0.81	2.27	
T × Sd × Sz	5.2	8.0	8	1.77	3.18*	
A × Sd × Sz	1.9	2.3	4	1.29	0.89	
T × A × Sd × Sz	0.9	11.4	8	0.31	4.51*	
Residual	22.0	20.2	60	48		
Total	100.0	100.0	119	95		
	(15.79)	(27.24)				

*Galeolaria* and the spirorbids were only abundant on the bottoms of rocks in the low-shore area. At 75 days both species were more abundant on unburied rocks (Fig. 2; Table 5). *Galeolaria* declined in abundance and by 341 days there were no differences among treatments. The spirorbids continued to be more abundant on the larger unburied rocks.

Similar analyses were done on the number of grazing species (Table 6). At 75 days all rocks had few grazing species but there were significantly more on the larger ( $> = 314 \text{ cm}^2$ ) unburied rocks (mean = 1.5) than in the other two treatments (means = 0.12). After 341 days there were differences among areas in results. All rocks high on the shore, and the tops of rocks low on the shore, had a similar number of species (mean = 0.16). There were again more species on the bottoms of large, unburied rocks low on the shore (mean = 2.0).

*Disturbance by waves.* Only two medium and two large fixed rocks survived low on the shore and so analyses used this number of replicates (two rocks were picked at random from those available), despite the fact that up to six rocks were present in other treatments. Furthermore, many of the bolts worked loose from the bolt-control rocks creating, in essence, a fourth treatment – rocks with a hole but no bolt. There were, however, no differences in any of the measured variables between rocks with only a hole and those with a hole and a bolt (McGuinness 1984b). Nor were there any significant effects at all of the hole and/or bolt on the communities developing (Fig. 3).

There were, however, differences between the communities on fixed rocks and those in other treatments (Table 7). There were more species of grazers on the tops and bottoms of fixed rocks high on the shore: no such pattern resulted in the low-shore area (Fig. 3). A slightly different result

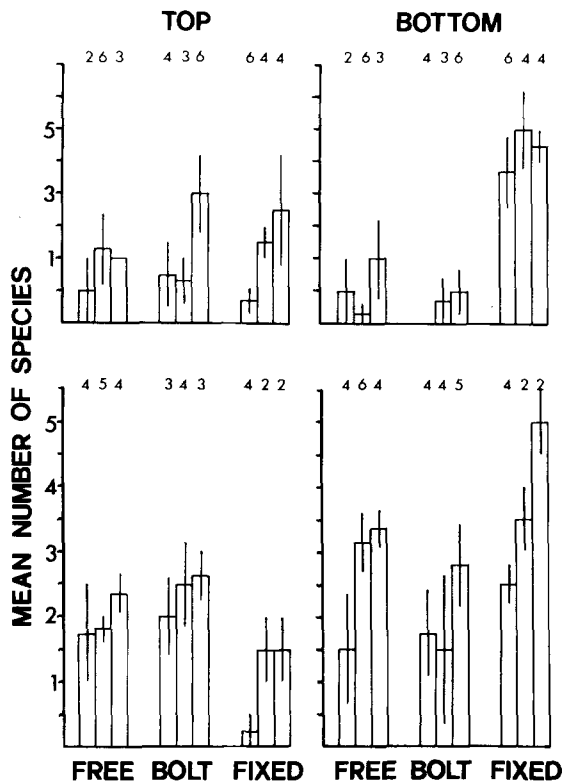


Fig. 3. Mean number of sessile species on free, bolt and fixed rocks of three sizes (127, 314 and 789 cm<sup>2</sup>, left to right) after 223 days. The upper two graphs are for the high-shore area; the bottom two are for the low-shore area. The lines above each bar give one standard error and the numbers the number of replicates

was seen with the sessile species (algae and sessile animals grouped together): there were more species on the bottoms of rocks in the fixed treatment than in other treatments but similar numbers on the tops of all the rocks (Fig. 3; Table 7). An important result of this experiment was that

species-area patterns developed for grazing and sessile species in all treatments, whether or not the rocks were fixed (Fig. 3; note the significance of the factor "size" in Table 7). Furthermore, the slope of the relationship between number of species and rock-size was not influenced by any of the treatments (note the lack of interactions between "treatments" and "size" in Table 7 indicating that the effect of size was the same for all treatments).

Four sessile animal species were commonly found on these rocks – the spirorbids, *Galeolaria caespitosa*, the barnacle *Tetraclitella purpurascens* and the anemone *Actinia tenebrosa*. Abundances were, however, very variable and the data could not be analysed by parametric techniques. Despite this, there was evidence that *Actinia*, *Galeolaria* and *Tetraclitella* were more abundant on fixed boulders, particularly high on the shore (Table 8; McGuinness 1984b). *Galeolaria* and *Actinia* were each most abundant on the fixed boulders in five of the six "area on shore × size of rock" combinations and the probability of this happening by chance alone (for each species) is only 0.018. In addition, in two of these situations for *Galeolaria*, and one for *Actinia*, the species was significantly more abundant on the fixed rocks by the Mann-Whitney-U test. *Tetraclitella* was also always more abundant on fixed rocks high on the shore, significantly so on medium and large rocks. Low on the shore, however, the barnacle was always most abundant on bolt rocks and the probability of this result occurring by chance alone was only 0.037: no explanation is offered for this result. The abundance of the spirorbids was extremely variable (e.g. values of 0, 2,480, 3,250 and 24,500 per m<sup>2</sup> on small stabilised rocks) and did not differ among treatments.

Three grazing gastropods were common – *Austrocochlea constricta*, *Nerita atramentosa* and the limpet *Cellana tramoserica* – and the latter two of these were affected by disturbance (McGuinness 1984b). *Nerita* was much more abundant on the undersides of fixed rocks high on the shore (mean = 41 per rock) than on free (mean = 14 per rock) or bolt-control rocks (mean = 2 per rock), but was unaffected

Table 7. Results of four-factor ANOVA's on the numbers of species of grazers and sessile organisms (animals and algae) settling onto the tops and bottoms of fixed, bolt and control rocks of four sizes high and low on the shore

	Sums of Squares		DOF	F-Ratio	
	Grazers	Sessile		Grazers	Sessile
Treatment	17.44	5.78	2	8.97*	2.81
Area	24.50	18.00	1	25.21*	17.51*
Side	3.56	5.56	1	3.66	5.41
Size	24.11	21.44	2	12.40*	10.43*
T × A	9.33	3.00	2	4.80*	1.46
T × Sd	1.44	24.11	2	0.74	11.73*
T × Sz	3.64	1.72	4	0.94	0.42
A × Sd	5.56	5.56	1	5.72*	5.41*
A × Sz	6.33	1.33	2	3.26*	0.65
Sd × Sz	2.11	0.78	2	1.09	0.38
T × A × Sd	1.78	0.44	2	0.91	0.22
T × A × Sz	2.08	1.17	4	0.54	0.29
T × Sd × Sz	1.64	2.06	4	0.42	0.50
A × Sd × Sz	0.11	4.78	4	0.06	2.32
T × A × Sd × Sz	1.31	5.72	4	0.34	1.39
Residual	35.00	37.00	36		
Total	139.94	138.45	71		

**Table 8.** Mean density (per m<sup>2</sup>) of four sessile animals on the undersides of free, bolt and fixed boulders. Values are pooled across the three sizes of rocks

	High			Low		
	Free	Bolt	Fixed	Free	Bolt	Fixed
<i>Actinia</i>	13	4	36	5	2	20
<i>Galeolaria</i>	0	0	140	340	320	480
<i>Tetraclitella</i>	200	47	1,220	253	780	107
spirorbids	0	0	0	10,427	4,033	8,450

by disturbance in other situations (overall mean = 4 per rock). *Cellana* was rare and equally abundant on all the small rocks (mean = 0.1 per rock), most abundant on medium-sized fixed rocks (mean = 2.1 per rock), and least abundant on rocks with a bolt (mean = 0.4 per rock). Finally, on large rocks *Cellana* was more abundant on fixed rocks (mean = 2.8 per rock) and those with a bolt (mean = 2.8 per rock) than on free rocks (mean = 1.5 per rock).

## Discussion

*Effects of disturbance.* Both types of disturbance were important to only some assemblages in these communities. Disturbance by waves did not effect the algae on the tops of rocks but did kill the sessile animals on the undersides. The latter effect was smaller low on the shore, probably because there was less disturbance in this area (McGuinness 1986a). Some grazing gastropods were also affected and this may have been a behavioural response to either the physical shifting of the boulder or to changes in the community. This has been seen before, notably in soft-bottom communities (Brenchley 1981; Thistle 1981; VanBlaricom 1982), and is suggested by the fact that not all grazers were affected similarly (see also McGuinness, unpublished work). Unfortunately, this experiment was too short to allow all the species normally present on the undersides to accumulate, or to determine whether the decline in diversity predicted by the Intermediate Disturbance Model would occur: most of the species which became abundant were "early-successional" forms (McGuinness 1984b, unpublished work).

Disturbance by sand was also important, retarding the development of the community and reducing the number and abundance of species in existing communities. Recruitment onto fully buried rocks was virtually zero but by the end of the experiment (after 341 days) normal communities had developed on unburied rocks; the usual foliose and encrusting algae, and polychaetes, bryozoans, ascidians and sponges were all present. The communities developing on half-buried rocks were intermediate between these extremes. All the algae were present, though in slightly smaller abundances than on unburied rocks – perhaps the result of minor shifts in the sand occasionally covering these rocks – but many of the species normally found on the undersides were never present. It is important to note that these comments apply only to the larger rocks, 177 cm<sup>2</sup> or greater. The small rocks in all treatments were equally depauperate. In retrospect this is not surprising since the difference among the three treatments in the extent to which rocks were buried in sand decreased with decreasing size (McGuinness 1987). On the basis of previous results, the small control

rocks could be expected to be buried to a greater extent and more frequently than the larger control rocks (McGuinness 1987), so at the smaller sizes the three treatments were effectively quite similar and no differences among them in the community would be expected.

The effects of sand on the number of sessile animal species took a long time to appear (more than 130 days). It was, however, difficult to tell when some of these organisms were actually dead. Many produced skeletons which persisted after the animal disintegrated and it was often impossible to determine whether an animal in a tube was dead from the state of the external covering. On normal, unburied rocks this was not a problem – the remains of species on these were degraded by the elements within a week. This could not happen on buried rocks so the experiment must have overestimated the time needed to kill some species. In fact, Brenchley (1981) found reductions in the abundance of a number of benthic species after only eight days of moderate burial and Taylor and Littler (1982) showed that more than 95% of the worm *Phragmatopoma californica* were killed by burial of only five days.

*Structure of the community.* Contrary to the conclusions of other workers (Osman 1977; Sousa 1979a, b, 1980; Littler and Littler 1981, 1984; Lieberman et al. 1984) disturbance by waves had no effect on the structure of the algal assemblage on the tops of boulders. Many of the differences between the results here and those of other studies are easy to understand once the biology of the organisms is considered. Of major importance to the assemblages studied by Sousa (1979a, b, 1980) was the overturning of rocks by waves. Once a rock had been overturned the foliose algae were removed by abrasion, deprivation of light and other effects of being on the wrong surface (Sousa 1979a). The dominant algae here, except on small rocks low on the shore at Long Reef, were thin encrusting species: *Hildenbrandia*, *Ralfsia* and a blue-green alga. These were tough, resistant to grazing, and probably also resistant to abrasion and light starvation (Andrew 1980; Underwood 1980; pers. obs.). In addition, these species grew part way underneath the rock. If a boulder was overturned, those parts of the plant then in the centre of the underside might die but the alga could "recolonise" by vegetatively regrowing from the edges of the rock up onto the top (see also Underwood 1980). The foliose, early-successional algae, *Ulva* and *Enteromorpha* sp., are much more susceptible to disturbance by waves (Sousa 1980) but are generally suppressed at Cape Banks by grazers (Underwood 1980; Underwood and Jernakoff 1981, 1984; Jernakoff 1983). At least one common grazer was not affected by disturbance by waves and most others were capable of quickly colonising or recolonising rocks (McGuinness, unpublished work), so the algae rarely "escaped" grazing to become abundant. When this did happen they grew very rapidly and could cover all the available space in twenty to thirty days (Underwood 1980; Underwood and Jernakoff 1984; McGuinness 1984b, unpublished work).

An important factor not considered by earlier workers was the increase in the period of emersion of the upper surface of a rock with rock-size. McGuinness and Underwood (1986) showed that a large rock low on the shore would be exposed for about two hours during an average low tide whereas a small rock would not be exposed at all. The growth rate of foliose algae decreases with emersion



(Underwood 1980; Underwood and Jernakoff 1984) so these species should grow much faster on the tops of the smaller rocks. At Cape Banks, however, there were more grazers on these small to medium rocks (McGuinness 1987) and they apparently compensated for the increased growth of the algae on these boulders. Just because the grazers were more common on the small boulders at low-tide does not, of course, mean that they did not feed elsewhere at other times. In fact, many grazers wandered over the larger rocks when the tide was in and retreated down the sides as the water fell. Even so, grazing pressure should still be greatest on the smaller rocks because these were not emersed by the average low-tide and would be little disturbed by waves at this time, so grazers could continue to feed (see also Paine 1966; Underwood and Jernakoff 1984).

Low on the shore at Long Reef, in contrast, grazers were less abundant overall and most common on the larger rocks (McGuinness 1987); those on small rocks were probably either killed or driven away by shifts in the sand. Since the algae were less affected by sand, their growth was largely unrestrained on the smaller rocks in these areas and one species could quickly cover much of the surface and reduce diversity (McGuinness 1984a). Emersion stress (increased heat, light, desiccation, etc. at low-tide) and grazing pressure were greater on rocks of intermediate size and sufficient to prevent any one species occupying all of the space. Finally, the combined effects of these two factors on the larger rocks was apparently so severe that only *Ralfsia* – a species relatively resistant to both factors – could survive (McGuinness 1987). The intermediate disturbance pattern in this assemblage (McGuinness 1984a) was apparently caused by the interaction of grazing and emersion, rather than disturbance and competition.

The situation on the undersides of boulders was quite different. Here disturbance had major effects on the number and abundances of species. Burial in sand could produce the increasing species-area and species-abundance curves seen on the undersides of boulders in most places (McGuinness 1984a, 1987) either by preventing organisms from recruiting or by killing those already present. Disturbance by burial was less for large rocks allowing more species to recruit or survive. Rocks were overturned but results suggest that this disturbance was less important than the abrasion caused by minor shifts in the position of the rock. The only estimates of this abrasion are the frequency of movement and mean distance moved by rocks. Both of these aspects of disturbance should be correlated with abrasion but neither was related to rock-size (McGuinness 1987). This is consistent with the results of stabilising rocks which showed no change in the slope of the species-area relationship, simply an overall increase in diversity.

Space was in short supply on the larger boulders low on the shore on both platforms (McGuinness 1987) and competition for this resource, by overgrowth and pre-emption, reduced the abundance of some species (McGuinness, unpublished work). Early-successional species initially dominated on all rocks (McGuinness, unpublished work). Species settling later (sponges, ascidians and bryozoans) could occupy more space and/or overgrow the early-successional forms (and see Jackson and Buss 1975; Jackson 1977; Connell and Keough 1984; Keough 1984) but no single species recruited often enough, or abundantly enough, to dominate more than a few rocks (McGuinness

1987). This sparse and sporadic colonisation of the later-successional forms meant that while diversity was smaller in this situation (McGuinness 1984a), there was no tendency for one or a few species to dominate undisturbed boulders.

In contrast, space was rarely in short supply in the high-shore area. Sponges, ascidians and bryozoans rarely settled on boulders in this area (McGuinness 1984b) and never became abundant (McGuinness 1987, unpublished work). Further, a transplant experiment showed that most could not survive in the area as adults in any case, even on large boulders (McGuinness 1984b). Thus, diversity in this situation was largely a simple function of disturbance and rock-size.

*Models of community Ecology.* No existing model of community ecology was adequate as a “general” explanation for these communities. This was the case for models explaining the occurrence of particular patterns (e.g. species-area curves) and for those accounting for the structure of certain communities (e.g. rocky shore communities). No model was consistent with the patterns of diversity and abundance in all situations, and frequently factors did not act as these models predict (Underwood 1980; Underwood and Jernakoff 1981, 1984; Underwood et al. 1983; Fairweather et al. 1984; McGuinness 1984a, 1987, unpublished work; McGuinness and Underwood 1986).

The most obvious pattern in the diversity of these communities was the species-area relationship, the tendency for the larger boulders with a greater surface-area to have more species (McGuinness 1984a, 1987). Current models for this relationship are the Equilibrium Theory (MacArthur and Wilson 1967; Simberloff 1974), the Habitat Diversity Model (Williams 1943; Connor and McCoy 1979) and the Disturbance Only Model (Riedl 1964). These all predict that the diversity of the community increases with area at a rate greater than that expected simply for sampling reasons (Connor and McCoy 1979; McGuinness 1984c), yet such patterns were only observed in *one* place – high on the shore at Long Reef (McGuinness 1984a). According to the Habitat Diversity Model this increase in diversity results from the greater variety of habitats present in large areas; the Disturbances Only Model considers it to be caused by the reduction in disturbance. However, *both* these factors were important, as were other factors – such as period of emersion and pre-emption of space – not mentioned in either model (McGuinness, unpublished work; McGuinness and Underwood 1986). The Equilibrium Theory explains the same pattern by proposing that populations are small in small areas and, therefore, more likely to go extinct. This may be true but it ignores the fact that some of the factors causing species to go extinct (e.g. disturbance) may affect small areas more severely (Osman 1977; Sousa 1979a; McGuinness 1984c), as seen here.

Several models exist which purport to explain the way in which factors act and interact in marine communities, particularly communities on rocky shores. Three of these – the Keystone Predator Model (Paine 1966, 1974), Menge and Sutherland’s (1976) model and Connell’s (1975) model – emphasise predation and competition. These models differ in complexity but all postulate that in benign environments predation prevents the domination of space by superior competitors. The commonest, and only abundant, predator here, the whelk *Morula marginalba* was, however, usually

most common in the harshest (most disturbed and exposed for longest at low tide) place examined – high on the shore at Long Reef (McGuinness 1987, Table 4). In addition, it preyed on only five of the sessile animals on these rocks (Fairweather and Underwood 1983; Fairweather et al. 1984; Fairweather pers. comm.; pers. obs.). Two of these settled only occasionally (*Balanus amphitrite* and *Crassostrea commercialis*), one was severely affected by disturbance (*Tetraclitella purpurascens*) and the remaining two (*Galeolaria caespitosa* and *Hydroides elegans*) were not preferred by the whelks and can be overgrown by other sessile forms. Thus, the whelk did not act as required by these models because it did not consume the species with the greatest abilities to overgrow others.

The models which came closest to explaining the structure of these communities were, not surprisingly, those involving disturbance: the Intermediate Disturbance Model (Grime 1973; Connell 1978; Sousa 1979a) and the Dynamic Equilibrium Model (Huston 1979). These two models propose that competitive exclusion at low levels of disturbance, and mortality of most species at high levels, results in diversity being greatest at intermediate levels of disturbance. However, according to Huston (1979), the Intermediate Disturbance Model is inadequate because it does not include factors which limit the abundance of organisms and reduce the likelihood of competition. Indeed, such was the case here and only in one of the several situations examined – on the undersides of boulders low on the shore – was space in short supply and competition for it likely. This was also the only place where patterns in diversity consistent with the predictions of the Intermediate Disturbance Model were observed (McGuinness 1984a).

In the Dynamic Equilibrium Model, in contrast, competitive exclusion occurs only slowly when population growth rates are small (Huston 1979). Growth rates themselves are determined by “the interaction of environmental variables, such as energy or nutrient availability, with the genetically determined maximum potential rate for the species” (Huston 1979, p 83). Some problems remain. Limited nutrient availability could promote competition (for the limited resource). Further, the model considers anything that kills organisms to be a disturbance, a definition which blurs the differences between biological and physical agents of mortality (McGuinness 1987). The distinction between, on the one hand, the disturbances which kill organisms and, on the other, the factors which reduce the growth rate of the population is also not clear. Finally, the model ignores important factors; one not included but known to affect communities on boulders is habitat diversity (McGuinness and Underwood 1986).

Overall, the models were too simple to account for the structure of these communities. Many factors affected the abundances of organisms and/or the diversity of the community in at least some situations (McGuinness 1984a, 1987, unpublished work; McGuinness and Underwood 1986). These factors – physical and biological – interacted in complex ways not predicted by any existing model and no model included all the important factors (see also the discussion in Underwood et al. 1983). It is at present difficult to see how any model could hope to combine these myriad complex interactions into a useful framework but, as others have noted, revolutions of any sort are usually unexpected in foresight and inevitable by hindsight (e.g. Kuhn 1970; Feyerabend 1975).

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