Disturbance and organisms on boulders

I. Patterns in the environment and the community

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Summary. Several aspects of disturbance by waves to intertidal boulders were monitored for one year high and low on the shore on two rock platforms on the east coast of Australia. These boulders were also subjected to burial by sand, and this disturbance was monitored in the same places for two years. The mobile and sessile organisms on the tops and bottoms of the rocks were sampled six times during the same period in order to determine patterns in community structure and assess the role of disturbance. Small rocks were overturned more often and buried to a greater extent than large rocks, but rocks of all sizes were moved similar distances with similar frequency. These contrasting results were probably caused by the fact that small rocks were rounder than large rocks. Rocks were buried in sand much more at Long Reef than at Cape Banks, but differences among places in disturbance by waves were not great.

Patterns in community structure were complex but suggested that disturbance was only important for sessile organisms on the undersides of boulders. The number of sessile species present was always related to the size of the rock but the total cover of algae on the tops of rocks never was. Some particular species were most abundant on large rocks but others showed the reverse pattern, covering more space on the smaller boulders. This latter pattern may have been due to the shorter period of exposure during low tide in this situation, though grazers were also abundant on these rocks in some places. In contrast, nearly all species on the undersides of rocks reached greatest abundance on the medium to large rocks, consistent with effects of disturbance. Space was in short supply low on the shore and overgrowth apparently reduced diversity but this was not the case elsewhere. Overall, the results indicate that disturbance was frequent and important, but not for all species nor in all places.

Key words: Intertidal communities on rocks – Disturbance – Community structure

One factor recognised as a strong influence on many marine and terrestrial communities is disturbance (e.g. Dayton 1971; Grime 1973, 1979; Connell 1978; Sousa 1979a; Thistle 1981; Taylor and Littler 1982; Connell and Keough 1983; Fletcher and Day 1983). Events called "disturbances" range from vast geological phenomena, such as earthquakes, affecting hundreds of hectares, to biological phenomena, such as grazing, which may damage less than a few square centimetres (Sousa 1984). Communities may

experience more than one type of disturbance and the same type of community may also experience different rates or regimes of disturbance in different places. For example, Sousa (1979a, b, 1980) noted that one disturbance to the assemblages of algae on intertidal boulders resulted when a boulder was overturned and another when one boulder was cast against another. Further, Osman (1977) observed that boulders were moved much more often intertidally than subtidally.

Many patterns in the diversity of communities, and in the abundances of particular species, are assumed to be due to disturbance (reviews by Connell 1978; Grime 1979; Connell and Keough 1983; Sousa 1984). In addition, this factor now figures as an important component in some models for the structure of natural communities (e.g. Connell 1978; Grime 1973; Paine and Levin 1981; Sousa 1984). Despite its presumed importance, there are still few studies reporting detailed measurements of natural rates of disturbance and relating these to the structure of the community. Some accounts of disturbance are merely anecdotal; others are given "after the fact" of disturbances of unusual magnitude (e.g. Ebling et al. 1985; Garwood et al. 1979). The latter observations do provide useful information about disturbance but give little indication of its normal importance.

Disturbance in intertidal communities is often linked to wave-action. Boulders may be overturned or cast about (Osman 1977; Sousa 1979a, b), organisms may be torn off the rock (Dayton 1971; Paine and Levin 1981), and sand may be scoured from one area and deposited in another (Taylor and Littler 1982; Turner 1983). The commonest physical disturbances in boulder fields are probably due to the movement of the boulders themselves and the movement of the surrounding sediments (Littler and Littler 1981; Osman 1977; Sousa 1979a, b, 1980). The present work had three aims. The first was to monitor the intensity and frequency of the common disturbances in boulder fields on the east coast of Australia. The second was to make detailed observations on the abundances of organisms in these communities (diversity was extensively sampled by McGuinness 1984b). Finally, the third aim was to formulate testable hypotheses about the way in which community structure is determined and the role of disturbance in this process.

Materials and methods

Location and description of study sites. The two rock platforms studied – Cape Banks and Long Reef – have been described elsewhere (McGuinness 1984b; McGuinness and

Underwood 1986; see also Pope 1937). An expanse of platform free of rocks divided the boulder fields on both shores into two areas: one in the low intertidal part of the shore (0.2 m–0.3 m above Mean Low Water); the other in the mid to high region (0.6–0.9 m above MLW; referred to as the "low-shore" and "high-shore" areas, respectively).

In order to compare variability in disturbance within each area to that among areas and shores I subdivided each area on each platform into three "fixed sites". These sites were not randomly placed – their location was largely determined by structural features of the platform, such as ridges, tide-pools and extremely large boulders. They were, therefore, considered a fixed, rather than random, factor in statistical analyses (Winer 1971) and will always be called "fixed sites". Other, smaller, sites were used in some studies. These were simply patches of the boulder field containing enough rocks for an experiment or sampling study. Again, at least two such sites were used so that variability among areas could be compared to that within areas. Because these "random sites" were only a few square metres in extent (less than one-fifth of the area of a fixed site), they could be randomly, or at least haphazardly, placed. They were a random factor in analyses (Winer 1971).

Measurement of disturbance. Ten rocks were put out at each of the fixed sites in each area on each shore in August 1981 to estimate the frequency with which rocks were moved, overturned and the average distance and direction moved. Further sets of five rocks were added to each site in November 1981, February 1982, and December 1982, to replace losses and increase the number of replicates (final total of 25 per site). The rocks at any site covered at least the size-range 20 cm^2 to 1,000 cm^2 in surface-area. These rocks were initially bare of organisms, being taken from above the high water mark, and had small plastic tags glued to the upper (U-side) and (L-side) lower surfaces. The distance from the centre of each rock to two nails planted in the platform was measured at approximately fortnightly intervals for one year. Note was also made of whether the rock was U-side or L-side uppermost. (Because the rocks were flattened, nearly all, when moved, came to rest with either the U-side or the L-side uppermost; in only 3 of more than 3,000 observations were rocks found lying on their edge with neither U-side or L-side up.) From these readings it was possible to estimate the displacement of each rock during each interval, and know whether it had been overturned (Underwood 1977). The smallest movement which could be detected was 10 cm (McGuinness 1984c), so rocks displaced less than this were considered not to have moved.

These observations will tend to underestimate disturbance. Estimates of the frequency of overturning will be biased because rocks which were overturned an *even* number of times would be recorded as not having been rolled at all, and rocks rolled an *odd* number of times could only be assumed to have been overturned once. The distance moved could be underestimated because straight-line displacement was always measured whereas the rock may have travelled by a longer, curved path. Since the disturbance to the community is likely to be a function of total distance moved, rather than simple displacement, the consequences of this error could be serious. A pilot study, however, revealed that biases would be minor if a sampling interval of two weeks was used (McGuinness 1984c).

The frequency with which rocks were overturned was examined by calculating the *percentage-overturning* of each rock: the percentage of the times which a rock could have been overturned that it was overturned (e.g. a rock observed 11 times and overturned 3 times would have 30% overturning since it could have been overturned 10 times). The *percentage-movement* of rocks was defined in a similar fashion as the percentage of the times which a rock could have been moved that it was moved. These statistics were used simply to compensate for some differences in numbers of observations among rocks.

The percentage of the underside of these rocks buried in sand was also sampled. This was done by examining the orientation of the rock with respect to the substratum, turning it over to inspect the underside for adhering sand, and visually estimating from these observations the percentage that was in contact with the sand. There was a statistically significant, but negligible (approximately -2%), bias in these visual estimates (McGuinness 1984c). Burial was sampled less often but for a longer period than movement – every 2 months for 28 months.

Comparisons among times, shores, areas and sites were made using four-factor Analyses of Covariance (AN-COVA) with disturbance as the variate and the log of rock-size as the covariate (see McGuinness 1987 for further details of statistical methods). Rock-size was transformed in order to eliminate heterogeneity of regression slopes and residuals and satisfy the assumptions of ANCOVA (Huitema 1980). The resulting exponential curves fit the data at least as well as linear relationships (as indicated by the value of the correlation coefficient, r) and usually better. Ordinary analyses of variance were done when there was no relationship between the variate and covariate (e.g. for percentage-movement; see Results).

Structure of the community. The community was defined as the group of macroscopic organisms present on a particular boulder at a particular time, with organisms on the upper and lower sides of the rock regarded as separate communities. These communities were sampled six times, at intervals of about four months, from 23 November 1981 to 4 November 1983. Ten rocks, covering the size-range 20 cm^2 to 1,000 cm^2, were sampled in two randomly selected sites in each area on each shore. I selected rocks by wandering away from the centre of each random site in a haphazardly chosen direction and sampling the first rock of each size encountered.

Preliminary analyses of these data indicated that there were no consistent seasonal variations in abundance (McGuinness 1984c; and see also Jernakoff 1985b), so some data were pooled to increase sample size for some analyses. The data used were for three similar times of year – November 1981, September 1982 and November 1983 – thus any biases resulting from undetected seasonal changes should be minor.

Variations in the abundance of species with size of rock were examined by calculating the mean abundance of the species on rocks in five size classes: 0–99, 100–199, 200–499, 500–1,099, and 1,100–2,500 cm^2. The extent to which the community was dominated by a species was examined by calculating, for each size class (except class 5 because of insufficient replicates), (1) the number of times each species was dominant, and (2) the number of different species dominating. The latter statistic could be influenced by the number of rocks sampled (more species should be found

the greater the number of rocks, and therefore area, sampled). To remove this bias eight rocks in each size class were sampled. This was done in two ways. First, I simply recorded the number of different species which were dominant on the *first* eight rocks selected. However, because species were much rarer in the high-shore area, the undersides of many of the smaller rocks in this area were completely bare. To take this into account, I sampled additional rocks until eight *occupied* rocks were found. Usually the two methods gave similar results. I always considered the dominant species simply to be that which covered more of the surface of the rock than any other.

Sampling of organisms on boulders. Data were taken from colour slides of the entire upper and lower sides of boulders. These slides were examined under a binocular microscope for:

1. the identity of all macroscopic species present, with the exception that both amphipods and spirorbids were counted as single species because accurate identification was not possible from slides (in any case amphipods were not common and boulders examined in the laboratory nearly always had only two species of spirorbid – *Janua pseudocorrugata* and *Pileolaria pseudomilitaris*);
2. the percentage cover of sessile species; and

3. the density of each mobile species (except amphipods).

Percentage covers were estimated by using 50 points superimposed on the slide and randomly located over the entire upper or lower surface of the boulder. Densities were estimated by either a total count of all individuals on the rock, or using five 4×4 cm or 2×2 cm quadrats (depending upon the abundance of the species). Surface-areas of the rocks were obtained from regressions relating surface-area to measurements of the length and breadth of the rock (McGuinness 1984c). The surface-areas given here are for one surface (upper or lower) of the rock.

Results

Frequency of disturbance

I present only a summary of the major results since the data were both lengthy and tedious (for detailed analyses see McGuinness 1984c). There were some variations in disturbance with time (see below), but since there were no consistent seasonal patterns (McGuinness 1984c; see also Underwood 1981) I will concentrate on variations in disturbance with size of rock, and differences among sites, areas and shores.
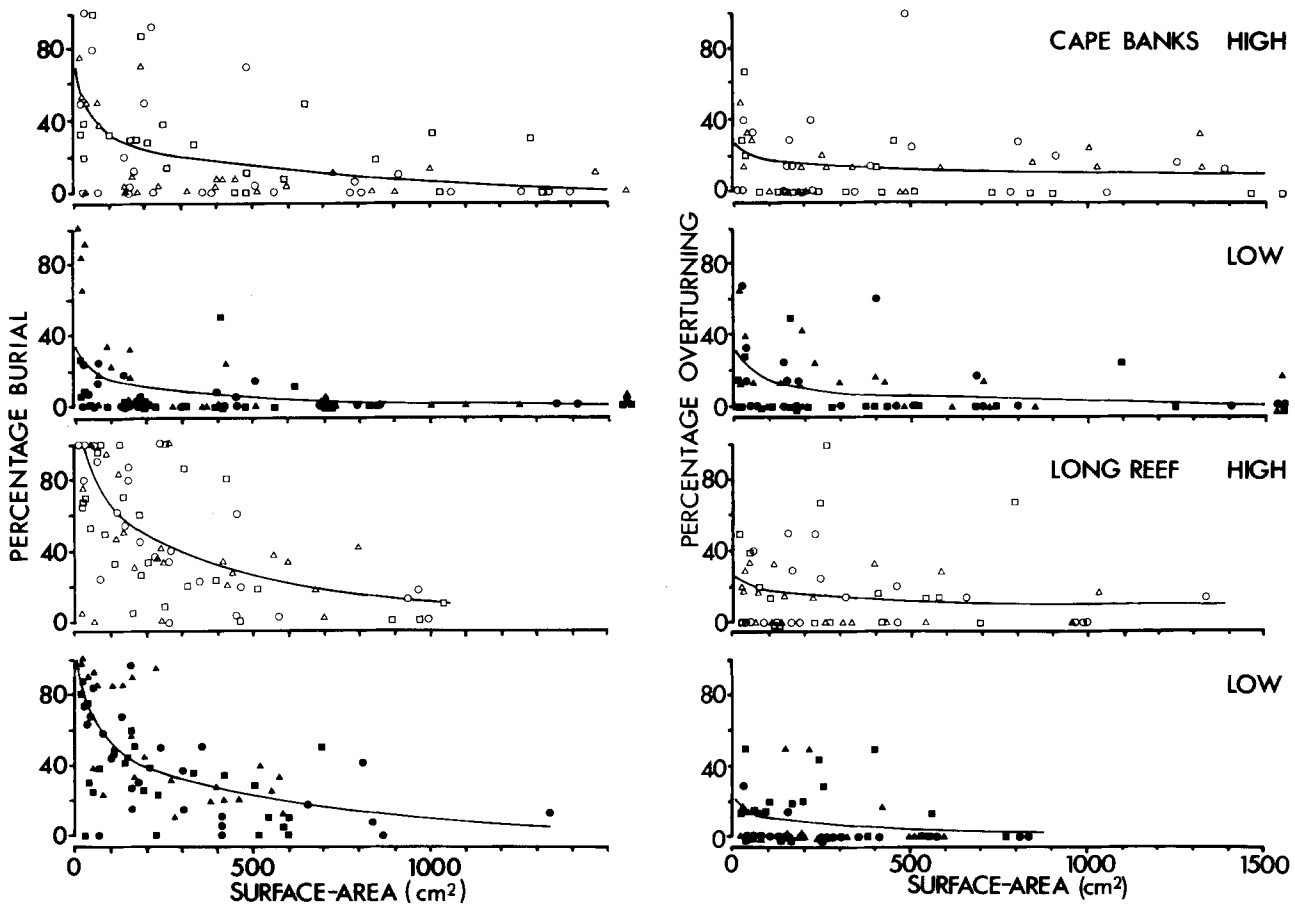

Fig. 1. Relationship between disturbance and rock-size high and low on the shore at Cape Banks and Long Reef for (a) percentage of underside buried in sand, and (b) frequency of overturning. The points give the mean disturbance for each rock during the study (12 months for overturning; 28 months for burial). The triangle, square and circle identify observations for the three sites within each area. Points grouped together to the right of 1,500 cm² were observations on rocks greater than 1,500 cm² (on average about 2,000 cm²). The exponential curves plotted were calculated using data pooled across sites and times to illustrate the overall relationship for each area and shore (analyses examined sites and times separately; see text)
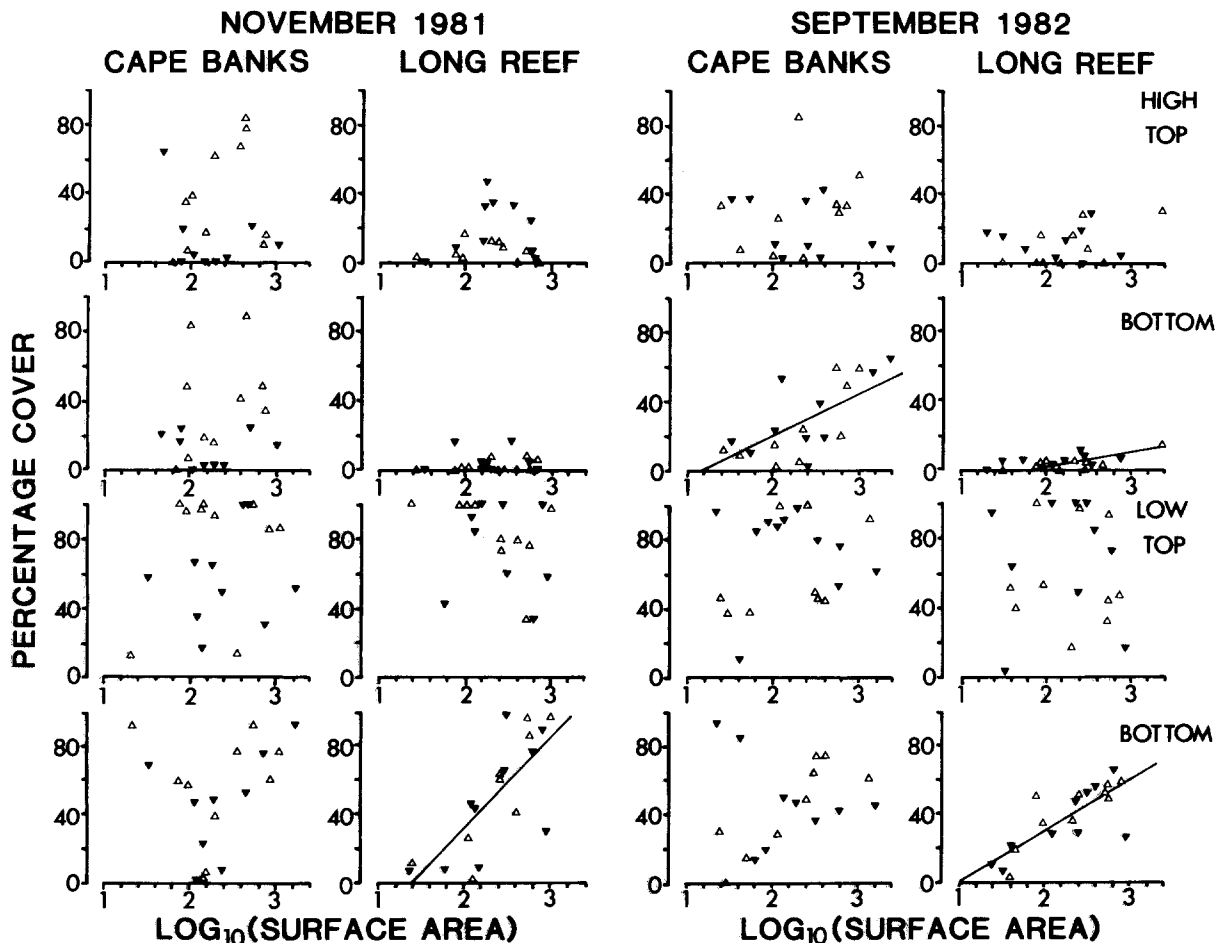
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Fig. 2. The total percentage of the tops and bottoms of rocks occupied by sessile species high (upper 2 rows) and low (bottom 2 rows) on the shore at Cape Banks and Long Reef for two of the sampling times. Open and closed symbols give results for two sites within each area. Solid lines indicate significant linear regressions ($P < 0.05$) calculated pooling data across sites

Burial in sand. There was an inverse relationship between the size of a rock and the percentage of its underside buried in sand (Fig. 1 a). These data were well fit by exponential curves and in 11 of the 12 "shore × area × fixed site" combinations the resulting relationship was significant (with P of the correlation coefficient, r, ranging from <0.05 to <0.001). On average, the relationship with size accounted for 32% of the variability in burial (for transformed data; see Methods). The three sites in each area differed in burial and the magnitude of these differences varied with time (McGuinness 1984c). Overall, however, rocks were buried to the greatest extent high on the shore at Long Reef (mean for a 300 cm^2 rock = 39% of the underside buried), less in the low-shore area there (mean = 32%) and least at Cape Banks (high = 21%, low = 8%).

Movement of rocks by waves. Percentage-overturning was negatively correlated with the size of the rock (combined r from ANCOVA = 0.31, df = 72, $P < 0.001$; Fig. 1 b) and no variations with time were detected. High-shore areas had greater percentage-overturning (mean for a 300 cm^2 rock = 14%) than low-shore areas (mean = 11%), but the difference was not great. There were again differences among the fixed sites within an area (Fig. 1 b). On average a small,

50 cm^2, rock was overturned about 22% of the sampling times, or once every two months (since rocks were observed about every two weeks), but large, 1,500 cm^2, rocks were overturned only once a year. It is worth noting, however, that the relationship between percentage-overturning and rock size accounted for only 10% of the variability in this aspect of disturbance by waves.

In contrast to percentage-overturning, there was no significant relationship between percentage-movement and the size of the rock (combined r from ANCOVA = 0.02, df = 72, $P > 0.10$), nor were there any differences among fixed sites, areas or shores. The overall mean percentage-movement for all places, times and sizes of rock was 52%, indicating that rocks were moved 10 cm or more about every second sampling time, or once a month. Note that this indicates that small rocks were overturned about once every second time that they were moved whereas for large rocks this frequency was somewhat less than once every 5 times.

As with percentage-movement, there was no correlation between distance moved and size of rock. Disturbance, by this measure, was greatest high on the shore at Cape Banks (mean = 0.50 m per 18 days), least in the low-shore area at Long Reef (mean = 0.19 m) and intermediate high on the shore at Long Reef (mean = 0.43 m) and low on the shore at Cape Banks (mean = 0.33 m).

Table 1. Relationship between percentage cover of all species combined and size of rock (transformed as $\log_{10}$). Data were pooled over the two sites in each area and the six sets of samples. Nsig gives the number of significant regressions if the six times were analysed separately; Corr. Coeff. is the correlation coefficient

Side	Area	Shore	N	Mean % cover	Intercept	Slope	Corr. coeff.	Nsig
Top	high	Cape Banks	119	34.8	22.8	5.4	0.08	0
		Long Reef	120	11.7	7.2	2.0	0.07	0
	low	Cape Banks	120	73.0	62.1	4.9	0.09	0
		Long Reef	120	68.2	54.0	6.3	0.10	0
Bottom	high	Cape Banks	119	26.7	−13.7	18.2	0.33*	2
		Long Reef	120	4.4	− 2.2	3.0	0.21*	1
	low	Cape Banks	118	51.0	8.7	18.9	0.34*	1
		Long Reef	119	37.2	−42.8	35.7	0.68*	6

$* = P < 0.05$

Table 2. Relationship between the percentage of the cover on the rock which was algal and size of rock (transformed as $\log_{10}$). Data were pooled over the two sites in each area and the six sets of samples. Nsig gives the number of significant regressions if the six times were analysed separately; Corr. Coeff. gives the correlation coefficient

Side	Area	Shore	N	Mean % cover	Intercept	Slope	Corr. coeff.	Nsig
Top	high	Cape Banks	110	86.7	107.2	− 9.1	−0.16	0
		Long Reef	94	91.5	114.5	−10.2	−0.20*	1
	low	Cape Banks	120	97.4	94.9	1.1	0.07	0
		Long Reef	118	95.8	89.0	3.0	0.11	1
Bottom	high	Cape Banks	106	63.5	86.8	−10.3	−0.13	1
		Long Reef	85	46.9	60.2	− 5.7	−0.05	0
	low	Cape Banks	116	48.7	97.3	−21.7	−0.34*	1
		Long Reef	119	25.0	49.0	−10.7	−0.17	1

$* = P < 0.05$

Structure of the existing community

Total space occupied. The major species on the tops of rocks were algae and these formed more than 80% of the cover present (Table 2). The amount of the upper surface occupied varied considerably but was never related to rock-size (Fig. 2; Table 2). About 70% of the tops of rocks low on the shore was occupied on average compared to 35% high on the shore at Cape Banks and only 12% at Long Reef (Table 1). Differences between the two sites sampled within each area were occasionally present (Fig. 2).

As might be expected, sessile animals were more important as occupants of space on the undersides of boulders, though algae still formed a significant proportion of the total cover – from 25% to 64%, depending upon place but tending to be less lower on the shore (Table 2). In contrast to the case for the tops, the total percentage of the undersurface of rocks occupied increased significantly with rock-size (Fig. 2; Table 1). In the low-shore area at Long Reef this relationship accounted for an average of 58% of the variability in cover at any time, but only 10% high on the shore and 16% in that area at Cape Banks. The pattern on the undersides of boulders in the low-shore area at Cape Banks was unusual. Cover on small boulders (< 50 cm^2) was either little (approx. 30%) or great (approx. 70%), but about 30–70% of the surface of medium-sized rocks (200–500 cm^2) was occupied and 50–100% on the larger rocks. Similar patterns were seen several times (see Fig. 2 and McGuinness 1984c). The tops of many of the rocks in this area were dominated by encrusting algae and

the pattern probably resulted from the overturning of some small rocks. Indeed, the proportion of the undersurface cover which was algal decreased with size of rock (Table 2).

Abundance of major species. In general, species showed one of four patterns: greatest abundance on small rocks, on large rocks, on rocks in the middle size-classes (2–4), or, lastly, no consistent variation in abundance with rock-size (Tables 4 and 5). These results were complicated by the fact that the same species often showed different patterns at different places. The encrusting alga *Ralfsia sp.* was common on the tops of rocks high and low on the shore at Cape Banks and low at Long Reef. At Cape Banks it was most abundant on the smaller rocks, covering 10–20% of the space (Table 3). It covered a similar amount of space on small rocks at Long Reef but 50% or more on larger rocks (Table 3 and unpub. obs.). Another crust, *Hildenbrandia prototypus* was very abundant at Cape Banks, occupying 25 to 50% of space on medium rocks (Table 3) but was rarely found at Long Reef. Low on the shore at Long Reef the foliose alga *Polysiphonia sp.* occupied about 31% of space on smaller rocks but cover decreased to nearly zero on larger rocks. At Cape Banks this species covered a maximum of 22% of the space and no relationship of abundance to rock-size was obvious.

Similar results were observed with species on the undersides of rocks. *Ralfsia* again decreased in abundance at Cape Banks with rock-size but increased at Long Reef. The polychaete *Hydroides elegans* and the spirorbids increased in abundance in the low-shore area at Cape Banks

Table 3. Mean percentage cover and variance of the common sessile species in five size-classes (see Methods). Values in parentheses give number of replicates

		Size 1		Size 2		Size 3		Size 4		Size 5	
		$\bar{x}$	s^2	$\bar{x}$	s^2	$\bar{x}$	s^2	$\bar{x}$	s^2	$\bar{x}$	s^2
CB-High-Top	*Hildenbrandia*	13	551	14	760	26	1,158	16	132	6	19
	Ralfsia sp1	9	239	1	7	6	95	3	30	2	16
	Ulva	1	7	2	28	0	0	3	87	0	0
	Galeolaria	0	1	1	10	1	15	6	85	9	261
		(20)		(14)		(13)		(9)		(3)	
CB-High-Bot	diatoms	2	31	5	72	1	3	2	22	23	1541
	Hildenbrandia	11	587	11	557	10	120	25	762	16	24
	Nerita eggs	1	3	1	3	2	5	3	24	1	1
	Galeolaria	3	122	3	38	4	49	10	38	1	1
		(20)		(14)		(12)		(9)		(3)	
LR-High-Top	blue-green	1	3	17	231	8	98	6	73	14	200
	Ulva	1	15	2	14	3	36	0	1	14	288
		(17)		(15)		(18)		(7)		(2)	
LR-High-Bot	*Ralfsia* sp1	1	15	3	33	2	18	3	8	2	5
		(17)		(15)		(18)		(7)		(2)	
CB-Low-Top	*Corallina*	0	2	1	2	0	0	3	59	1	1
	Hildenbrandia	23	919	31	786	52	915	28	522	32	306
	Neogoniolithon	5	94	5	30	2	7	6	148	4	80
	Ralfsia sp1	18	433	15	349	5	84	4	18	8	86
	Ralfsia sp2	0	2	9	506	1	2	2	32	1	3
	Polysiphonia	5	157	7	337	2	13	22	1,407	2	12
	Petrospongium	2	59	2	17	1	14	7	86	4	65
	Ulva	13	394	6	106	2	13	3	28	0	0
		(20)		(16)		(10)		(8)		(5)	
CB-Low-Bot	*Hildenbrandia*	17	661	9	280	15	263	21	146	24	984
	Neogoniolithon	7	183	4	94	5	53	6	28	6	11
	Ralfsia sp1	10	591	3	26	4	41	0	0	0	0
	Nerita eggs	1	1	1	3	2	25	1	4	5	81
	Galeolaria	1	2	1	1	2	13	9	127	2	2
	Hydroides	1	14	2	6	1	0	4	80	10	223
	spirorbids	2	8	5	64	7	34	10	50	11	99
	Bajalus	2	21	1	7	4	96	4	111	0	0
		(20)		(15)		(10)		(8)		(4)	
LR-Low-Top	*Corallina*	1	1	1	6	0	2	0	0	–	–
	Ralfsia sp1	21	942	24	755	41	859	49	662	–	–
	Polysiphonia	31	1,037	34	1,287	18	740	3	41	–	–
	Ulva	3	21	13	236	5	27	5	72	–	–
	Zonaria	5	215	3	38	2	20	0	0	–	–
	Idanthrysus	0	1	2	13	0	1	0	2	–	–
		(16)		(11)		(17)		(15)		(0)	
LR-Low-Bot	*Ralfsia* sp1	3	27	5	64	5	40	11	200	–	–
	Galeolaria	0	1	1	2	2	3	4	20	–	–
	Hydroides	2	11	1	4	4	17	3	10	–	–
	Idanthrysus	1	4	4	76	4	31	4	26	–	–
	spirorbids	1	1	3	16	8	30	14	145	–	–
	Phyllochaetopterus	22	22	53	4	26	2	1	3	–	–
	Watersipora	2	45	3	28	4	39	2	17	–	–
	Bajalus	0	0	1	18	3	135	6	129	–	–
		(15)		(11)		(17)		(15)		(0)	

CB = Cape Banks; *LR* = Long Reef

and Long Reef, as did the sponge *Bajalus sp.* at Long Reef (Table 3). The polychaete *Phyllochaetopterus sp.* decreased low on the shore at Long Reef, whereas another polychaete, *Galeolaria caespitosa*, was most abundant on rocks 500–1,100 cm² (size class 4). Other species of sponges, ascidians and bryozoans covered little space on average, but as groups, were more abundant on the larger rocks.

The common grazers in all places were the molluscs

Table 4. Density of mobile species on boulders in five size classes at Cape Banks and Long Reef

			Na	Ac	Ct	Bn	Pe	Mc	Mm
high	1	x̄	114	89	0	25	10	0	0
		s	290	215	0	107	30	0	0
C	2	x̄	70	39	0	15	0	0	0
		s	118	61	0	43	0	0	0
A	3	x̄	172	27	6	21	13	0	0
		s	141	32	17	19	48	0	0
P	4	x̄	146	17	8	22	2	1	2
		s	129	21	8	23	3	3	5
E	5	x̄	139	16	13	38	0	1	5
		s	115	20	5	33	0	2	8
B low	1	x̄	85	63	0	0	151	0	3
		s	106	134	0	0	295	0	13
A	2	x̄	54	88	9	0	54	6	10
		s	51	104	17	0	68	17	25
N	3	x̄	64	66	35	2	52	24	17
		s	54	75	40	7	28	28	35
K	4	x̄	40	83	32	0	51	18	9
		s	15	76	25	0	34	12	17
S	5	x̄	46	58	26	2	52	3	5
		s	16	59	17	4	58	6	4
high	1	x̄	54	7	8	0	31	0	19
		s	27	20	23	0	87	0	37
L	2	x̄	58	22	15	2	2	0	6
		s	76	35	25	7	8	0	12
O	3	x̄	44	35	10	1	1	2	12
		s	54	43	15	4	3	6	24
N	4	x̄	39	20	33	2	0	0	20
		s	30	23	38	4	0	0	20
G	5	x̄	6	27	9	2	3	0	37
		s	8	26	6	3	4	0	43
R low	1	x̄	0	0	28	0	34	0	0
		s	0	0	67	0	62	0	0
E	2	x̄	0	0	4	0	32	10	0
		s	0	0	14	0	53	24	0
E	3	x̄	1	13	31	0	18	13	9
		s	4	26	39	0	18	22	14
F	4	x̄	0	32	44	1	39	9	20
		s	0	39	47	4	40	10	20
	5	x̄	–	–	–	–	–	–	–
		s	–	–	–	–	–	–	–

Na = *Nerita atramentosa*, Ac = *Austrocochlea constricta*, Ct = *Cellana tramoserica*, Bn = *Bembicium nanum*, Pe = *Patiriella exigua*, Mc = *Montfortula conoidea*, Mm = *Morula marginalba*. x̄ = number per m² (pooled over two sides of rock) and s = standard deviation

Nerita atramentosa, *Austrocochlea constricta*, *Bembicium nanum*, *Cellana tramoserica* and *Montfortula conoidea*, and the starfish *Patiriella exigua*. Abundances were generally great and variable at Cape Banks with several patterns observed, whereas at Long Reef species were less abundant and showed similar patterns (Table 4). In the high-shore area at Long Reef all species were most abundant on rocks in size-classes 2–4, except *Nerita* and *Patiriella* which were most abundant on smaller rocks (Table 4). Low on the shore all species were most abundant on larger rocks. Again

Nerita and *Patiriella* were exceptions: *Nerita* was rare and *Patiriella* was equally abundant on all rocks.

The situation at Cape Banks was more complex. *Patiriella* was most abundant on small rocks and *Cellana* on larger rocks, but patterns in other species varied with height on the shore. *Nerita* was most abundant on rocks of intermediate size high on the shore but decreased in abundance with rock-size in the low-shore area. *Austrocochlea* decreased in the high-shore area but showed no relationship with rock-size low on the shore. *Bembicium* was least abundant on rocks of intermediate size high on the shore and rare low, whilst *Montfortula* was rare high and most abundant on rocks of intermediate size high on the shore.

The only abundant predator was the whelk *Morula marginalba*. It increased in abundance with rock-size in all places except high on the shore at Cape Banks where it was most abundant on rocks in the middle size classes (Table 4).

Dominance in the community. There was one species which tended to dominate more of the tops of rocks in the larger size classes but the identity of this species varied among places (Table 5). High and low on the shore at Cape Banks the dominant was *Hildenbrandia*. *Ralfsia sp.* dominated nearly all the rocks in the low-shore area at Long Reef but high on the shore a blue-green alga (unidentified) was dominant. Some species, notably diatoms at Cape Banks and *Polysiphonia sp.* at Long Reef, dominated more rocks in the smaller size classes but other species, such as *Ulva lactuca* and *Neogoniolithon sp.*, showed no consistent tendency to increase or decrease in dominance. The tops of the smaller rocks high on the shore were often completely bare (Table 3).

The case for the undersides was somewhat different. High on the shore at Cape Banks *Hildenbrandia* and *Galeolaria* increased in dominance with rock-size. A similar pattern was seen high on the shore at Long Reef but here the two species increasing in dominance were the spirorbids and the blue-green alga. In the low-shore area at Long Reef *Phyllochaetopterus sp.* dominated fewer of the larger rocks but the spirorbids and the sponge *Haliclona sp.* dominated more. The only clear pattern low on the shore at Cape Banks was for the algae as a group to become less dominant on the larger rocks.

The number of different species found as dominants on the tops of rocks low on the shore at Long Reef declined asymptotically from four on the smallest size class to only one in the largest size class (Fig. 3). On the bottoms of rocks in both low shore areas the number of dominants appeared to increase asymptotically with size of rock. Observations of rocks greater than 1,100 cm² in surface-area revealed no tendency for the number of dominants to decline on larger rocks. Patterns were not obvious in other situations.

Discussion

Disturbance. As expected, large rocks were buried and overturned to a lesser extent than small rocks. These relationships were curved: disturbance decreased approximately exponentially to close to zero. Two results which at first seem surprising were the lack of relationships between the size of rocks and either the frequency with which rocks were moved, or the mean distance moved. Osman (1977) and

Table 5. The percentage of the tops and bottoms of rocks in four size classes dominated by different species high and low on the shore at Cape Banks and Long Reef

| | | High shore area | | | | | | | | Low shore area | | | | | | | |
| | | Cape Banks | | | | Long Reef | | | | Cape Banks | | | | Long Reef | | | |
		1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Top of rock																	
diatoms	E	12	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hildenbrandia	E	24	38	62	70	12	0	0	0	30	60	90	50	0	0	0	0
Neogoniolithon	E	0	0	0	0	0	0	0	0	15	7	0	13	0	0	0	0
Ralfsia sp1	E	24	19	31	10	24	69	41	63	15	7	10	0	27	36	76	94
Polysiphonia	F	0	0	0	0	0	0	0	0	0	7	0	25	47	36	18	0
Ulva	F	12	6	0	10	24	6	24	25	25	7	0	0	0	28	0	0
Galeolaria	P	0	6	7	10	0	0	0	0	0	0	0	0	0	0	0	0
Other		0	0	0	0	0	0	0	0	15	12	0	12	26	0	6	6
Bare		28	25	0	0	40	25	29	12	0	0	0	0	0	0	0	0
Bottom of rock																	
diatoms	M	29	13	0	10	0	0	0	0	0	0	0	0	0	0	0	0
Corallina	E	0	0	0	0	0	6	0	0	0	0	0	0	7	0	6	0
Hildenbrandia	E	29	31	46	50	0	0	0	0	40	19	40	37	7	0	0	0
Neogoniolithon	E	0	0	0	0	0	0	0	0	25	13	10	13	0	0	0	0
Ralfsia sp1	E	6	13	23	10	12	44	17	62	0	0	0	0	32	18	23	31
blue-green	E	0	0	0	0	0	0	0	0	15	7	0	0	0	0	0	0
Ulva	F	6	6	0	0	0	0	6	0	0	0	0	0	7	0	0	0
Cnidopus	A	6	0	0	0	6	0	0	0	0	7	0	0	0	0	0	0
Galeolaria	P	12	6	23	30	12	6	12	0	0	7	0	13	7	0	0	13
Hydroides	P	0	0	0	0	0	0	6	0	0	7	0	12	7	0	6	0
Idanthrysus	P	0	0	0	0	0	0	0	0	0	7	10	0	7	18	6	0
Phyllochaetopterus	P	0	0	0	0	0	0	6	0	0	0	0	0	12	19	6	0
spirorbids	P	0	0	0	0	6	6	12	25	10	26	10	13	0	9	23	25
Haliclona	S	0	0	0	0	0	0	0	0	0	0	20	0	0	9	0	6
Bajalus	S	0	0	0	0	0	0	0	0	0	0	10	12	0	9	6	13
Trachiopsis	S	0	0	0	0	0	0	0	0	0	0	0	0	7	0	12	6
Watersipora	B	0	0	0	0	0	0	6	0	0	0	0	0	7	9	12	6
Other		0	0	0	0	6	0	18	0	0	7	0	0	0	0	0	0
Bare		12	31	8	0	58	38	23	13	10	0	0	0	0	0	0	0

The size classes are: *1* 0–99 cm^2; *2* 100–199; *3* 200–499; *4* 500–1,099. Letters after species names give groups, as follows: *E* encrusting alga; *F* foliose alga; *M* microalga; *A* anemone; *B* bryozoan; *P* tube-building polychaete; *S* sponge

Sousa (1979b) did find negative relationships between frequency of movement and rock-size, but they estimated disturbance differently. Osman (1977) placed rocks on a line one metre below low tide and recorded the number and size of rocks moved from this line over time. Sousa (1979b) photographed fixed quadrats within his boulder field and determined the frequency with which rocks were moved by comparing slides from one time to the next. Both workers, therefore, did not measure the frequency of movement of a random sample of the rocks present within the area but rather of those rocks on the top of the pile. This may have led them to overestimate the actual difference in the frequency of movement between small and large rocks, and the intensity of this aspect of disturbance. A random sample was not used in this study either, but after a few months many of the smaller rocks did become buried in sand, or lodged firmly underneath larger rocks, and prevented from being moved for long periods of time. In fact, large rocks were buried less because they sat upon small rocks and were held up out of the sand. The inverse relationship between overturning and size observed might well occur simply because the smaller rocks were rounder (McGuinness 1984c) and so could be more easily rolled by a given force. This is consistent with the observation that small rocks were overturned a greater proportion of the times that they were moved than were large rocks.

There are other problems with measurements of disturbance in the literature. These arise because some workers have defined disturbance in terms of its effects on the community (e.g. Paine and Levin 1981; Dethier 1984; Ebling et al. 1985) and then attempted to measure its frequency and intensity by observing changes in the community (see also Connell and Sousa 1983; Rykiel 1985). Dethier (1984), for instance, studied the communities in rock pools and considered that a disturbance had occurred when the percentage cover of a sessile organism declined by more than 10% within a period of less than six months, except for the "senescence of annual or emphemeral species...which *seem[ed]* to occur even in the absence of disturbance", "cases of 'chronic' herbivory", "losses of motile organisms ...were *generally* not counted as disturbances" and, of course, "the diatoms present[ed] a *problem*" (my italics throughout). By this measure, however, pools which had consistently less than 10% cover could never be disturbed yet disturbance might be the primary factor limiting abundance, and seasonal changes in abundance might themselves
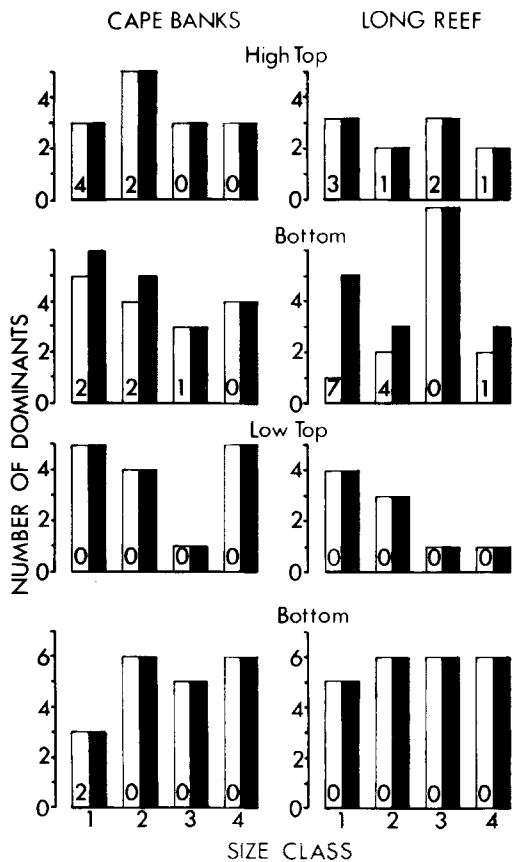
Fig. 3. Number of different species found as dominants on rocks in four size-classes (see Table 5 for actual sizes). Open bars give results from sampling the first eight rocks encountered (value inside bar is number of rocks unoccupied by any species); closed bars give results of examining the first eight occupied rocks

by caused by seasonal variations in disturbance (e.g. Taylor and Littler 1982). Measurements of the frequency and intensity of disturbance should be made in some way that is not dependent on the responses of the organisms present (because sometimes there are no organisms present) and this is often not difficult (e.g. Dayton 1971; Osman 1977; Sousa 1979a; Fletcher and Day 1983).

The list of things now regarded as "disturbances" includes fires, storms, logs, waves, sand, grazers, predators, starvation, rocks, mudslides, uplifting, trampling, earthquakes and treefalls, to name but a few (Dayton 1971; Grime 1973; Osman 1977; Connell 1978; Sousa 1979a, b, 1980, 1984; Paine and Levin 1981; Taylor and Littler 1982; Fletcher and Day 1983; Turner 1983; Dethier 1984). Central to the idea of a "disturbance" in most ecological models is the creation of free space or resources within the community, and all the factors listed above may do this. Also important, however, is the idea of an interruption to a sequence of species replacements (Connell 1978; Sousa 1979a, 1984). It follows from this that disturbance should not permanently change the environment, alter the pattern of development, and lead to the formation of a completely different community with different species abundant and new patterns in distribution and diversity (White and Pickett 1984). A log, for example, removes organisms but causes no major changes to the platform and the patch created is, eventually, re-occupied by similar species (Dayton 1971;

Paine and Levin 1981). In contrast, events such as uplifting or earthquakes may cause major changes to the habitat which make the re-establishment of a similar community unlikely.

For quite different reasons, factors such as grazing and predation should be distinguished from physical disturbances. First, the effects of grazers and predators may be greatly influenced by other organisms – either predators, competitors or prey – in the habitat, or their behaviour may change as a result of their own earlier actions. For example, whether or not the predatory whelk Morula marginalba creates free space by removing the barnacle, Tesseropora rosea, depends on the size and abundance of alternate prey (Underwood et al. 1983; Fairweather 1985). It is true that the observed effects of a physical disturbance may depend on the type of organism present – some may be more resistant or may modify the intensity of the disturbance (e.g. Wulff and Buss 1979) – but the physical action itself continues. The second difference is simply that agents of "biological disturbance" may themselves be affected by physical disturbance. Referring to all of these factors as "disturbance" ignores these potentially important interactions. Additional clarification of these concepts comes from Canny (1981) who notes that disturbances in thermodynamics are definable as increases in the rate of energy flow across the boundary to a system. Since agents of biological disturbance are part of the system (i.e. the community) their actions do not alter this rate; their energy is always contained within the system.

The community. Patterns in the community were not consistent with the role of disturbance as the single most important factor in all places. The percentage of the tops of rocks occupied by sessile species, predominantly algae, was never related to the size of the rock (Fig. 2; Table 1). Further, while some algae were less abundant on the smaller rocks, consistent with effects of disturbance, others were most abundant on these rocks, or occasionally on rocks in the middle size-classes. The assemblages on the largest rocks were more diverse (McGuinness 1984b), but this could result from their larger surface-area sampling more of the available colonists (Osman 1977; Connor and McCoy 1979; McGuinness 1984a). Analyses taking this effect into account (McGuinness 1984b), revealed that for boulders at Cape Banks diversity was essentially equal on rocks of all sizes, further downplaying the importance of disturbance. At Long Reef, however, patterns consistent with an effect of disturbance were seen (McGuinness 1984b).

These results differ sharply from those observed in similar habitats elsewhere. Sousa (1979a, b, 1980) studied algal assemblages on boulders of similar sizes at a similar tidal height but found that total space occupied did increase with rock-size, with nearly 100% cover on all large rocks. Diversity, in contrast, was greatest on rocks of intermediate size. He explained these results by the Intermediate Disturbance Model (Grime 1973; Connell 1978). Diversity was small, and cover great, on the largest rocks because one foliose alga, resistant to physical stress and grazing, was able to outlast other species and dominate space. The greater rates of disturbance on somewhat smaller rocks prevented domination and allowed more species to co-exist. The very small rocks were so disturbed, however, that only the few species able to colonise and grow quickly were present.

Few of the patterns in abundance observed here could

result from domination of space in the absence of disturbance. Space was sometimes in short supply on the tops of rocks low on the shore, but the dominant species were always encrusting forms, *Ralfsia* and *Hildenbrandia*. In other places on the same shores these are readily overgrown by foliose species, such as *Polysiphonia* and *Ulva* (Jernakoff 1983; Underwood 1980, 1985) and the same was true on boulders (McGuinness, unpublished work; pers. obs.). Thus the decline in abundance of the foliose species with rock-size could not be due to a lack of space on the larger rocks.

An alternate explanation for these patterns involves the interaction of the effects of exposure during low tide and grazing, both known to be important on the open platform (Underwood 1980, 1985; Underwood and Jernakoff 1981, 1984). The time for which the top of a rock was exposed above water increased with rock-size (McGuinness and Underwood 1986). The difference was especially pronounced in the low-shore area where, during the average low-tide, small rocks were not exposed at all but the tops of large rocks were out of the water for up to two hours (McGuinness and Underwood 1986). The decline in the abundance of crusts with rock-size on this shore may have be due to this increase in period of exposure. At Cape Banks grazers were very abundant and were probably responsible for eliminating foliose algae; they are known to do this on the open platform nearby (Jernakoff 1983, 1985a; Underwood 1980, 1985; Underwood and Jernakoff 1981, 1984). Grazers were not abundant at all at Long Reef, especially on the smaller rocks (Table 4). This might well be due to the presence of much sand on this shore burying 60–100% of the undersides of the medium to small rocks and could have allowed foliose algae to become more abundant in this situation.

Disturbance by sand and waves did, however, appear to be of major importance to sessile species on the undersides of boulders. Patterns in diversity consistent with the Intermediate Disturbance Model were observed in the low-shore areas on both platforms (McGuinness 1984b). Further, with very few exceptions, species were most abundant on the medium to large rocks (Table 3). Indeed, most space was typically occupied on the largest rocks and total cover often approached 100% (Fig. 2; Table 1). Sponges, ascidians and bryozoans often overgrew the more solitary forms, notably polychaetes and barnacles, and experiments revealed that the abundance of the latter forms was limited by a lack of space for settlement (McGuinness, unpublished work). High on the shore these interactions were not observed and competition for space could not reduce abundance on larger rocks.

These differences between upper and undersurface communities may in part result from the difference in frequency of disturbance. Sand rarely affected the tops of any but the very smallest rocks, though once or twice a year severe storms moved large amounts of sediment around and buried much of the high-shore area on both platforms leaving only the tops of the largest rocks exposed. In addition, rocks were moved two to five times more often than they were overturned, so undersides probably experienced more abrasion than the upper sides. Conclusive statements about processes in these communities await experimental tests of these hypotheses (see McGuinness 1987, unpublished work; McGuinness and Underwood 1986) but it nonetheless seems clear that the general, uncritical application of the

Intermediate Disturbance Model to these communities is unjustified.

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