

Recolonization of intertidal macroalgae in relation to gap size and molluscan herbivory on a rocky shore on the east coast of southern Africa

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ABSTRACT: The low intertidal on rocky shores in the Transkei region of southern Africa is characterized by extensive turfs of coralline algae. These turfs are punctuated by small gaps maintained by patellid limpets. Recolonization of macroalgae in experimentally cleared gaps of different sizes (0.5, 0.125 and 0.03 m²) was monitored over 1 yr in an initial experiment and then repeated and monitored over a 2 yr period. All quadrats were rapidly recolonized by a green/brown algal component, consisting of *Ralfsia* spp., *Ulva* spp., *Enteromorpha* spp. and *Iyengaria* sp. Although this component remained dominant there was some growth of coralline algae (*Arthrocardia* spp. and *Jania* spp.). Rate of recolonization was directly related to gap size, with the smallest gaps remaining relatively free of algae, and the largest showing greatest recovery after 12 mo. Even after 24 mo, however, the total algal cover was only between 10 and 50 % of that in undisturbed control quadrats. Grazer density (*Patella longicosta*, *P. oculus*, *Oxystele tabularis*) was highest in small gaps and there was a direct relationship between the number of grazers and the ratio of bare rock to algae. A model of the interactions between grazers and algae is discussed in terms of human exploitation of patellid limpets and the implications of this for low-shore community structure.

INTRODUCTION

The structure of rocky intertidal communities reflects the spatial and temporal integration of a number of biotic and abiotic factors. In the case of plant communities numerous studies have attested to the importance of such factors as herbivory (Southward 1956, Raffaelli 1979, Underwood 1980, Underwood & Jernakoff 1981, Cubit 1984, Jara & Moreno 1984, Duggins & Dethier 1985, Geller 1991, Beovich & Quinn 1992), recruitment (Jernakoff 1983, Sousa 1984), competition (Duggins & Dethier 1985, Steneck et al. 1991) and disturbance (Emerson & Zedler 1978, Sousa 1984). These factors generally exert their influence directly by acting on individual plants or their propagules. The complexity of interactions between the components of intertidal communities may, however, result in indirect effects which, although sometimes subtle, can alter community structure in important ways. External forces, such as human exploitation, acting on one or more components of the community, may also affect

community structure by causing release from predation or grazing pressure (Moreno et al. 1984, 1986, Oliva & Castilla 1986).

Some sections of the east coast of southern Africa are subject to shellfish gathering by local people (Lasiak & Dye 1989, Lasiak 1991). The lower tidal levels of these exploited rocky shores are usually dominated by an extensive turf of coralline algae. Although stable and persistent the turf is often punctuated by gaps of 'bare' rock apparently maintained by grazing molluscs (Branch 1975). The structure of this mosaic, however, differs between exploited areas, where the turf is extensive, and those in which shellfish gathering is restricted and the mosaic consists of mussels, bare rock and coralline algae.

There has been much speculation about the consequences of shellfish gathering on these shores (Siegfried et al. 1985, Hockey & Bosman 1986, Hockey et al. 1988, Lasiak & Dye 1989, Lasiak 1991, Dye 1992). One of the major problems has been the difficulty of separating natural variability from anthropogenic ef-

fects (Dye 1988). Such problems can be resolved by using manipulative experiments to simulate natural disturbance and grazing (Underwood et al. 1983). The aim of the present study was to assess the response of the algal turf community on an exploited shore to experimental disturbance and to make testable predictions about the effects of grazer removal.

METHODS

Study sites. The study was carried out on an exposed rocky shore at Nqabara, 4 km south of the Dwesa Nature Reserve, on the east coast of southern Africa (28° 50' E; 32° 18' S). The shore, which consists of wave-cut shale platforms, experiences moderate to heavy wave action emanating from a southwesterly direction. The low shore (between the neap and spring low tide levels) is covered by an extensive turf of coralline algae about 20 mm thick consisting mainly of *Arthrocardia* sp. and *Jania* sp. (Table 1). Within this turf patellid limpets, such as *Patella longicosta* and *P. oculus*, and pulmonate limpets, such as *Siphonaria aspera*, maintain gaps of bare rock varying in area from ca 100 to 400 cm². Periwinkles (*Oxystele tabularis*) also graze in these gaps. Although a number of other macro-herbivores occur on these shores, only the key-hole limpet *Fissurella natalensis* is conspicuous during low tide. The gaps, although devoid of macroalgae, support a biofilm which includes bacteria and microalgae.

Experimental manipulations. Three 10 m long transects, ca 30 m apart, were established parallel to the sea and permanently marked with stainless steel rawl

bolts at each end. Three treatments, consisting of different sized quadrats from which macroalgae were removed, were established in triplicate at random intervals along each transect, giving a total of 9 replicates per treatment. The dimensions of the cleared areas were 71 × 71 cm, 35 × 35 cm and 18 × 18 cm respectively and the minimum distance between treatments was 1 m. Macroalgae were cleared from these experimental areas in spring (September) 1989, using a paint scraper and wire brush to simulate heavy grazing. No chemical treatment was applied as this may have contaminated surrounding algae and would have represented an unnatural level of disturbance. Triplicate 71 × 71 cm control areas were located in the undisturbed algal turf adjacent to each transect. Composition of the algal turf, on a wet mass basis, was determined from the material obtained from the largest cleared areas. The following September (1990) a second series of manipulations was initiated on the same experimental areas.

The recovery of algae was monitored at monthly intervals using 35 mm colour slides taken through stainless steel quadrats of appropriate size, divided in the case of the 2 larger sizes, into 100 squares using yellow nylon line. The smallest quadrat was divided into 25 squares. To facilitate correct placement of the quadrats a nylon rope, marked with the positions of the treatments, was stretched between the rawl bolts. The percentage cover of algae and the number of grazers were assessed only in the inner 75 % of the quadrats, leaving the remainder as a buffer zone. The surface area sampled in each treatment was the same each month. Two groups of algae were distinguished, i.e. green/browns and corallines (see Table 1). Monthly sampling was done over a 12 mo period in each experiment, with an additional survey being undertaken 24 mo after the start of the second experiment. Controls were surveyed at the start and after 12 mo in each experiment, as well as after 24 mo in the second experiment. Surveys of algal cover and grazer density (9 × 0.5 m²) were conducted concomitantly in the nearby Dwesa Nature Reserve.

In order to reduce temporal and spatial dependence, data on grazer density, coralline and green/brown algal cover were obtained from 3 separate subsets (n = 4) of each treatment selected randomly each month. Percent cover data were transformed to arcsin and all data tested for normality and homoscedasticity (Zar 1974) prior to analyses of variance which were performed after 3, 6, 9 and 12 mo in each experiment. An additional analysis was performed after 24 mo in the second experiment. Where significance was revealed Tukey's HSD test was used for further analysis (Wilkinson 1989). *T*-tests and Pearson correlation analyses were also used where appropriate.

Table 1. Wet-mass composition of the low-shore algal turf at Nqabara. (n = 9 × 0.5 m²). Species composition and density of grazers (ind. m⁻²) are also given

Species	% Wet mass (±SD)
Corallines	
<i>Arthrocardia</i> sp.	85.2 (12.6)
<i>Jania</i> sp.	5.3 (2.1)
Green/brown algae	
<i>Ralfsia</i> sp.	5.1 (4.5)
<i>Ulva rigida</i>	1.8 (1.2)
<i>Acrosorium</i> sp.	1.8 (1.1)
<i>Iyengaria stellata</i>	0.8 (0.8)
<i>Enteromorpha</i> sp.	0.5 (0.3)
Species	Density
Primary space grazers	
<i>Patella longicosta</i>	10.1 (1.0)
<i>Siphonaria concinna</i>	1.4 (1.2)
<i>Oxystele tabularis</i>	2.0 (1.1)

RESULTS

Figs. 1 & 2 show the recovery of algae and grazers following clearance in Expts 1 and 2 respectively. Patterns of algal recovery were similar in both experiments. Gaps were initially recolonized by green/brown algae, mainly *Ralfsia* sp. and *Enteromorpha* sp., which reached maximum cover (50 to 80 %) after 1 to 2 mo. Although some variability was evident, green/brown algae generally declined in all treatments and by the end of the experiments accounted for less than 10 % cover (Figs. 1 & 2).

Coralline algae (*Arthrocardia* sp. and *Jania* sp.) took longer to re-establish and reached maximum cover (30 to 40 %) 4 mo after clearing. This was despite the fact that the coralline algal crust could not be removed en-

tirely. It was observed, however, that the remains of the crust became bleached and either died off or were smothered by green/brown algae. The coralline algae also died back during the experiment but this was most evident in the small clearings where they accounted for approximately 10 % by the end of the experiments (Figs. 1 & 2). Algal cover was considerably lower by the end of the experiments than in adjacent control areas (see below). The ratio of bare rock to algae after 12 mo varied between 0.80 (± 0.05): 1 in the largest gaps and 5.67 (± 1.25): 1 in the smallest. Although data on the cover of algae in the peripheral buffer zone was not used in the present analysis, it was noted that coralline algae had encroached from the surrounding turf and dominated the periphery by the end of each experiment.

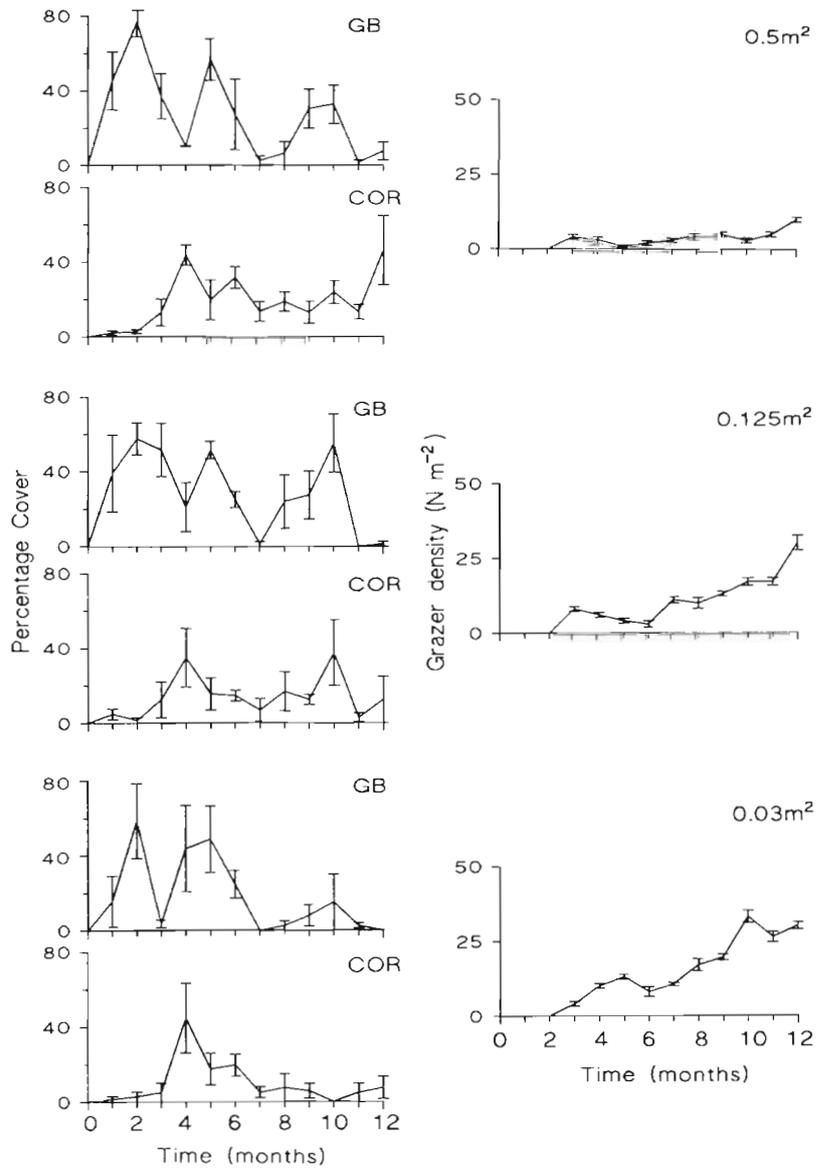


Fig. 1. Recovery of algae and grazers following clearance in Expt 1 (1989 to 1990) GB = green/brown, COR = corallines. Figures on the right indicate gap size. Vertical lines are standard errors (n = 4)

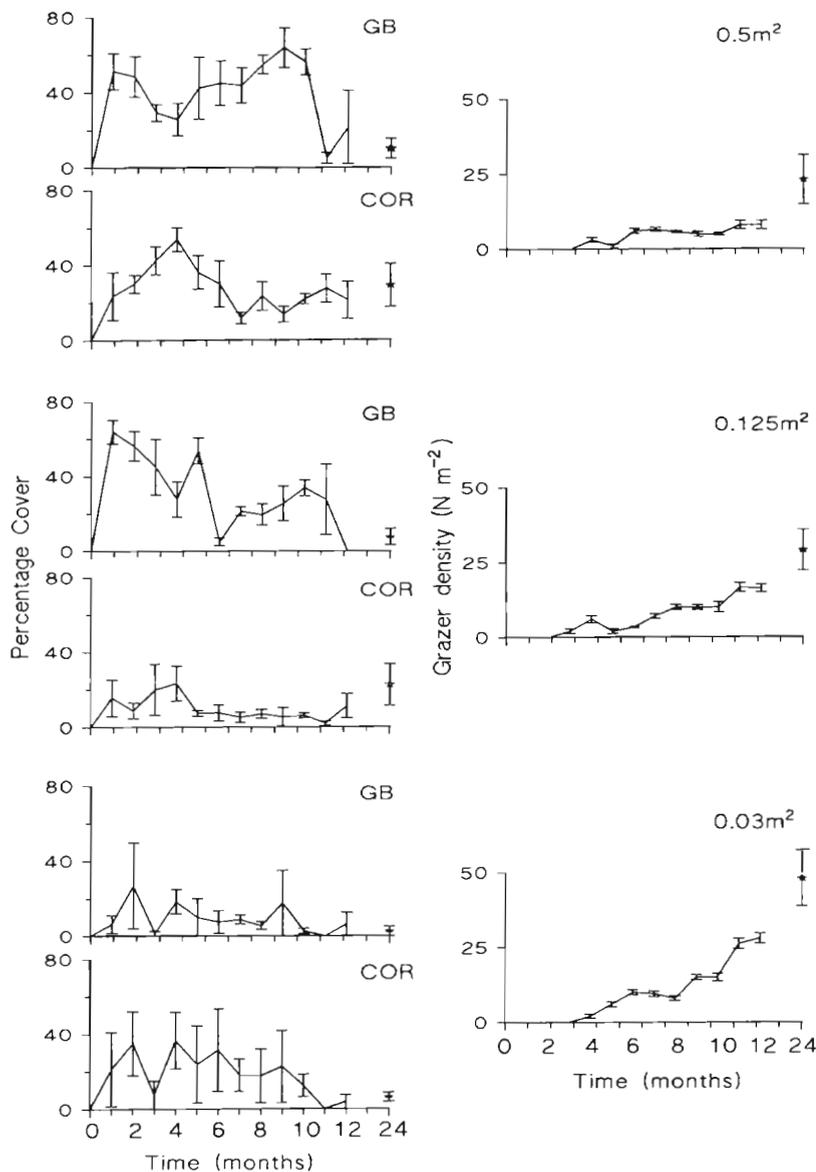


Fig. 2. As in Fig. 1 but for Expt 2 (1990 to 1992)

In contrast to the algae, the density of grazers, mainly *Patella longicosta* and *Oxystele tabularis*, increased steadily in all treatments after a 2 to 3 mo delay. By 12 mo grazer density was between 8 and 30 m^{-2} (Fig. 1), and by 24 mo there were 20 to 48 m^{-2} (Fig. 2). The smallest clearings supported the greatest density of grazers.

Fig. 3 shows the condition of control areas at the beginning and end of each experiment. Also shown are the results of a concomittant survey of algal cover and grazer density in the nearby Dwesa Reserve. In each case the first 12 mo point also serves as the initial survey for the second experiment. Little change occurred in the structure of the community at either site during the experimental periods. At Nqabara coralline algae accounted for more than 80 % cover with only a

small amount of green/brown algae present. Total algal cover was rarely less than 95 %. At Nqabara the mean ratio of bare rock to algae was 0.14 (± 0.05):1 after 12 mo and 0.11 (± 0.05):1 after 24 mo. The number of grazers varied between 10 and 15 m^{-2} , but declined to 5 m^{-2} by 24 mo.

The cover of algae was significantly lower at Dwesa than at Nqabara (Table 2). Coralline algae rarely exceeded 50 % cover, while 40 % of the substratum was devoid of macroalgae. The green/brown algal component was also slightly more abundant at about 10 % cover. The mean ratio of bare rock to algae was 0.77 (± 0.08):1 which was significantly higher than at Nqabara (t -test, $p < 0.007$, $n = 9$). The number of grazers (16 to 24 ind. m^{-2}) was significantly higher at Dwesa (t -test, $p < 0.03$, $n = 9$).

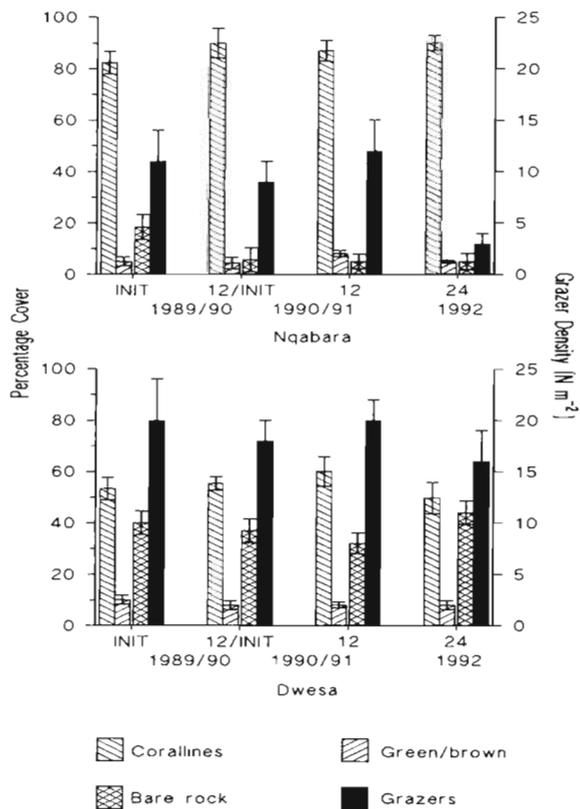


Fig. 3. Algal cover, bare rock area and grazer density, at the beginning and end of each experiment, in 0.5 m² control quadrats at Nqabara and Dwesa. Vertical lines indicate standard errors (n = 9)

Table 2. Comparisons of algal cover, bare rock and grazer density in control quadrats at Nqabara and Dwesa. *t*-tests, n = 9. NS: not significant

Time	<i>t</i>	<i>p</i>
Initial (1989)		
Corallines	26.854	<0.0001
Green/brown	-5.116	<0.0009
Bare rock	-6.030	<0.0004
Grazers	-10.444	<0.0001
12 mo (Expt 1) ^a		
Corallines	15.901	<0.0001
Green/brown	-3.920	<0.004
Bare rock	-8.605	<0.0005
Grazers	-11.627	<0.0001
12 mo (Expt 2)		
Corallines		<0.0001
Green/brown	-1.164	NS
Bare rock	-11.186	<0.0001
Grazers	-15.179	<0.0001
24 mo (Expt 2)		
Corallines	58.357	<0.0001
Green/brown	-5.000	<0.001
Bare rock	-18.127	<0.0001
Grazers	-19.404	<0.0001

^a Also represents the initial condition for Expt 2

Table 3. Analysis of variance of percent cover (arcsin) with the factors gap size and algal group for Months 3, 6, 9 and 12 in Expt 1 and Months 3, 6, 9, 12 and 24 in Expt. 2. n = 24 (3 treatments × 2 algal groups × 4 replicates). NS: not significant

Elapsed time	Factor	df	MS	<i>F</i>	<i>p</i>
Expt 1					
3 mo					
Size		2	0.388	5.425	<0.014
Algae		1	0.578	8.074	<0.011
Size × Algae		2	0.152	2.125	NS
6 mo					
Size		2	0.048	3.841	<0.041
Algae		1	0.005	0.442	NS
Size × Algae		2	0.012	0.980	NS
9 mo					
Size		2	0.159	2.853	<0.084
Algae		1	0.141	2.537	<0.0001
Size × Algae		2	0.044	3.930	NS
12 mo					
Size		2	0.166	4.122	<0.034
Algae		1	0.227	5.628	<0.029
Size × Algae		2	0.040	1.000	NS
Expt 2					
3 mo					
Size		2	0.618	12.983	<0.0001
Algae		1	0.000	0.001	NS
Size × Algae		2	0.075	1.580	NS
6 mo					
Size		2	0.282	9.431	<0.002
Algae		1	0.011	0.378	NS
Size × Algae		2	0.023	0.781	NS
9 mo					
Size		2	0.180	3.307	<0.060
Algae		1	0.480	8.803	<0.008
Size × Algae		2	0.113	2.071	NS
12 mo					
Size		2	0.072	4.295	<0.030
Algae		1	0.005	0.280	NS
Size × Algae		2	0.010	0.607	NS
24 mo					
Size		2	0.051	3.089	<0.070
Algae		1	0.051	3.104	NS
Size × Algae		2	0.015	0.894	NS

Analyses of variance at 3, 6, 9 and 12 mo in the first experiment, as well as at 24 mo in the second, revealed that gap size had a significant influence on the recovery of algae (Table 3). Post-hoc tests consistently revealed that all treatments differed from each other (Tukey HSD; *p* < 0.05 in each case). The largest clearings supported the greatest cover of algae, and by the end of the experiments these gaps had broken up into a mosaic of small areas of bare rock separated by patches of coralline algal turf. In contrast, the small

Table 4. Analysis of variance of grazer density (ind. m⁻²) with the factor gap size for Months 3, 6, 9 and 12 in Expt 1 and Months 3, 6, 9, 12 and 24 in Expt 2. n = 12. NS: not significant

Elapsed time Factor	df	MS	F	p
Expt 1				
3 mo Size	2	64.000	36.000	<0.0001
6 mo Size	2	134.333	36.636	<0.0001
9 mo Size	2	149.333	20.364	<0.0001
12 mo Size	2	533.333	48.980	<0.0001
Expt 2				
3 mo Size	2	5.333	6.000	<0.022
6 mo Size	2	46.083	24.761	<0.0001
9 mo Size	2	100.000	37.583	<0.0001
12 mo Size	2	404.083	47.384	<0.0001
24 mo Size	2	169.333	0.301	NS

cleared quadrats were usually devoid of macroalgae. There were no significant interaction terms indicating that gap size affected both groups of algae in a similar way.

Table 4 shows the results of single factor analyses of variance of grazer density as a function of gap size at various times. Gap size had a significant influence on

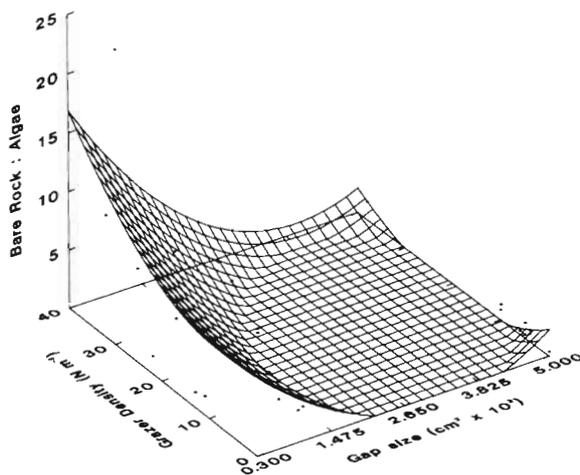


Fig. 4. Graphical representation of the relationship between gap size, grazer density and the ratio of bare rock to algae over time at Nqabara. Expts 1 and 2 combined

Table 5. Pearson correlations between green/brown and coralline algal cover and between grazer density (ind. m⁻²) and algal cover as a function of time (excluding Month 1). NS: not significant

Time Factor	r ²	p
Expt 1 (1989 to 1990; n = 33) ^a		
Green/brown vs corallines	NS	
Grazers vs green/brown	-0.461	<0.007
Grazers vs corallines	NS	
Grazers vs total cover	-0.486	<0.004
Expt 2 (1990 to 1992; n = 36) ^b		
Green/brown vs corallines	NS	
Grazers vs green/brown	-0.507	<0.002
Grazers vs corallines	NS	
Grazers vs total cover	-0.546	<0.001
Expt 1 vs Expt 2 (excluding 24 month point) (n = 33) ^a		
Green/brown	0.586	<0.0001
Coralline	0.490	<0.004
Total algal cover	0.717	<0.0001
Grazers	0.902	<0.0001

^a n = 11 × 3 treatments
^b n = 12 × 3 treatments

the recruitment of grazers during the first 12 mo in both experiments. Grazer density was invariably highest in the small clearings (Figs. 1 & 2). Once again post-hoc tests revealed that all treatments differed significantly from each other (Tukey HSD; p < 0.001 in all cases). Gap size had ceased to influence grazer density by 24 mo when all treatments supported a similar density of grazers.

Table 5 shows the results of correlation analyses of algal cover and grazer density with time, which are based on the combined data from the 3 treatments each month (excluding Month 1). There were no significant correlations between the algal groups or between grazer density and coralline algal cover. There were, however, significant negative correlations between green/brown algal cover and grazer density as well as between total algal cover and grazer density. This suggests that the temporal decline in algal cover was due to grazing effects. Also shown in Table 5 are correlations between the 2 experiments in the recovery of the algal groups and grazers (excluding Month 24 in Expt 2). The high positive correlations confirm the impression gained from Figs. 1 & 2 that the patterns of recovery were similar in each experiment.

The above results indicate that there were significant interactions between gap size, algal recolonization and grazer density. These interactions are summarized in 2 multiple regression models. They are derived from a combination of the data from both experiments and all treatments for Months 3, 6, 9 and 12,

as well as Month 24 in the second experiment. In the first model the ratio of bare rock to algae (BR:A) is related to time from disturbance (t) and intensity of disturbance (s ; expressed as gap size in cm^2) as follows:

$$\text{BR:A} = 7.300 + 0.694t - 8.461s - 0.020t^2 + 1.273s^2$$

and $r = 0.661$, $n = 27$, $p < 0.01$.

In the second model grazer density (G) is related to time and disturbance as follows:

$$G = -0.390 + 2.346t - 3.915s - 0.413t^2 - 0.025s^2$$

and $r = 0.909$, $n = 27$, $p < 0.0001$.

Fig. 5 gives a graphical representation of the relationship between these 3 parameters. The figure shows that, in the absence of grazers, any gap will tend to become covered by algae and exhibit a low BR:A ratio. This tendency is, however, modulated by increasing grazing pressure. Since this is generally greatest in small gaps, these will tend to have the highest BR:A ratios. The graininess of the low shore mosaic of turf and gaps is thus determined to a large extent by grazing pressure.

DISCUSSION

The present study has shown that gap size has a significant influence on algal recolonization. Smaller gaps in general exhibit poor recovery compared to large gaps. A similar finding was reported by Sousa (1984) who cleared gaps in beds of *Mytilus californianus* in northern California, USA. He found that algal recovery was poor at the periphery of gaps and related this to grazing pressure. Grazers, particularly limpets, which invaded the clearings from the surrounding mussel bed, were able to eliminate the grazer-vulnerable algae. The situation at Nqabara differs in that gaps were created within an algal turf which supports relatively few grazers. Recolonization of algae therefore arises through settlement of spores and regrowth of existing thalli as well as through encroachment from the periphery. By the end of the study the cover of algae was higher at the periphery than in the centre in all but the smallest gaps. Grazer-resistant corallines dominated the periphery while the centre was dominated by grazer-vulnerable species such as ulvoids. As found in previous studies it appears that grazer abundance is the key factor in determining the extent and type of algal recolonization (Suchanek 1978, Underwood 1980, 1981, Paine & Levin 1981, Sousa 1984).

Although the effects of seasonal disturbance were not investigated in the present case, some studies have

shown that succession, if not the climax state, is affected by the timing and frequency of disturbance (Dayton 1971, Emerson & Zedler 1978). Such effects have been short-lived and, given the relative stability and uniformity of the algal turf at Nqabara, it seems unlikely that seasonal fluctuations have long-lasting effects.

How do grazers become established and maintain gaps in the face of encroachment by grazer-resistant algae such as corallines? Since most of the grazers in the present study cannot cross the algal turf because of lack of adhesion (Underwood 1981) only 2 possibilities exist for the establishment of grazers in the cleared areas. Grazers could invade clearings by cutting through from adjacent gaps (see below) or larvae could settle directly into cleared areas. The former was not observed in the present study and it must be concluded that direct settlement occurred. This is supported by the observation that initial grazers were small and, although no measurements were made, appeared to increase in size with time. The grazers studied at Nqabara feed largely on bacteria, diatoms and spores of larger algae. Their control of primary space is therefore indirect and acts through preventing the establishment of macroalgae. In a recent study on the Oregon (USA) coast Farrell (1991) found that limpets initially slowed the rate of recolonization of macroalgae. The eventual establishment of barnacles, however, facilitated the growth of macroalgae by inhibiting the grazing activity of limpets. In a similar study on the east coast of Australia Beovich & Quinn (1992) found that the limpet *Siphonaria diemenensis* had a significant effect on the abundance of mid-littoral foliose algae.

The foraging behavior of limpets offers another possibility for maintaining primary space. Individuals of species such as *Patella longicosta* and *P. oculus* are often found at the edge of gaps partially wedged under the surrounding algal turf. This continual undercutting of the turf could presumably prevent encroachment provided that the gap size was small enough for the grazers to cover the periphery frequently. Large gaps would either break up into smaller gaps by recolonization from within or be reduced in size by encroachment. Furthermore, large grazers would be expected to maintain large gaps and the resulting mosaic would be a function of both the abundance and size of grazers (Geller 1991). The presence of limpets also appears to facilitate the activity of other primary space grazers which, on their own, would be unable to maintain bare rock. Species such as *Oxystele tabularis*, *Cellana capensis* and *Siphonaria aspera* may be favoured by the presence of limpets provided that microalgal productivity is high enough (Dye & White 1992).

One indicator of low-shore mosaic structure is the

ratio of bare rock to algae (BR:A). The model derived from the Nqabara data clearly shows the relationship between grazer abundance and BR:A ratio. It predicts that any factor which influences the abundance of grazers will affect the structure of the mosaic. A gap created on a shore on which grazers are scarce will be rapidly recolonized by algae while gaps will persist on shores where grazers are abundant. A comparison of the mosaic at Nqabara with that at Dwesa reveals a much higher ratio of bare rock to algae at Dwesa. According to the model this would result from increased grazing pressure at Dwesa and indeed there are almost twice as many grazers at Dwesa than at Nqabara. Furthermore, Lasiak (1991) found that, among low-shore limpets, *Patella oculus* was not only more abundant at Dwesa but was also 32 % larger than at Nqabara. Her findings clearly showed that differences in grazer population structure between the 2 shores resulted from human shellfish exploitation. In the present study a significant number of grazers, particularly limpets, colonized the gaps. Presumably these will be removed when they reach harvestable size at 35 mm (Lasiak 1991) and, unless they are replaced by new recruits, the gaps will become covered by algal turf.

A number of studies have attempted to quantify the effects of this exploitation (Mills 1985, Hockey et al. 1988, Lasiak & Dye 1989). Some studies have suffered from inadequate temporal and spatial replication (Siegfried et al. 1985, Hockey & Bosman 1986) and only one has involved limited experimental manipulation (Dye 1992). In that study it was shown that exploitation of mussels (*Perna perna*) from the infratidal on these shores often results in the establishment of coral-line algal turf. It was predicted that grazing pressure would modify the recolonization of mussels in a similar way to that for algae in the present study. The model proposed in the present paper, although limited by its deterministic nature, provides a framework for understanding the structure of the low shore in this region. Extensive algal turfs with small gaps which close rapidly would be predicted on shores subjected to shellfish gathering. In protected areas, however, a more open or grainy mosaic of grazed rock and algal patches would be expected. A greater abundance of grazer species that are normally unexploited would also be expected in protected areas. However, while the evidence at hand is compelling, verification of the model awaits the completion of further experiments which involve the manipulation of grazing pressure.

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