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Primary succession on a seasonal tropical rocky shore: the relative roles of spatial heterogeneity and herbivory

Gray A. Williams[1,*], Mark S. Davies[2], Sanjay Nagarkar[1]

[1]Department of Ecology and Biodiversity, The Swire Institute of Marine Science, The University of Hong Kong, Pokfulan Road, Hong Kong

[2]Ecology Centre, University of Sunderland, Sunderland SR1 3SD, United Kingdom

ABSTRACT: Hong Kong is within the tropics and has a seasonal climate. In winter, shores support patches of ephemeral macroalgae and areas of seemingly bare rock close to crevices where molluscan herbivores are abundant. Using a factorial design of herbivore exclusions in areas far and close to crevices, the development of algal assemblages was monitored in mid-shore, cleared areas, in winter. To estimate the role of herbivore mucus deposition, half the treatments received a mucus application. Algal development was estimated from macroalgal and biofilm development and chlorophyll *a* levels. In all areas, biofilms (diatoms, unicellular cyanobacteria) developed rapidly in herbivore exclusions followed by ephemeral macroalgae (*Enteromorpha* spp. and *Porphyra suborbiculata*). In herbivore access treatments, however, the algal assemblage was influenced by treatment location; few macroalgae developed in areas close to crevices, and the rock was dominated by cyanobacteria. A negative relationship between macroalgae and biofilms suggested that ephemeral algae were competitively dominant. In areas distant from herbivore refuges, ephemeral macroalgae did develop, illustrating that the effectiveness of molluscan herbivores was limited to 50 to 100 cm from these refuges. The absence of large herbivorous fish, and the sparse numbers of herbivorous crabs at this site, means that algae can achieve a spatial escape from consumption, and where this occurs competition between producers is important in assemblage development. Mucus appeared to play a limited role, only sometimes stimulating initial stages of unicellular cyanobacteria and macroalgae. With the onset of summer, macroalgae died back, and rock space became available for colonization. Unicellular cyanobacteria developed rapidly but were replaced in all treatments by the encrusting macroalga, *Hapalospongidion gelatinosum*, which dominated treatments until the end of the experiment. On seasonal, tropical shores processes influencing community structure can, therefore, be temporally variable and their relative importance, even at the same shore level, can change with season.

KEY WORDS: Biofilm · Cyanobacteria · Herbivory · Hong Kong · Mucus · Spatial heterogeneity · Succession · Tropical rocky shore

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INTRODUCTION

Herbivores influence the distribution, diversity and abundance of macroalgal assemblages on shores of varying exposures world-wide (reviewed by Hawkins & Hartnoll 1983, Vadas 1985). The direct impacts of herbivores are dependant on a number of factors, of which environmental conditions have a great influence in moderating algal-herbivore interactions (Underwood & Jernakoff 1981, Underwood 1985). Herbivores also influence the biomass and diversity of microalgal assemblages (Nicotri 1977) although studies on this role are scarce. The physical act of grazing is not, however, the sole impact of herbivores as deposition of mucus can trap and stimulate microalgal growth (see Davies & Hawkins 1998 for review), and herbivore excretion may fertilize algal growth (Carpenter 1986) and aid dispersal (Santelices & Ugarte 1987).

*E-mail: hrsbwga@hkucc.hku.hk

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Herbivores are rarely evenly distributed, and as a consequence, predation pressure is spatially and temporally variable resulting in density effects on the prey species (Underwood et al. 1983, Hartnoll & Hawkins 1985). Variation in herbivore density within a shore can influence spatial patterns of algal abundance resulting in patches of different species which have escaped grazing, are stimulated by low or high grazing pressure, or often bare areas of rock (commonly referred to as halos) within areas of high algal abundance. Such halos are often focused on spatial refuges in the rock surface where herbivores aggregate when at rest, and leave to forage (Hawkins & Hartnoll 1983, Chapman & Underwood 1992).

On some tropical shores, where environmental conditions are relatively constant, species distribution patterns and abundance are very patchy (e.g. the Bay of Panama, Lubchenco et al. 1984) and set by predation pressure from a diversity of consumers in the low-shore and availability of refuges from thermal and desiccation stress in the mid-shore (Menge & Lubchenco 1981, Garrity 1984, Menge et al. 1985, 1986). As a result, species are found in cracks and crevices which provide shelter from predators and a relatively cool or damp habitat (reviewed by Brosnan 1992). The distribution of these habitats, and the limited movement of species from these areas can cause a patchy mosaic of species (Levings & Garrity 1983).

Spatial heterogeneity can, therefore, have direct (species distribution patterns) and indirect (impact of consumers, especially herbivores) influences on community dynamics on tropical rocky shores. On a small scale, near refuges, consumer pressure is likely to have a strong influence, as these areas would be heavily cropped but areas further away would receive little influence. High grazing pressure may also have positive effects, stimulating algal production (Carpenter 1986) and indirectly enhancing microalgal and bacterial growth (Davies & Hawkins 1998), which may increase primary production. There may, therefore, be an interaction between grazing removing algae and bacteria, and a possible influence of enhanced productivity, especially in the epilithic biofilm, which on tropical shores is mainly composed of cyanobacteria (Nagarkar & Williams 1997, 1999, Nagarkar 1998a,b).

The relative importance of predation/herbivory has been hypothesized to vary with environmental conditions (Brosnan 1992), following models proposed by Menge & Sutherland (1976, 1987). In physically harsh environments, predation is assumed to be unimportant, whereas in more benign environments herbivory plays a strong role in community structure. The importance of herbivory may also vary temporally where shores experience both benign and harsh environments in different seasons (Brosnan 1992). Such is the case for many seasonal, tropical shores with monsoonal climates (e.g. Hong Kong, India and West Africa). Hot summers kill foliose macroalgae and invertebrates, freeing primary space, and mobile species retreat lower on the shore and take refuge in crevices (Lawson 1966, John et al. 1992, Kaehler & Williams 1996, Nagarkar & Williams 1999). In winter, conditions ameliorate, macroalgae flourish and mobile invertebrates extend their vertical range and their foraging periods (Banaimoon 1988, Murthy et al. 1989, Williams & Morritt 1995). The structuring role of spatial heterogeneity and environmental harshness can, therefore, vary temporally on such seasonal tropical shores.

This paper investigates small scale (metres) spatial patterns of macroalgal and biofilm distribution relative to herbivore refuges on a seasonal, tropical, rocky shore. Spatial patterns of succession were monitored on cleared rock surfaces in close proximity to crevices and areas distant from these habitats. Variation in succession in these areas may be the result of a location effect (i.e. algal development being influenced by the habitat itself) or an interaction between the crevices and grazing pressure, associated with the fact that grazers seek refuge in these areas and forage over a limited range around these crevices. This was tested using herbivore exclusions in areas close to and far away from crevices, where the interaction between these factors would elucidate the processes affecting algal distribution. Direct and indirect impacts of herbivores on macroalgal and biofilm assemblages were tested by allowing herbivores to leave mucus trails in herbivore exclusions in a factorial design with the location and exclusion treatments. Temporal changes in algal development in these treatments were followed between winter and summer (i.e. from benign to harsh conditions).

MATERIALS AND METHODS

Study site and timing. Experiments were conducted on a moderately exposed, gently sloping, granodiorite shore at Cape d'Aguilar, Hong Kong (22° 20′ N, 114° 10′ E). Maximum tidal range at this site is 2.5 m and tides are predominantly mixed semi-diurnal (Morton et al. 1996). The experimental area (~40 m^2, between 1.50 and 1.75 m above Chart Datum) was subdivided into a grid and 50 × 50 cm, double-strung 100-point quadrats were sequentially placed to assess macroalgal and herbivore distribution.

Experiments were initiated in April 1995 (end of winter) and terminated in mid-July 1995 (summer). Hong Kong has a hot and wet summer (July to September; mean surface seawater temperature ~27°C, mean air temperature ~28°C, maximum air temperature = 36°C, rock temperatures can exceed 50°C) and a cool and

dry winter (December to March; mean water temperature ~17°C, mean air temperature ~15°C). The period from April to May represents the transition from winter to summer. Air temperatures in April 1995 were relatively cool (mean ~26°C) but increased during the experiment and after ~40 d (mid-May) reached ~30°C (maximum temperature = 33.6°C). Tidal height also varied temporally, the height of low water tides decreasing towards summer (by ~0.4 m).

Manipulative experiments. A 4-factor experiment was used to investigate whether the pattern of macroalgal distribution was a result of herbivore grazing, mucus deposition by herbivores, a location effect or interactions between these main treatments. Ten areas (Areas) of the shore were selected, which either had a high cover of erect macroalgae (>70% cover) and were >1 m away from a crevice (designated +A [Algae] areas, n = 5) or a relatively sparse cover (<20% cover) and within 50 cm of a crevice (designated –A areas, n = 5). This treatment, therefore, accounted for both variation in algal cover and distance from crevices as these influences were linked. Within these areas molluscan herbivores were either excluded, or allowed access to 23 × 23 cm areas. Completely fenced areas (–H [herbivores]), using 25 × 25 cm (1 cm edge) wire mesh (5 × 5 mm) fences, prevented molluscs from entering the experimental areas; however, fish and herbivorous crabs could potentially enter these areas. In herbivore access areas (+H), a partial fence (2 L-shaped corners) was used to control for possible procedural effects. Two of each treatment were randomly established in each of the algal areas and in 1 of each (randomly assigned) herbivores were allowed to lay mucus trails (see below). This treatment, in herbivore exclusions, allowed the influence of grazing and mucus deposition to be separated experimentally. The full experimental design included 2 herbivore treatments and 2 mucus treatments in locations with dense and sparse algal cover replicated in 5 areas ($\sum n = 2 \times 2 \times 2 \times 5 = 40$). This experimental design did not include a natural control treatment (i.e. open plots which allow herbivores access) which may have limited the generality of the findings. Partial fence treatments, in similar manipulations on Hong Kong's moderately exposed shores, proved not significantly different to unfenced, open areas, suggesting that results from this treatment are comparable to unmanipulated areas (Williams 1994). Rock surfaces were scraped clean and then blowtorched to white hot on 3 consecutive days prior to the initiation of the experiment.

Mucus application. To achieve a coating of mucus (+M) 4 *Cellana toreuma*, 10 *Nerita albicilla* and 20 *Monodonta labio* (the most abundant species, Table 1) were stimulated, by spraying with seawater, to crawl over the experimental surfaces for 15 min, at approximately weekly intervals. The molluscs grazed slightly upon these treatments whilst moving; however, this effect is thought to have been minimal. Treatments which did not receive a mucus application (–M) were also sprayed with seawater as a procedural control. Individual molluscs were used on 2 experimental areas and then replaced with new ones.

Pedal mucus production was estimated by stimulating molluscs to crawl over 25 × 25 cm glass plates in the laboratory. After 15 min, the individuals were removed, the mucus was scraped from the glass and first wet and then dry weighed (70°C to constant weight). An average of 0.0132 g dry weight ($\pm 1.06 \times 10^{-3}$ SD, n = 4) was laid down by the herbivores.

Macroalgal and biofilm abundance. To investigate changes in macroalgal (i.e. visual) abundance, the percentage cover was scored using a 23 × 23 cm, 100-point, double-strung quadrat at approximately 7 to 14 d intervals (depending on tidal conditions). Macroalgae were scored to species, except the turfs of green algae which were scored as 'green turfs' (primarily *Enteromorpha* spp.). A change in the rock colour (usually a green colour) was scored as a 'biofilm'.

Rock chips (~1.5 cm^2) were also removed, fixed in 2.5% (v/v) glutaraldehyde, air-dried, gold-palladium coated and viewed under the scanning electron microscope (SEM, Leica Cambridge S440). The percentage cover of biofilm species was scored from 10 random fields of view at fixed magnification (500×) using a 100-point grid (see Nagarkar & Williams 1997). Species were scored in 9 broad groups: diatoms; sporelings of *Porphyra subaorbiculata, Enteromorpha* spp. (macroalgae); unicellular cyanobacteria; *Phormidium* spp.; *Lyngbya* spp.; *Calothrix* spp.; and the encrusting algae *Hapalospongidion gelatinosum* and *Hildenbrandia rubra*. Only abundant groups (>5% cover at each time period) were statistically analyzed.

Changes in overall algal biomass (macroalgae and biofilm) were assessed by chlorophyll *a* (chl *a*) analysis of rock chips (~2.5 cm^2) taken from each treatment, again at 7 to 14 d intervals and extracted using hot methanol (see Nagarkar & Williams 1997). Areas from which rock chips were removed remained visible in the treatments and accounted for <10% of individual areas at the end of the experiment. These areas were not scored during the percentage cover estimates, nor were subsequent rock chips taken from the same areas.

Statistical analysis. A 4-way, mixed model, analysis of variance (ANOVA) was used to investigate variation in percentage cover of visible algae, and the biofilm scored under the SEM. Herbivore exclusion or access (– or +H) and mucus application (+ or –M) were fixed, orthogonal effects. The treatment with sparse algal cover (–A, close to crevices) and high algal cover (+A, far from crevices) was also a fixed effect. A fourth factor, the individual areas (Areas, n = 10), was random

and nested within the algal cover treatment. The use of unreplicated treatments within specific locations (algal areas) means that the analysis cannot detect small-scale changes in the effects of herbivores and mucus coating in the individual areas (interactions with the term Areas [A]). Time was not included as a factor as temporal readings were non-independent. The percentage cover data were arc-sine transformed prior to analysis and Student-Neumann-Keuls tests used to separate significant means (Underwood 1997). As rock chips were also repeatedly sampled from the same treatment for chl *a* analysis, these data are also temporally non-independent. Chlorophyll data were, therefore, only analysed for the time of peak levels (t = 32 d, 18 May). Chl *a* data failed Cochran's test for homogeneity of variances, despite subsequent transformations. The outcome of this ANOVA should, therefore, be interpreted with caution, although as group sizes were equal, ANOVA is thought to be relatively robust to such heterogeneity (Underwood 1997).

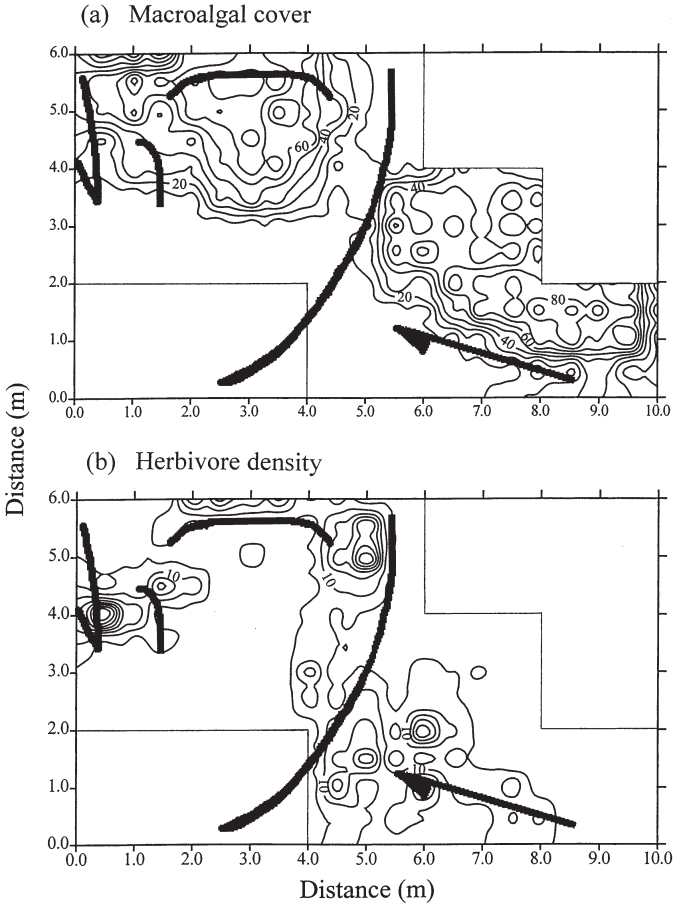

Fig. 1. (a) Contour map to illustrate variation in percentage cover of macroalgae (turf forming green algae) at the experimental site at Cape d'Aguilar, Hong Kong, in May 1995. Contours connect 10% isolines; (b) Contour map to illustrate variation in abundance of herbivorous molluscs (see Table 1 for species list) at the experimental site, Cape d'Aguilar, Hong Kong, in May 1995. Contours connect 10 molluscan herbivores 0.25 m^{-2} isolines. For both panels, the location of crevices (impressions in the rock surface greater than 3 cm) in the rock substratum are indicated by the thick lines

RESULTS

Initial assemblage structure

Dense green algal turfs (e.g. *Enteromorpha* spp. and *Ulva* spp.) were found on relatively homogeneous bedrock (Fig. 1), whilst areas in close proximity to crevices and surface irregularities tended to have low algal cover, or a thin film of *Hildenbrandia rubra.* Numerous herbivorous molluscs were patchily distributed in these crevices and depressions (Fig. 1, Table 1). Lower on the shore, films of *H. rubra* and patches of *Hapalospongidion gelatinosum* and *Ralfsia expansa* were found as well as a number of other herbivores (e.g. *Lunella coronata* and *Chlorostoma* spp., see Williams 1993a, Kaehler & Williams 1996). Overall there was a negative relationship between cover of green turfs and the abundance of herbivores (Slope = –0.55; ANOVA, $F_{1, 158}$ = 5.88, p = 0.016).

Macroalgal and biofilm abundance (visual cover)

Succession from burnt rock surfaces was rapid in all treatments where biofilms quickly developed (after 8 d, Fig. 2) especially in herbivore exclusions (~80% cover

Table 1. Mean densities (±SD) of abundant species (>0.1 0.25 m^{-2}) and maximum densities of molluscan herbivores at the study site at Cape d'Aguilar, Hong Kong

Species	Density 0.25 m^{-2}		
	Mean	SD	Maximum
Monodonta labio	3.95	7.72	44
Nerita albicilla	0.90	2.2	18
Cellana toreuma	0.80	1.9	14
Patelloida pygmea	0.39	1.0	5
Lunella coronata	0.39	0.96	5
Acanthopleura japonica	0.32	1.4	11
Chlorostoma spp.	0.12	0.59	5
Total herbivores	**7.14**	**10.1**	**54**
Also recorded (<0.1 0.25 m^{-2})			
Siphonaria japonica			2
Siphonaria atra/sirius			2
Patelloida saccharina			2
Nodilittorina vidua			2
Individuals recorded *Planaxis sulcatus*; *Monodonta neritoides*; *Nipponoacmea* sp.			

as compared to ~20 to 40% in herbivore access treatments, Fig. 2; Table 2). There were consistent differences in the algal assemblage supported in treatments with and without herbivores, in areas with and without algae, and also in the interaction between these 2 factors. There were also interactions between herbivore and mucus treatments and at one time a 3-way interaction (Table 2). Herbivore exclusions showed a succession from biofilms to green turfs (principally *Enteromorpha* spp., Fig. 2) which dominated (~80% cover) these treatments, in both locations, between Days 20 and 60. After 61 d, however, the green turfs bleached white and died and were replaced by colonies of the encrusting brown alga *Hapalospongidion gelatinosum*, which dominated until the end of the experiment (Fig. 2).

Areas which allowed herbivores access, in general, did not develop such dense green turfs (Fig. 2), but maintained a persistent, visual biofilm for most of the experiment (Table 3). These films also burnt off and were replaced towards the end of the experiment by *Hapalospongidion gelatinosum*. Treatments in originally dense algal cover areas far from crevices (+A areas), supported a significantly higher cover of green turfs than treatments in originally sparse algal cover areas close to crevices where biofilms persisted (Fig. 2, Table 3).

The application of mucus alone had no impact on the development of the algal assemblage, but it had an interactive effect with herbivore treatments (Table 2). In the early stages of succession, in herbivore exclusions, green turfs were more abundant in areas which did not receive a mucus coating, whereas later in the succession biofilm cover was greater in areas which received a mucus coating (Table 3).

The interaction between algal areas and herbivore presence/absence revealed that where herbivores were excluded in areas with algae far from crevices, green turfs developed between 40 and 60 d, but did not persist (Fig. 2, Table 3). At the peak of their dominance (May 26), green turfs had the greatest cover in herbivore exclusions in originally high algal cover areas, followed by herbivore exclusions in originally sparse algal cover areas close to crevices (Fig. 2, Table 3). In treatments which allowed herbivore access, green turfs were also more abundant in originally dense algal cover areas far from crevices as compared to areas which originally had a sparse cover and were close to crevices (Table 3), indicating an interaction of location and herbivore presence/absence. Biofilm abundance was negatively associated with green turfs, being highest in herbivore access treatments where algal abundance was initially low, i.e. close to crevices (Fig. 2, Table 3). Biofilm cover was very low in herbivore exclusions in either algal location, owing to the high abundance of green turfs. The 3-way interaction (June 13) revealed that green turfs were more abundant in areas which originally supported algae, where a mucus coating was applied and where herbivores were allowed access (Table 3).

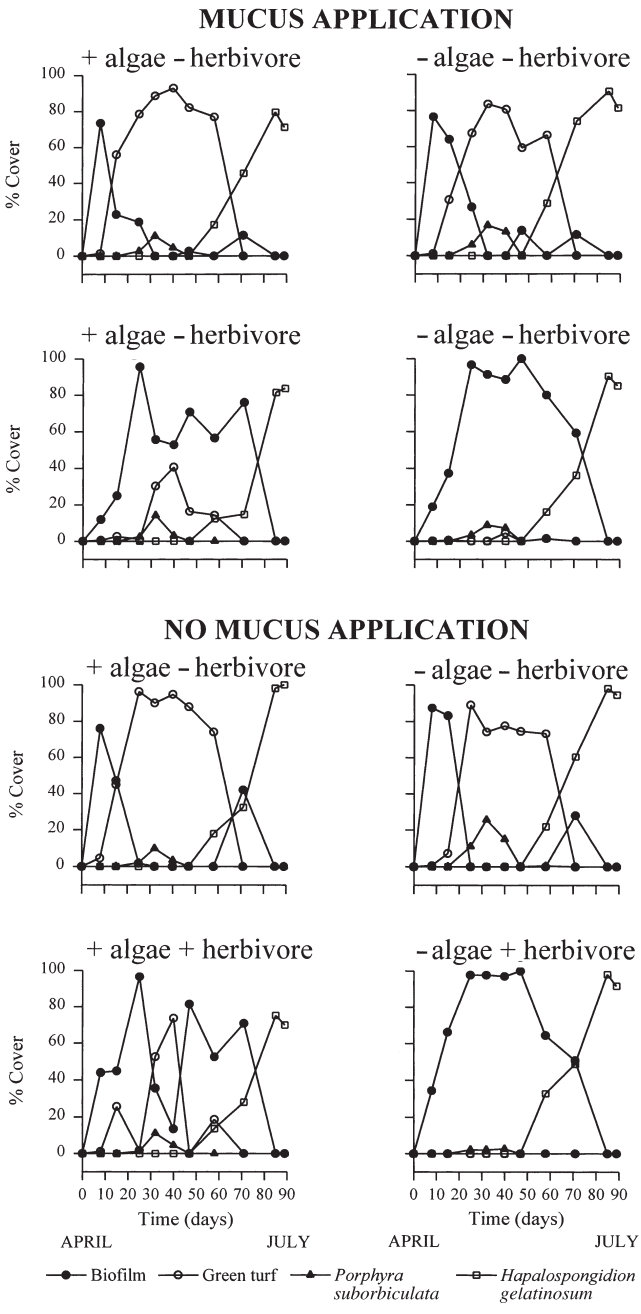

Fig. 2. Variation in mean percentage cover (n = 5) of visible macroalgae and biofilms in different experimental treatments with time (+algae = areas originally with dense algal cover; –algae = areas with sparse algal cover; +herbivores = partially fenced areas which allow herbivores access, –herbivores = fully fenced areas that excluded molluscan herbivores). Error bars have been omitted for clarity

Table 2. Summary of 4-way ANOVAs to investigate variation in visual cover of algae (F = biofilms; G = green turfs; *P* = *Porphyra suborbiculata*; *H* = *Hapalospongidion gelatinosum*) with time in experimental treatments (for denominators of *F*-ratios see Table 7). Data were arc-sine transformed prior to analysis. N = not significant, *p < 0.05

Algal groups		Sampling date									
	df	Apr 24	May 1	May 11	May 18	May 26	Jun 2	Jun 13	Jun 26	Jul 10	Jul 14
		F	F G	F G *P*	F G *P*	F G *P*	F G	F G *H*	F *H*	*H*	*H*
Algae (A)	1	N	* N	N N N	* * N	* * N	N N	N N N	N *	N	N
Mucus (M)	1	N	N N	N N N	N N N	N N N	N N	N N N	N N	N	N
Herbivores (H)	1	*	N *	* * *	* * *	* * N	* *	* * N	* N	N	N
A × M	1	N	N N	N N N	N N N	N N N	N N	N N N	N N	N	N
A × H	1	N	N N	N N N	* N *	* * N	N N	N N N	N N	N	N
M × H	1	N	N *	N N N	N N N	N N N	N N	N N N	* N	N	*
A × M × H	1	N	N N	N N N	N N N	N N N	N N	N * N	N N	N	N
Areas (Algae, A)	8	No test									
Areas (A) × M	8	No test									
Areas (A) × H	8	No test									
Areas (A) × M × H	8	No test									
Total	39										

Table 3. Student-Neumann-Keuls tests for significant factors from ANOVAs to investigate variation in visual cover of macroalgae at various sample dates (+A = areas originally with dense algal cover, –A = areas originally with sparse algal cover, +H = partial fence, herbivore access, –H = complete fence, herbivore exclusion). Where factors were involved in higher-order interactions, these have not been tested (NT)

	Sample date							
	Apr 24	May 1	May 11	May 18	May 26	Jun 2	Jun 13	Jun 26
Algal area								
Biofilms		–A > +A		NT	NT			
Green turfs				+A > –A	NT			
Hapalospongidion gelatinosum								–A > +A
Herbivore								
Biofilms	–H > +H		+H > –H	NT	NT	+H > –H	+H > –H	NT
Green turfs		NT	–H > +H	–H > +H	NT	–H > +H	NT	
Porphyra suborbiculata			–H > +H	NT				

Algal area × Herbivore	Algal area		Herbivore	
Biofilms (May 18)	+A	+H > –H	+H	–A > +A
	–A	+H > –H	–H	–A = +A
Porphyra suborbiculata (May 18)	+A	+H = –H	+H	+A > –A
	–A	–H > +H	–H	–A = +A
Biofilms (May 26)	+A	+H > –H	+H	–A > +A
	–A	+H > –H	–H	–A = +A
Green turfs (May 26)	+A	–H > +H	+H	+A > –A
	–A	–H > +H	–H	+A = –A

Mucus × Herbivore	Mucus		Herbivore	
Green turfs (May 1)	+M	–H > +H	+H	+M = –M
	–M	–H > +H	–H	–M > +M
Biofilms (Jun 26)	+M	+H > –H	+H	–M = +M
	–M	+H > –H	–H	+M > –M
Hapalospongidion gelatinosum (Jul 14)	+M	–H = +H	+H	–M = +M
	–M	+H = –H	–H	+M > –M

Algal area × Mucus × Herbivore

Green turfs (Jun 13)

Algal area × Mucus: All interactions: –H > +H

Mucus × Herbivore: All interactions: +A = –A, except +M × +H where +A > –A

Herbivore × Algal area: All interactions: –M = +M

The foliose red alga *Porphyra suborbiculata* appeared briefly between 20 and 40 d and was most abundant in herbivore exclusions in originally sparse algal cover areas and herbivore access treatments in areas which originally had a dense algal cover close to crevices (Fig. 3, Table 3). After 71 d, the encrusting brown alga *Hapalospongidion gelatinosum* settled and was more abundant in areas that had supported a sparse algal cover close to crevices and at the end of the experiment was more abundant in herbivore exclusions which had received a mucus coating although all treatments were dominated by a cover >65% of *H. gelatinosum* (Figs. 2 & 3, Table 3).

Microalgal and biofilm abundance (SEM)

A total of 13 cyanobacterial species, a variety of diatoms (e.g. *Melosira* sp., *Achnanthes* spp. and *Cocconeis* spp.), sporelings of macroalgae (*Porphyra suborbiculata* and *Enteromorpha* spp.) and crusts of *Hapalospongidion gelatinosum* could be identified under the SEM. Cyanobacteria species could be separated into 3 major groups (Table 4). Within these groups *Aphanocapsa sesciacensis* and *Dermocarpa* sp. were most abundant in the unicellular group and *Borzia* sp. within the non-heterocystous filamentous group. *Calothrix* spp. and *Lyngbya semiplena* were, in general, rare (<5% cover). There was a general pattern of succession from diatoms to macroalgal sporelings and unicellular cyanobacteria, then *Phormidium* (including *Borzia* sp.), and finally the encrusting brown alga *H. gelatinosum* together with unicellular cyanobacteria (Figs. 3 & 4).

Overall, the principal impact on species observed under the SEM was the exclusion of herbivores (Table 5), although the presence of mucus and 2-way interactions between algal area, mucus and herbivore exclusion were sometimes important and at one time (June 2) there was a significant 3-way interaction (Table 5). Initial colonization occurred within 8 d by diatoms, which were more abundant (~30%) in herbivore exclusions, and after ~3 wk, in areas which had received a mucus coating (Fig. 3, Table 6).

Porphyra suborbiculata and *Enteromorpha* spp. recruited after 2 wk and sporelings of these algae were dominant in all herbivore exclusions (>60%, Fig. 3, Tables 5 & 6). After ~1 mo, macroalgae were more abundant in herbivore exclusions, especially in areas which originally had a dense algal cover far from crevices, and in herbivore access treatments in areas which originally had a sparse algal cover, close to crevices (Table 6). By June 13, macroalgae were still more abundant in herbivore exclusions, irrespective of their location. In herbivore access treatments that had received a mucus application, however, macroalgae were more abundant as compared to areas which had not received an additional mucus coating (Fig. 3, Table 6).

Unicellular cyanobacteria and *Phormidium* species (Table 4) were more abundant in areas which allowed

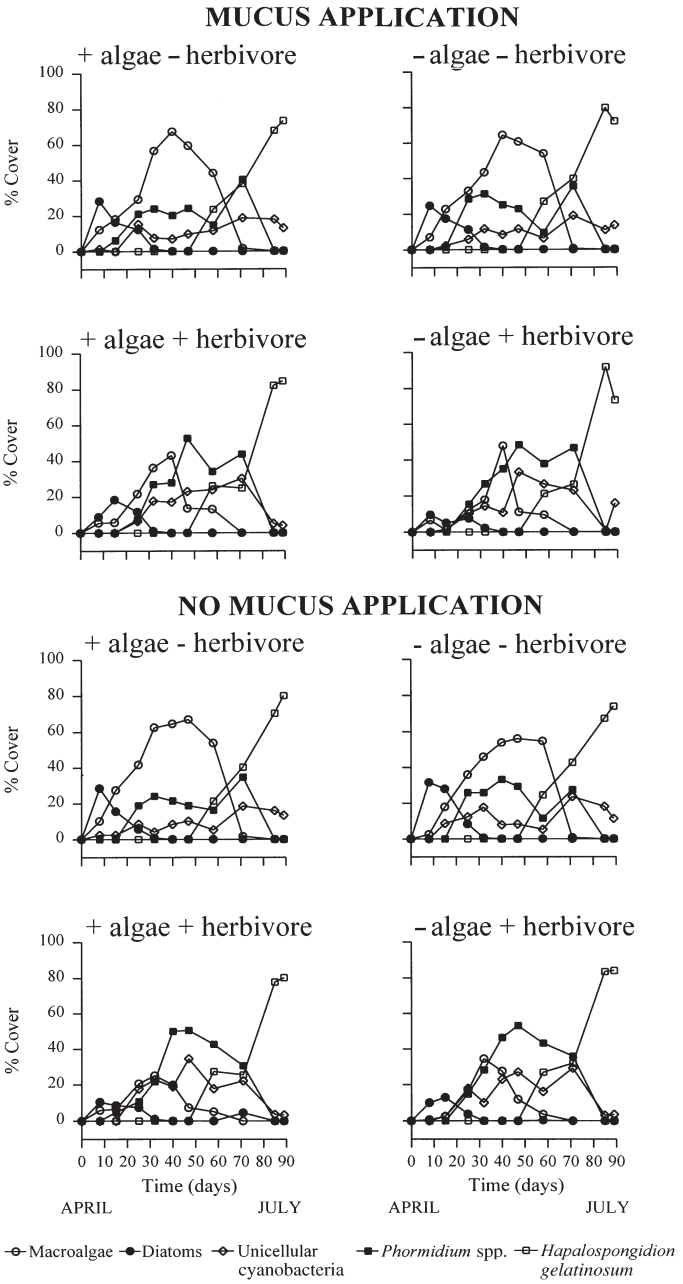

Fig. 3. Variation in mean percentage cover (n = 5) of various species/groups scored from rock chips under the SEM in different experimental treatments with time (+algae = areas originally with dense algal cover; –algae = areas with sparse algal cover; +herbivores = partially fenced areas which allow herbivores access, –herbivores = fully fenced areas that exclude molluscan herbivores). Error bars have been omitted for clarity

herbivores access, suggesting a negative association between abundance of macroalgae and these cyanobacteria and, at one time (May 26) for *Phormidium* species, treatments which had not received an extra mucus application (Table 6). After 32 d (May 18), the abundance of unicellular cyanobacteria interacted with algal area and herbivore exclusion, being higher in areas which originally had a dense algal cover far from crevices and which allowed herbivores access.

Foliose macroalgae started to decrease after ~60 d in all treatments to be replaced by *Hapalospongidion gelatinosum* (Fig. 3), which initially was more abundant in herbivore exclusions, but later in herbivore access treatments and treatments that had received a mucus coating (Table 6). As the macroalgae died back the 3-way interaction (June 2, Table 6) revealed that the highest abundance was maintained in areas which allowed herbivore access, in areas that originally supported a dense algal cover far from crevices and re-

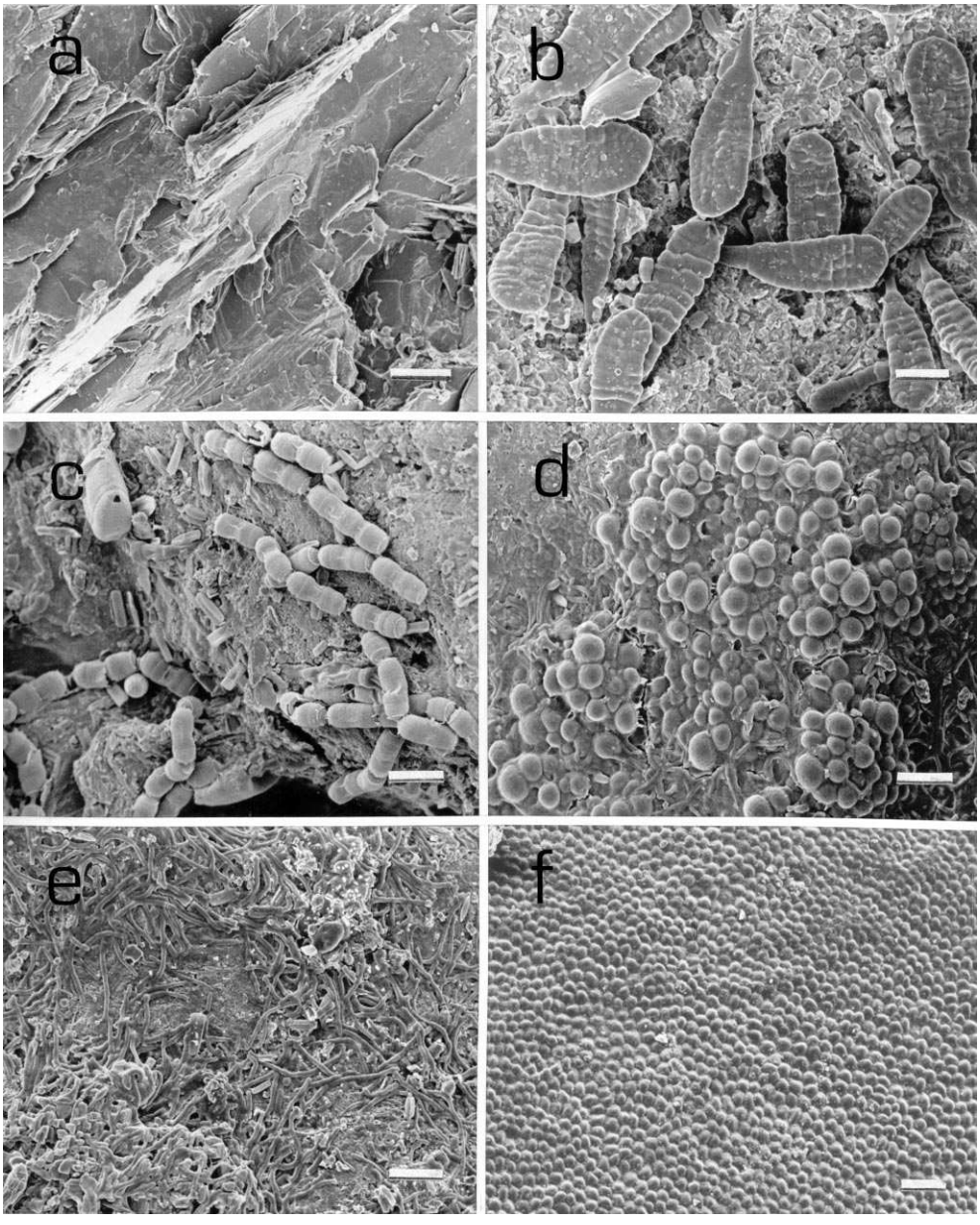

Fig. 4. Selected SEM photographs of the biofilm during primary succession. (a) Newly created, bare rock surface just after burning with a blowtorch; (b) sporelings of *Porphyra suborbiculata*; (c) initial colonization of diatoms (*Melosira* sp.); (d) colonies of unicellular cyanobacterium *Aphanocapsa sesciacensis*; (e) filaments of *Phormidium* spp.; (f) surface layer of the encrusting alga *Hapalospongidion gelatinosum*. Scale bars = 20 µm

ceived a mucus coating. Associated with the dieback of the macroalgae, *Phormidium* species were more abundant in treatments which received additional mucus in late June (Table 6). All species, however, had died back by the end of the experimental period, except for unicellular cyanobacteria spp., which were more abundant in herbivore exclusions, and *H. gelatinosum* which dominated all treatments.

Microalgal and biofilm biomass (chl *a* levels)

Chlorophyll *a* levels increased in the early stages of the experiment and peaked after 32 d (May 18, Fig. 5), after which levels decreased to stabilise at ~2 µg cm^{-2} after 85 d (July 10), similar to the first 2 wk of the experiment. At the time of peak abundance, chl *a* levels were significantly higher in herbivore exclusions (Table 7) and in herbivore access treatments in the high algal cover areas far from crevices (Fig. 5, Table 7), indicating an interaction between location and herbivore impact. The lowest chl *a* levels were recorded in the originally sparse algal cover areas close to crevices which allowed herbivore access (Fig. 5, Table 7). The application of mucus had no impact on chl *a* levels. The effects of herbivore exclusion appeared to vary with time (Fig. 5). There was little apparent difference between herbivore access and exclusion treatments at the start of the experiment (up to 2 wk) or at the end of the experiment (the last 30 d, June 26 to July 25) and it was only in the middle stages of the experiment, that chl *a* levels were generally high, when exclusions had higher chl *a* levels than treatments which allowed herbivore access (Table 7).

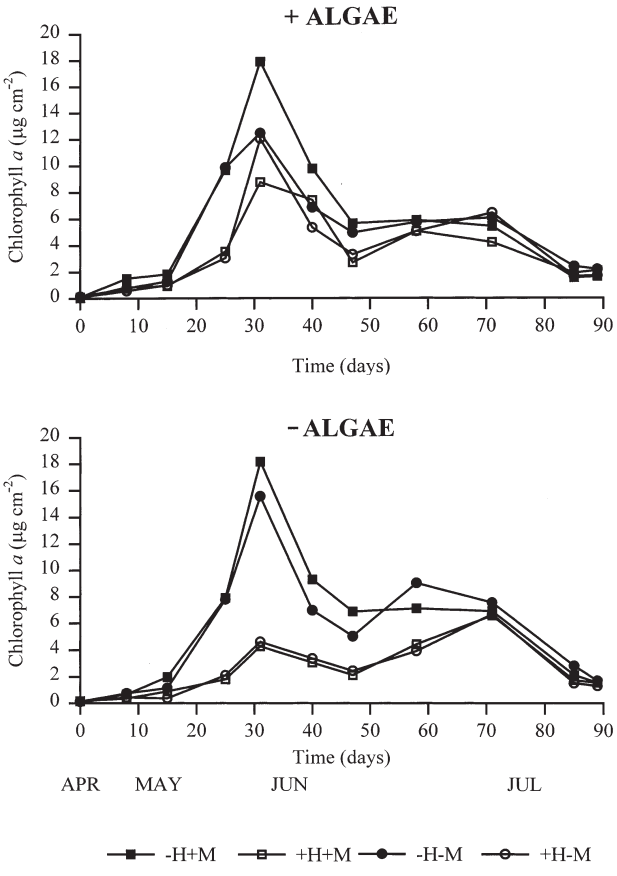

Fig. 5. Variation in mean chl *a* concentration (n = 5) in different experimental treatments with time. +H = partially fenced areas which allow herbivores access, –H = fully fenced areas that exclude molluscan herbivores, +M = mucus treatments, –M = no mucus applied. Error bars have been omitted for clarity

Table 4. Qualitative changes in cyanobacteria species abundance in experimental treatments with time. A = most abundant species in group; C = common in group but <25% as compared to the most abundant species; R = rare (<1% cover)

	Sample date									
	Apr 24	May 1	May 11	May 18	May 26	Jun 2	Jun 13	Jun 26	Jul 10	Jul 14
Unicellular group										
Aphanocapsa sesciacensis	A	A	A	A	A	A	A	A	A	A
Dermocarpa sp.	A	A	A	A	A	A	A	A	A	A
Gloeocapsa crepidinum	C	C	C	C						
Chroococcus minor	C	C	C	C	C					
Non-heterocystous-filamentous group										
Borzia sp.		A	A	A	A	A	A	A		
Phormidium tenue		C	C	C	C					
Phormidium corium		C	C	C	C	C	C			
Symploca laete-viridis			R	R	R	R				
Spirulina labyrinthiformis		R	R	R	R	R	R	R		
Lyngbya semiplena		R	R							
***Calothrix* group**										
Calothrix contarenii				C	R	R	R	R	R	R
Calothrix crustacea				C						
Calothrix scopulorum				C						

Table 5. Summary of 4-way ANOVAs to investigate variation in cover of algae and biofilm species/groups scored under the SEM (MA = macroalgae; *Porphyra suborbiculata* and *Enteromorpha* spp.; D = diatoms; U = unicellular cyanobacteria; *PM* = *Phormidium* spp.; *H* = *Hapalospongidion gelatinosum*) with time in experimental treatments (for denominators of *F*-ratios see Table 7). Percentage data were arc-sine transformed prior to analysis. N = not significant, *p < 0.05

Algal groups		Sampling date																													
	df	Apr 24		May 1		May 11				May 18			May 26			Jun 2			Jun 13				Jun 26			Jul 10		Jul 14	
		MA	D	MA	D	MA	D	U	*PM*	MA	U	*PM*	MA	U	*PM*	MA	U	*PM*	MA	U	*PM*	H	U	*P*	*H*	U	*H*	U	*H*
Algae (A)	1	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
Mucus (M)	1	N	N	N	N	N	*	N	N	N	N	N	*	N	*	N	N	N	N	*	N	N	N	*	N	N	*	N	N
Herbivores (H)	1	N	*	*	N	*	N	N	*	*	N	N	*	*	*	*	*	*	*	*	*	N	N	N	*	*	*	*	N
A × M	1	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
A × H	1	N	N	N	N	N	N	N	N	N	*	N	*	N	N	N	N	N	*	N	N	N	N	N	N	N	N	N	N	N	N
M × H	1	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	*	N	N	N	N	N	N	N	N	N	N	N	N
A × M × H	1	N	N	N	N	N	N	N	N	N	N	N	N	N	N	*	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
Areas (Algae, A)	8	No test																													
Areas (A) × M	8	No test																													
Areas (A) × H	8	No test																													
Areas (A) × M × H	8	No test																													
Total	39																														

Table 6. Student-Neumann-Keuls tests for significant factors from univariate 4-way ANOVAs to investigate variation in cover of algae and biofilm species/groups scored under the SEM at various sample dates (for abbreviations see Table 3). Where factors were involved in higher-order interactions, these have not been tested (NT)

	Sample date									
	Apr 24	May 1	May 11	May 18	May 26	Jun 2	Jun 13	Jun 26	Jul 10	Jul 14
Mucus										
Macroalgae					NT					
Diatoms			+M > −M							
Unicellular							+M = −M			
Phormidium spp.					−M > +M			+M > −M		
Hapalospongidion gelatinosum									+M > −M	
Herbivore										
Macroalgae		−H > +H	−H > +H	−H > +H	NT	NT	NT			
Diatoms	−H > +H									
Unicellular					+H > −H	+H > −H	+H > −H		−H > +H	−H > +H
Phormidium spp.			−H > +H		+H > −H	+H > −H	+H > −H			
Hapalospongidion gelatinosum								−H > +H	+H > −H	

Algal area × Herbivore	Algae		Herbivore	
Unicellular (May 18)	+A	+H > −H	+H	+A = −A
	−A	−H = +H	−H	−A = +A
Macroalgae (May 26)	+A	−H > +H	+H	−A > +A
	−A	−H > +H	−H	+A > −A
Macroalgae (Jun 13)	+A	−H > +H	+H	+A = −A
	−A	−H > +H	−H	−A = +A

Mucus × Herbivore	Mucus		Herbivore	
Macroalgae (Jun 13)	+M	−H > +H	+H	+M > −M
	−M	−H > +H	−H	−M = +M

Algal area × Herbivore × Mucus
Macroalgae (Jun 2)
Algal area × Mucus: All interactions: −H > +H
Mucus × Herbivore: All interactions: −A = +A
Herbivore × Algal area: All interactions: −M = +M except +H × +A where +M > −M

DISCUSSION

Spatial patterns of species distributions

In contrast to aseasonal tropical shores, where distribution patterns are temporally stable (e.g. the Bay of Panama, Lubchenco et al. 1984), Hong Kong shores of moderate exposure often support patches of ephemeral macroalgae in winter (Hodgkiss 1984, Williams 1993b, Kaehler & Williams 1996). The causes of these temporal and spatial patterns have been suggested to be physical stresses in the summer, limiting ephemeral algae to the more benign winter (Hodgkiss 1984) or where physical stress is reduced (Kaehler & Williams 1996). Grazing pressure may also limit algae to areas of the shore where herbivores are reduced in density or effectiveness, or to times when herbivory is reduced and/or algal productivity exceeds herbivore cropping (Williams 1993b, Kaehler & Williams 1996).

Small-scale (i.e. 50 × 50 cm areas) patterns at Cape d'Aguilar, Hong Kong, showed that the distribution of *Ulva* spp. and *Enteromorpha* spp. in winter was associated with open areas of substrate away from cracks and crevices in the rock. These irregularities in the rock provided a shelter for a variety of herbivorous molluscs (16 species) and areas close to these refuges were generally devoid of macroalgae. The resulting mosaic of bare rock areas and patches of algae on the shore is presumably mediated by the relative distance of these areas from herbivore refuges. A negative relationship between ephemeral macroalgae and herbivore abundance is common (Lein 1980), and where herbivores are limited spatially, this can cause a mosaic of patches on the shore (Vadas 1992). On tropical shores many mobile species are limited in their distribution to cracks and crevices, which provide a refuge against physical stresses (e.g. *Nerita funiculata*, Levings & Garrity 1983) or predation (Menge et al. 1983, 1985). The actual cause of this pattern of algal distribution, therefore, appears to be substratum heterogeneity and its indirect impact of limiting the foraging range of herbivores (see Menge et al. 1985, Menge & Olson 1990, Hixon & Menge 1991).

Most herbivores in Hong Kong leave their crevices to feed on the flooding tide and retreat to suitable refuges on the ebbing tide (Hutchinson 1999, G.A.W. pers. obs.) a pattern which is common for tropical herbivores (Bertness et al. 1981, Garrity 1984, Williams & Morritt 1995). The foraging distance which can be achieved is, therefore, a function of travel distance within a tidal period from a refuge (Levings & Garrity 1983). Although other molluscan herbivores migrate into the intertidal zone with the flooding tide in Hong Kong, there is not the influx of highly mobile consumers (fish and crabs) recorded from other tropical shores (Menge & Lubchenco 1981, Brosnan 1992, and see discussion in Sutherland & Ortega 1986) which limits species to refuges from consumer pressure. The highly mobile

Table 7. Four-way ANOVA to investigate variation in chl *a* abundance on 18 May with the factors: the presence or absence of algae (+A = original dense algal area, –A = original sparse algal area), mucus (+M = mucus applied, –M = no mucus application) and herbivores (+H = partial fence, herbivore access, –H = full fence, herbivore exclusion) (n = 5). It was not possible to transform data to meet assumptions of homogeneity of variances (see 'Materials and methods'). Significant differences indicated (*) and further examined by Student-Neumann-Keuls tests, although tests were not performed for factors involved in significant higher-order interactions

Source	df	MS	Denominator for *F*	*F*
Algae (A)	1	45.38	Area (Algae, A)	1.01
Mucus (M)	1	12.31	Area (A) × M	3.96
Herbivores (H)	1	740.9	Area (A) × H	58.84*
A × M	1	0.006	Area (A) × M	0.00
A × H	1	146.3	Area (A) × H	11.62*
M × H	1	85.06	Area (A) × H × M	3.35
A × H × M	1	20.59	Area (A) × H × M	0.81
Areas (Algae, A)	8	45.15	No test	
Areas (A) × M	8	3.11	No test	
Areas (A) × H	8	12.59	No test	
Areas (A) × M × H	8	25.43	No test	
Total	39			

Student-Neumann-Keuls tests:
Algal area × Herbivore

Algae		Herbivore	
+A	–H > +H	+H	+A > –A
–A	–H > +H	–H	–A = +A

herbivorous crab *Grapsus albolineatus* is present at this site but was not abundant during the study period. As a result, ephemeral algae can achieve spatial escapes at distances from herbivore refuges, resulting in patches of algae within areas of high grazing pressure.

Patterns of succession

In herbivore exclusions, irrespective of location or whether mucus was added, there was a predictable pattern of colonization starting with a biofilm (diatoms and unicellular cyanobacteria) followed by a macroalgal phase (e.g. *Enteromorpha* spp. and *Porphyra suborbiculata*) after 20 to 30 d. The rapid establishment of macroalgae is common following herbivore exclusion on temperate (reviewed by Sousa & Connell 1992) and tropical shores during periods of reduced physical stress, or low on the shore (e.g. Lawson 1966, Sauer Machado et al. 1992, Williams 1993a,b, Kaehler & Williams 1998).

In herbivore access treatments, succession was affected by treatment location. Herbivores maintained treatments close to crevices (the formerly sparse algal areas) in an arrested state of succession where a biofilm persisted. Herbivores, therefore, can prevent the development of ephemeral turfs when they have access to such areas. In treatments distant from herbivore refuges (the dense algal areas), green turfs did develop in herbivore access treatments. This indicates that either herbivores were unable to reach these areas to effectively crop the algae, or that these areas recruited more macroalgae as compared to areas near herbivore refuges (Benedetti-Cecchi & Cinelli 1995). If the latter explanation was the case, then it would be expected that algal turf abundance in the herbivore exclusions in the 2 locations (i.e. near and far from crevices) should vary, but this did not occur. Herbivore effectiveness appears the most likely explanation, and this is in agreement with Levings & Garrity (1983), who showed that *Nerita funiculata* maintained a 10 cm bare area around its refuges, and when removed, crustose algae grew in these areas. *N. funiculata* maintains small-scale (10 cm scale) patchiness on Panamanian shores, whereas the guild of molluscan herbivores in the present experiment were able to maintain bare areas ~50 cm away from their refuges.

Mucus application had little effect, except on the biofilm when, in herbivore access treatments, macroalgal cover was almost twice as great in treatments which received a mucus coating as those which did not. This may represent a fertilizing impact of mucus on the early stages of ephemeral algal development. Mucus also had a limited impact, stimulating diatoms, unicellular cyanobacteria, *Phormidium* species, early settling stages of *Hapalospongidion gelatinosum* and visible biofilms following the dieback of green algae, especially in herbivore exclusion treatments. It was difficult to gauge the effectiveness of this treatment. The anticipated influence was in the initial stages of the experiment, mucus increasing microalgal settlement (Davies & Hawkins 1998, Davies & Beckwith 1999), but such impact was not clear (but may be present for settlement of diatoms), although the sampling interval (8 d) may have been too long to detect this. The influence of mucus following the dieback of ephemeral algae may, however, represent such an impact. Mucus from limpets in Hong Kong has a shorter half-life (1 to 2 d) and traps less microalgae as compared to temperate species (Davies & Williams 1995), suggesting that the possible role of mucus as a seeding layer in tropical areas is relatively less important than proposed for temperate shores.

There was a clearly negative relationship between cyanobacteria abundance and macroalgal cover. The competitive inhibition of other species by ephemeral algae is a well documented phenomenon (Sousa 1979). Such competition between species at low trophic levels has been proposed to take place only when predation pressure is reduced (see Brosnan 1992 for a review of the Menge & Sutherland 1976, 1987 models), which would appear to be the case in the present situation; herbivore exclusion allows the development of ephemeral algae which dominate the rock surface and inhibit cyanobacterial films or other algae.

Seasonal patterns

There was a rapid change in algal assemblages with the onset of summer. Irrespective of herbivore access, area location or the application of mucus, macroalgae died back in all treatments after ~60 d (mid-June) to be replaced by crusts of the brown alga *Hapalospongidion gelatinosum*. This alga can recruit during the winter, if space is available (Kaehler & Williams 1997), but is competitively inferior to ephemeral species such as *Enteromorpha* spp. and *Ulva* spp. (Kaehler 1996). Once settled, however, recruits of *H. gelatinosum* are relatively resistant to physical stress (Kaehler & Williams 1998). There was little consistent influence of any of the treatments on *H. gelatinosum,* the remaining epilithic biofilm or chl *a* levels at the end of the experiment, suggesting that the dominant structuring factor was physical stress.

The advent of the hot season on many seasonal tropical shores has a great impact on assemblages, causing high shore kills of both mobile and sessile species (e.g. Lawson 1966, Banaimoon 1988, Murthy et al. 1989; in

Hong Kong, Williams 1994, Williams & Morritt 1995, Kaehler & Williams 1996, Nagarkar & Williams 1999). The relative impact of herbivory is also seasonally variable in the Hong Kong mid-intertidal zone (Williams 1993b). In the present example, the competitive dominance of green algae is broken by physical stress, removing the stress-intolerant ephemeral algae and allowing more tolerant algae (the encrusting alga *Hapalospongidion gelatinosum*) to colonize. This is an annual event on seasonal tropical shores where rock space is liberated for colonization with the advent of the hot season, and this disturbance plays an important role in subsequent community structure (Williams 1993b, Kaehler & Williams 1996).

On seasonal tropical shores, therefore, the dominant factors controlling assemblage structure vary with environmental conditions. In winter, assemblage structure in the mid-shore is controlled by grazing pressure, which is directly set by spatial refuges for molluscan herbivores. Processes appear similar to those described by Menge et al. (1986) on the low shore of the Bay of Panama, where consumer pressure controls species distribution patterns; only where species escape such pressure will competition be important. In Hong Kong, escapes from such pressure can be achieved spatially, if the rock surface available is far enough removed from refuges for the molluscan herbivores. In summer, however, physical conditions control assemblage structure, removing the fast-growing ephemeral algae and leaving only grazer-resistant and stress-tolerant species, the distribution of which is little affected by consumers in the mid-shore (see Sauer Machado et al. 1996). In tropical regions which experience strong monsoon conditions, the relative influences of physical and biological factors will vary seasonally. The relative roles of these factors are therefore likely to be variable between tropical regions (Sauer Machado et al. 1996) owing to climatic differences; hence even on a small-scale, generalizations concerning the importance of different processes should be made with caution.

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Erratum

Primary succession on a seasonal tropical rocky shore: the relative roles of spatial heterogeneity and herbivory

Gray A. Williams, Mark S. Davies, Sanjay Nagarkar

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- On page 85, Fig. 2, the plus and minus signs were incorrect in the second row of graphs. The corrected figure is shown here.

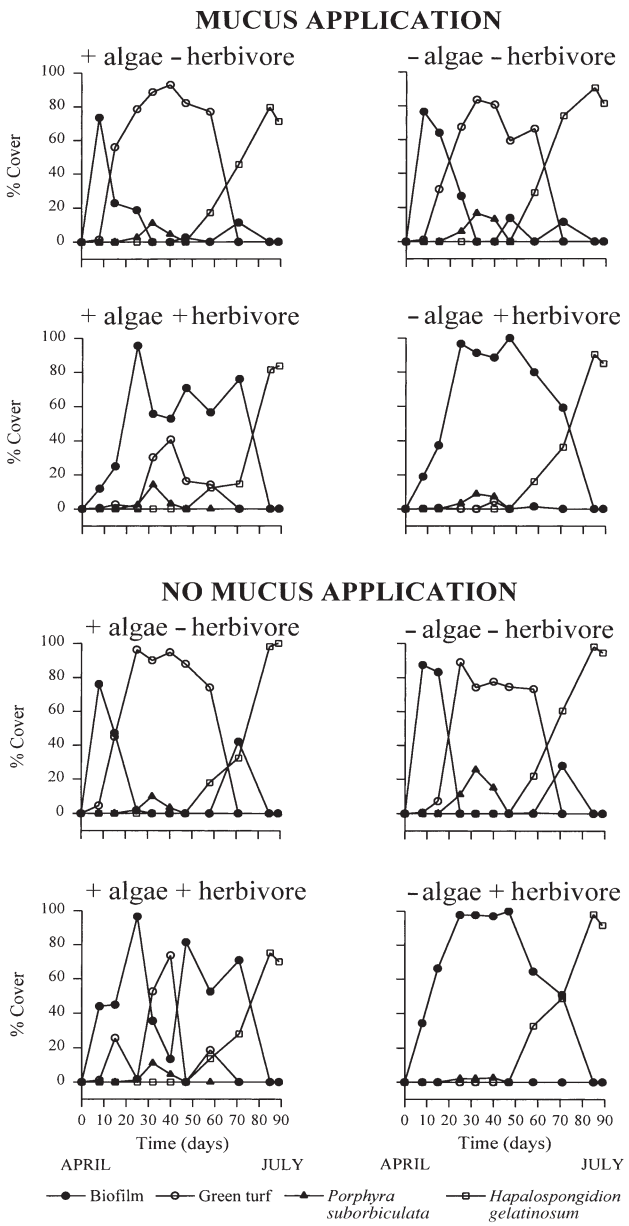

Fig. 2. Variation in mean percentage cover (n = 5) of visible macroalgae and biofilms in different experimental treatments with time (+algae = areas originally with dense algal cover; –algae = areas with sparse algal cover; +herbivores = partially fenced areas which allow herbivores access, –herbivores = fully fenced areas that excluded molluscan herbivores). Error bars have been omitted for clarity