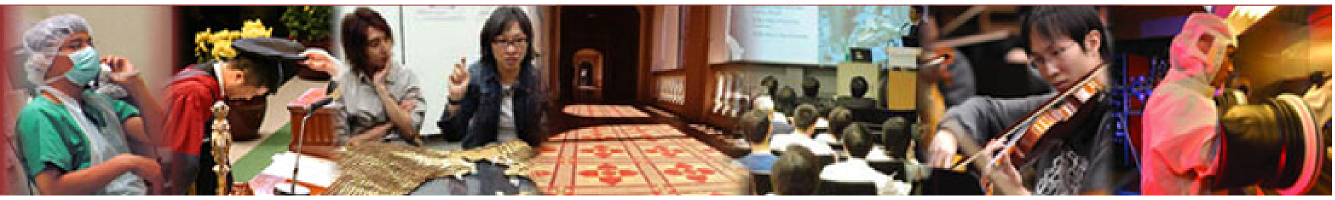

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Do factors influencing recruitment ultimately determine the distribution and abundance of encrusting algae on seasonal tropical shores?

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ABSTRACT: Similar to many low-latitude shores, encrusting algae are the dominant space-occupying organisms on moderately exposed rocky shores in Hong Kong. A multifactorial experiment assessed the roles of herbivory, season, tidal height and substratum inclination on the initial recruitment of encrusting algae to artificial surfaces. Herbivores reduced recruit densities at certain times of the year and tidal heights, but did not prevent settlement. In contrast, the relative timing of recruitment and the prevailing environmental conditions greatly affected recruit success. No species recruited at any time to the high shore, and species recruited as high as the mid shore only during cooler months. Species that recruited during the cooler months (e.g. *Hapalospongidion gelatinosum* and coralline crusts) could colonise the mid shore, while *Ralfsia expansa*, which recruited primarily during the hot season, was restricted to the low shore and subtidal. Recruitment also varied with substratum inclination; cool-season recruits were found in greater densities on horizontal surfaces, whereas hot-season recruits exhibited no difference between horizontal and vertical plates. Seasonal availability of free space may influence the life-history strategies of encrusting algae. *R. expansa* recruited during the hot season to the low shore, when free space was available following the annual die-back of algae. In contrast, cool-season recruits (e.g. *H. gelatinosum*) have less free space to colonise and as a result become established in greater densities higher on the shore, resulting in increased physical stress and mortality during the following hot season. The timing of recruitment relative to spatial and temporal variation in the physical environment, therefore, greatly affects the potential distribution of mature encrusting algal populations on Hong Kong shores.

KEY WORDS: Encrusting algae · Recruitment · Herbivores · Physical stress · Hong Kong · Seasonal variation · Settlement · Tropical shores

INTRODUCTION

The distribution and abundance of marine macroalgae vary both spatially and temporally under the influence of a variety of physical and biological factors (reviewed by Dayton 1985, Norton 1985, Underwood 1985). Compared to numerous studies of the effects of herbivory, physical disturbance and stress on the abundance of adult macroalgae relatively little is known about the importance of early settlement and recruitment processes in establishing algal distribution patterns, especially of encrusting algae on tropical shores (Underwood & Denley 1984, Underwood 1985, 1991, Menge & Farrell 1989, Underwood & Fairweather 1989, Brosnan 1992). This stage, however, is crucial as the establishment of algal populations is often directly dependent on the ability of algae to initially colonise the substratum. Furthermore, in highly disturbed habitats where adult mortality is greater than lateral re-growth, the persistence of a species may depend on successful recruitment of propagules onto

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newly liberated surfaces (Reed et al. 1988, Fletcher & Callow 1992, Benedetti-Cecchi & Cinelli 1993, Kendrick & Walker 1994).

Unlike the planktonic larvae of many marine invertebrates, algal propagules exhibit little to no motility (Fletcher & Callow 1992) and active site selection is thought to be of little importance in determining colonisation patterns (Chamberlain 1976, Norton & Fetter 1981). Instead, the distribution of new recruits is influenced by a wide variety of physical and biological factors that act on propagule availability and dispersal (e.g. Deysher & Norton 1982, Hoffmann & Ugarte 1985), the arrival and establishment of settlers on the shore (e.g. Norton & Fetter 1981, Hoffmann 1987, Benedetti-Cecchi & Cinelli 1992) and early post-settlement mortality (e.g. Underwood 1980, Jernakoff 1983, Santelices & Ojeda 1984, Ang 1991, Geller 1991, Kendrick 1994). Recruitment (the addition of individuals to a unit of population; Doherty & Williams 1988) is thus determined by all processes that affect settlement (the point when individuals first take permanent residence on the substratum) and the early survival of the settlers up to the time of the first census (Keough & Downes 1982, Connell 1985).

In Hong Kong, shores of intermediate exposure are frequently dominated (in terms of total cover) by encrusting algal species, many of which exhibit distinct spatial and temporal distribution patterns (Williams 1993a, b, Kaehler 1994, Kaehler & Williams 1996). The distribution of these populations may be related to physical (e.g. heat and desiccation stress) and biological factors (e.g. herbivory and competition) that act on adult mortality (Kaehler & Williams 1996), but little is known about the importance of recruitment. In Hong Kong, recruitment is likely to be of great importance in determining species distributions, as large areas of mid and low shore substratum are annually made available due to die-backs of space-occupying species with the advent of the hot season (Kaehler & Williams 1996).

This study investigates the importance of early (≤1 mo) recruitment processes in determining the distribution patterns of encrusting algae with reference to season, tidal height and inclination. The effect of herbivory on recruitment was also investigated by experimentally excluding molluscan and echinoid grazers, therefore allowing an assessment of the interaction between physical and biological factors in determining the potential distribution of encrusting algae.

MATERIALS AND METHODS

Study site. A 15 m, west facing, stretch of shoreline located inside Lobster Bay on the Cape d'Aguilar peninsula, Hong Kong (22° 13′ N, 114° 12′ E) was selected as being typical of local rocky shores of intermediate exposure. Encrusting algae were the most abundant macroalgae present and exhibited a 4-banded zonation pattern consisting of a *Kyrtuthrix* zone on the high shore, a Bare zone on the mid shore, a Mixed zone on the low shore and a Coralline-crust zone in the subtidal. Sessile invertebrates and erect macroalgae were rare (overall <5 % cover). Herbivores occurred in high densities and consisted of echinoids in the subtidal and molluscs at all tidal heights. During the cool season, the high shore was dominated by littorinids (densities of >200 m^{-2}), the mid and low shore by limpets (mainly *Cellana* spp., up to 80 m^{-2}), chitons (*Acanthopleura japonica*, up to 30 m^{-2}), and low densities of *Monodonta labio* and *Nerita albicilla*. The subtidal supported rhipidoglossan snails (mainly *Lunella* sp., *Chlorostoma* sp., *M. labio* and *N. albicilla*, up to 200 m^{-2}) and urchins (*Anthocidaris crassispina*, several m^{-2}) and low numbers of herbivorous fish (*Entomacrodus stellifer*) and hermit crabs. Low densities of the herbivorous crab *Grapsus albolinetaus* foraged over the intertidal. During the hot season many molluscs are killed or migrate down shore, resulting in the densities of many species being reduced by ~50% (for more details see Williams 1993b, Kaehler & Williams 1996). Some of these herbivores (limpets, chitons and urchins) preferentially consume encrusting algae, but all of the herbivores are capable of ingesting newly settled spores and juvenile algae (Kaehler 1996).

Experimental design. To remove the confounding effects of substratum heterogeneity and therefore facilitate comparison of recruitment rates from different seasons, tidal heights and inclinations, uniform settlement surfaces (roughened PVC plates, 160 × 90 × 3 mm) were used. This material allows recruitment of coralline as well as non-calcified encrusting algae (Adey & Vassar 1975) and, except in situations of heavy fish grazing, supports similar assemblages of algae as compared to natural surfaces (Hixon & Brostoff 1985). Plates were fixed onto the shore by attaching them to plastic bolts cemented (Wet Surface Epoxy Putty, Devcon) into holes in the rock surface. Plates remained on the shore for 1 mo, after which they were removed and scored in the laboratory. At 1 mo most recruits were large enough (1 to 5 mm) for identification but still small enough not to interfere with each other.

The experiment utilized an orthogonal design to investigate the factors herbivory, season, tidal height and inclination on recruit density (Fig. 1). Three treatments were used to investigate the influence of herbivores. Herbivores were excluded from the plates, using 3 cm high, 18 × 11 cm stainless steel mesh 'exclusion fences' (4 × 4 mm mesh size). Weekly observations were made at high tide, either by snorkelling or

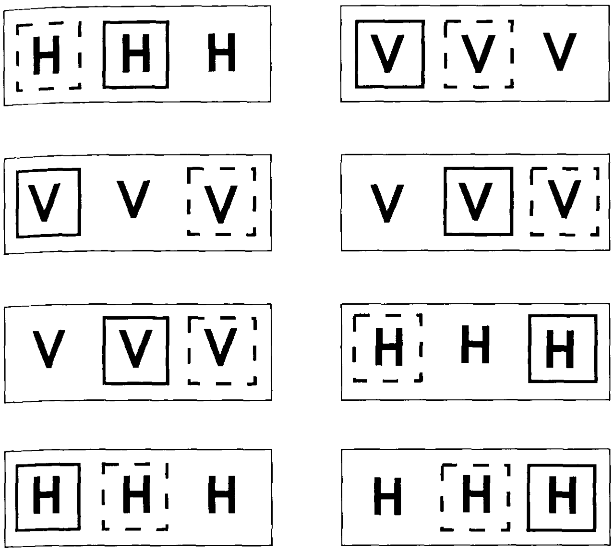

Fig. 1. Schematic representation of plate arrangement at one tidal height. Blocks contain all 3 randomly allocated herbivore treatments and are interspersed on horizontal (H = 0 to 30°) and on vertical surfaces (V = 60 to 90°). The design was repeated at 4 tidal heights and during 5 sampling periods. Full box: exclusion fence; dashed box: fence control (half fence); no box: open plates (unmanipulated grazer density)

SCUBA, of experimental areas. At only one time was a molluscan herbivore (*Chlorostoma* sp.) seen in the exclusion treatment. Echinoids were never present, but fish and hermit crabs were occasionally seen to graze in subtidal exclusion treatments. The fences were, therefore, successful at excluding molluscan and echinoid herbivores but allowed access, having no roof, to highly mobile hermit crabs and fish. 'Open plates' allowed full access to all herbivores and 'half-fence plates' (fences along 2 opposite sides of the plates) permitted herbivore entry while providing a control for possible fence effects. The effects of inclination on recruitment were tested by fixing plates onto both horizontal (0 to 30°) and vertical rock surfaces (60 to 90°, west facing where possible). Variation in recruitment patterns with tidal height were investigated by attaching plates at 4 different tidal heights corresponding with the 4 main algal zonation bands (*Kyrtuthrix* zone ≈ 1.75 m, Bare zone ≈ 1.25 m, Mixed zone ≈ 0.75 m, Coralline-crust zone ≈ −0.25 m above chart datum). For simplicity, the 4 tidal heights are referred to as high, mid, low shore and the subtidal. Finally, temporal patterns in recruitment were investigated by repeating the entire design, with new plates, at 3 mo intervals from April 1992 to April 1993. July 1992 and January 1993 were representative of the extremes of the hot and cool seasons respectively, while April and October were monsoonal transition periods (see Kaehler & Williams 1996).

The arrangement of treatments of the 3 factors herbivory, inclination and tidal height was based on a randomised block design (see Hurlbert 1984). The smallest block consisted of the 3 randomly allocated herbivore treatments which were interspersed on horizontal and vertical surfaces (Fig. 1), at 4 tidal heights. There were 4 replicates of each treatment and the experiment was repeated over 5 time periods ($\sum n$ = 480 plates).

Determination of recruitment density. The density of recruits on the plates was determined in the laboratory. Two randomly chosen areas (16 cm^2) were studied at low power under a dissection microscope (Wild), and where possible, individuals were identified and scored. Areas were selected at random from within an area of 84 cm^2, allowing at least 1 cm distance from the plate perimeter to eliminate possible edge effects (Foster 1975). The mean number of recruits per unit area (cm^{-2}) was calculated from the 2 subsamples for each plate.

The effects of herbivory, inclination, tidal height and time of year on density of algal recruitment were analysed using multifactorial ANOVAs. Data were square-root-transformed to normalise distributions and/or homogenise variances when these assumptions were initially violated (Zar 1984). Bonferroni corrections were applied to maintain the probability of an overall Type I experimental error at 5%. SNK multiple comparison procedures were used to further investigate significant differences (Zar 1984).

RESULTS

Due to the small size of encrusting algal recruits (usually <5 mm), only individuals of *Hapalospongidion gelatinosum*, *Ralfsia expansa*, the coralline crusts, *Hildenbrandia* sp., *Dermocarpa* sp. and *Peyssonnelia* spp. could be distinguished and identified on the plates (Table 1). Of these, only the first 3 were sufficiently abundant to warrant statistical analysis. Several of the species (i.e. *Hildenbrandia* sp., *Dermocarpa* sp., *Ulva* sp. and *Colpomenia sinuosa*) were extremely rare (overall <30 individuals during all 5 study periods), while other organisms (erect algae and sessile invertebrates) were slightly more abundant but were patchily distributed (Table 1).

Effects of herbivory on recruitment

Herbivory generally reduced the recruitment of all 3 abundant encrusting algal groups (Tables 2–4, Figs. 2–4). There was, however, no significant difference between half-fenced plates (fence controls) and

Table 1. Overall mean recruitment densities cm^{-2} (SE in parentheses, n = 96) of all organisms identified on the experimental plates with time. nr: no recruitment

	Apr 1992	Jul 1992	Oct 1992	Jan 1993	Apr 1993
Encrusting algae					
Hapalospongidion gelatinosum	4.57 (0.92)	0.67 (0.30)	0.07 (0.02)	21.0 (2.95)	8.75 (1.58)
Ralfsia expansa	nr	8.67 (1.96)	1.76 (0.64)	nr	nr
Coralline crusts	1.31 (0.32)	2.12 (0.73)	2.93 (0.64)	9.78 (1.46)	3.16 (1.09)
Dermocarpa sp.	<0.01	nr	nr	nr	nr
Hildenbrandia sp.	0.02 (0.01)	nr	nr	nr	nr
Peyssonnelia spp.	nr	1.89 (0.87)	<0.01	0.04 (0.02)	0.01 (0.01)
Erect algae					
Colpomenia sinuosa	nr	nr	nr	<0.01	<0.01
Gelidium spp.	nr	nr	nr	0.02 (0.01)	<0.01
Porphyra sp.	nr	nr	nr	0.64 (0.26)	nr
Ulva sp.	nr	nr	nr	<0.01	<0.01
Brown spores	nr	nr	nr	0.22 (0.15)	0.10 (0.09)
Green spores	nr	nr	2.11 (0.89)	0.11 (0.03)	0.29 (0.19)
Sessile invertebrates					
Barnacles	0.02 (0.01)	0.04 (0.02)	<0.01	0.01 (0.01)	0.76 (0.27)
Spirorbids	0.38 (0.14)	1.60 (0.50)	0.27 (0.09)	0.04 (0.01)	0.34 (0.11)

open plates, suggesting that the fences successfully excluded molluscan and echinoid herbivores, but did not otherwise affect recruitment.

Interaction terms revealed that for most groups the effect of herbivory was highly dependent on the time of year and/or on tidal height (Tables 2 & 3). For both *Hapalospongidion gelatinosum* and *Ralfsia expansa*, the effect of herbivory was only significant during times of increased recruitment (January and July respectively), and in the case of *R. expansa* herbivory effectively reduced recruitment only on the low shore and not in the subtidal (Tables 2 & 3, Figs. 2 & 3).

Variation in recruitment with physical factors

All 3 abundant encrusting algal groups exhibited variation in recruitment density with time (Tables 2–4, Figs. 2–4). While the coralline crusts recruited throughout the year with a peak in January (Table 4, Fig. 4), the 2 brown crusts had periods of greatly reduced or no recruitment. *Hapalospongidion gelatinosum* recruited mainly during the cooler months, especially January, with a significant reduction during the hot season (Table 2) while *Ralfsia expansa* recruited primarily during the hot season, with a peak in July (Tables 1 & 3). No recruits of *R. expansa* were observed during January or either April (Fig. 3).

For most of the time, recruitment was restricted to the low shore and subtidal. No species recruited onto the high shore at any time and only during times of reduced physical stress (cool air temperatures and higher low tides, January and April) did recruitment occur onto the mid shore (Figs. 2–4). *Ralfsia expansa*, which recruited only during the hottest months, was always restricted to the low shore and subtidal (Fig. 3). In contrast, species that recruited during the cooler months (*Hapalospongidion gelatinosum* and the coralline crusts), colonised higher on the shore (Figs. 2 & 4).

Recruitment also varied with substratum inclination (Tables 2 & 4). For both *Hapalospongidion gelatinosum* and the coralline crusts, recruitment was significantly greater on horizontal surfaces than on vertical surfaces (Figs. 2 & 4). In both species, however, the effect of inclination interacted with time and, for the coralline crusts, with tidal height (Fig. 4). Recruitment of both *H. gelatinosum* and the coralline crusts was more dense on horizontal plates only during the cooler months and exhibited no difference during the hot season (Tables 2 & 4). Coralline-crust recruits were significantly more abundant on horizontal surfaces in the subtidal, for most of the year (Table 4, Fig. 4). *Ralfsia expansa*, which recruited only during the hot season, did not exhibit any differences with surface orientation, either alone or in combination with time and/or tidal height (Table 3, Fig. 3).

Recruitment patterns of rare species

Although no statistical tests were performed on the rare and patchily distributed species (Table 5) several broad patterns were apparent. In all species (algae as well as invertebrates), recruitment varied with time (Table 1). While the majority of species recruited during the cooler months (January, April 1992 and 1993),

Table 2. *Hapalospongidion gelatinosum*. Four-way ANOVA of recruit densities (mean number of individuals cm^{-2}) by time, tidal height, herbivory and inclination. Sign.: significance after Bonferroni correction; *p < 0.05 (0.0166); **p < 0.01 (0.0033); ns: not significant. Significant differences were further analysed using SNK multiple comparison tests. Treatment abbreviations are: M: mid shore; L: low shore; S: subtidal; O: open plates; C: fence control; E: exclusion plates (fully fenced); V: vertical; H: horizontal

Source	df	MS	*F*	p	Sign.
Time (T)	4	193.45	270.99	<0.001	**
Height (Ht)	2	92.90	130.14	<0.001	**
Herbivory (Herb)	2	10.32	14.46	<0.001	**
Inclination (Inc)	1	25.05	35.09	<0.001	**
T x Ht	8	15.73	22.05	<0.001	**
T x Herb	8	1.88	2.63	0.009	*
T x Inc	4	11.23	15.74	<0.001	**
Ht x Herb	4	1.88	2.64	0.034	ns
Ht x Inc	2	0.162	0.23	0.797	ns
Herb x Inc	2	0.202	0.28	0.754	ns
T x Ht x Herb	16	0.470	0.66	0.833	ns
T x Ht x Inc	8	2.141	3.00	0.003	*
T x Herb x Inc	8	0.317	0.44	0.894	ns
Ht x Herb x Inc	4	0.197	0.28	0.893	ns
T x Ht x Herb x Inc	16	0.224	0.31	0.995	ns
Error	270	0.714			

SNK tests

Time	July = October < April 92 < April 93 < January
Height	Mid shore < Low shore = Subtidal
Herbivory	Open = Control < Exclusion
Inclination	Vertical < Horizontal

Time	x Height	x Herbivory	x Inclination
April 92	M < L = S	O = C = E	V < H
July 92	M = L = S	O = C = E	V = H
October 92	M = L = S	O = C = E	V = H
January 93	M < L > S	O = C < E	V < H
April 93	M < L = S	O = C = E	V = H
Time x Height x Inc	H > V at all heights during January and on the low shore during April 92; otherwise V = H		

some species (e.g. *Peyssonnelia* spp., green spores and spirorbids) recruited in greatest abundance during July and/or October.

The effect of molluscan and echinoid herbivory on recruitment was most pronounced for the erect macroalgae (Table 5). Herbivory did not seem to effect recruitment success of *Peyssonnelia* spp. or the sessile invertebrates. Recruitment was generally greatest on the low shore and in the subtidal and no species recruited at any time onto the high shore. *Peyssonnelia* spp. was, however, most abundant on, and *Porphyra* only colonised, the mid shore (Table 5). Except for *Porphyra* sp. and spirorbids most algal species either recruited in greater numbers on horizontal surfaces than vertical surfaces or were equally distributed (Table 5).

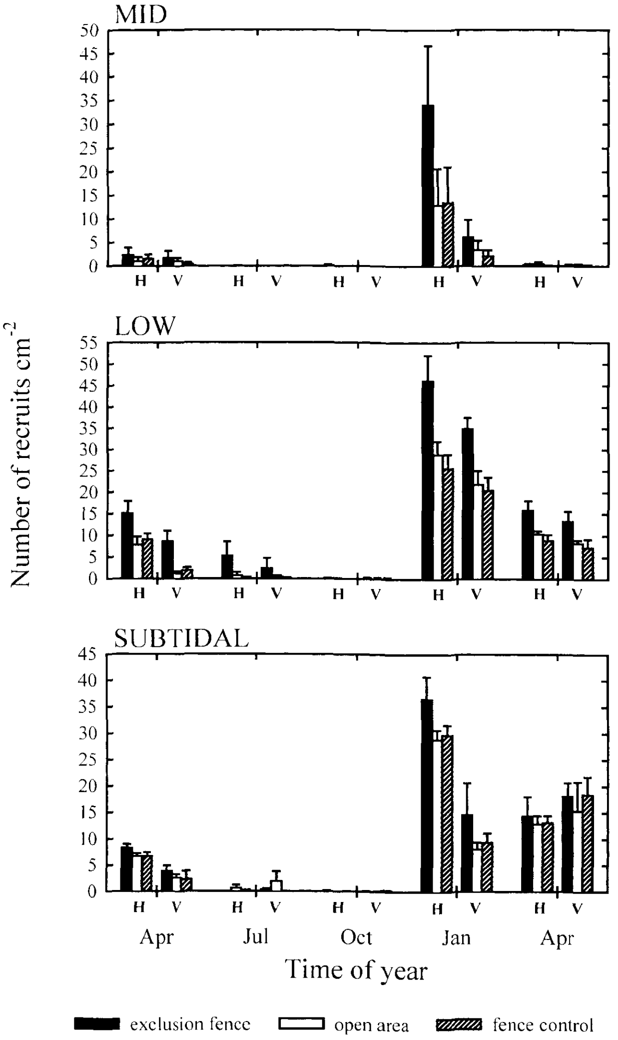

Fig. 2. *Hapalospongidion gelatinosum*. Effects of herbivory (fence, fence control and open treatments), time and inclination (horizontal vs vertical surfaces) on recruit density (+SE) at 3 tidal heights; n = 4

DISCUSSION

Effects of herbivory on recruitment

Molluscan and echinoid herbivores occasionally reduced, but did not prevent, recruitment of algae. For *Hapalospongidion gelatinosum* and *Ralfsia expansa* recruit densities were reduced only during times of peak recruitment. During these periods, herbivore exclusions resulted in up to a 3-fold increase in recruitment although, even in the presence of natural herbivore densities, large numbers of recruits survived (up to 17000 recruits m^{-2}). It is unlikely that herbivory effectively limits the distribution of mature algal populations within the first month of recruitment.

Table 3. *Ralfsia expansa*. Four-way ANOVA of recruit densities (mean number of individuals cm^{-2}) by time, tidal height, herbivory and inclination, followed by SNK multiple comparison tests for significant results. Abbreviations as in Table 2

Source	df	MS	*F*	p	Sign.
Time (T)	1	112.905	252.28	<0.001	••
Height (Ht)	1	2.588	5.78	0.019	ns
Herbivory (Herb)	2	12.079	26.99	<0.001	••
Inclination (Inc)	1	0.017	0.04	0.844	ns
T × Ht	1	59.328	132.57	<0.001	••
T × Herb	2	4.943	11.04	<0.001	••
T × Inc	1	0.159	0.36	0.553	ns
Ht × Herb	2	5.031	11.24	<0.001	••
Ht × Inc	1	0.1215	0.27	0.604	ns
Herb × Inc	2	0.293	0.66	0.522	ns
T × Ht × Herb	2	0.120	0.27	0.765	ns
T × Ht × Inc	1	0.004	0.01	0.925	ns
T × Herb × Inc	2	0.185	0.42	0.662	ns
Ht × Herb × Inc	2	0.189	0.42	0.657	ns
T × Ht × Herb × Inc	2	0.285	0.64	0.531	ns
Error	72	0.447			

SNK tests

Time	July > October
Herbivory	Open = Control < Exclusion

Time	× Height	× Herbivory
July 92	L < S	O = C < E
October 92	L > S	O = C = E

Height	× Herbivory
Low shore	O = C < E
Subtidal	O = C = E

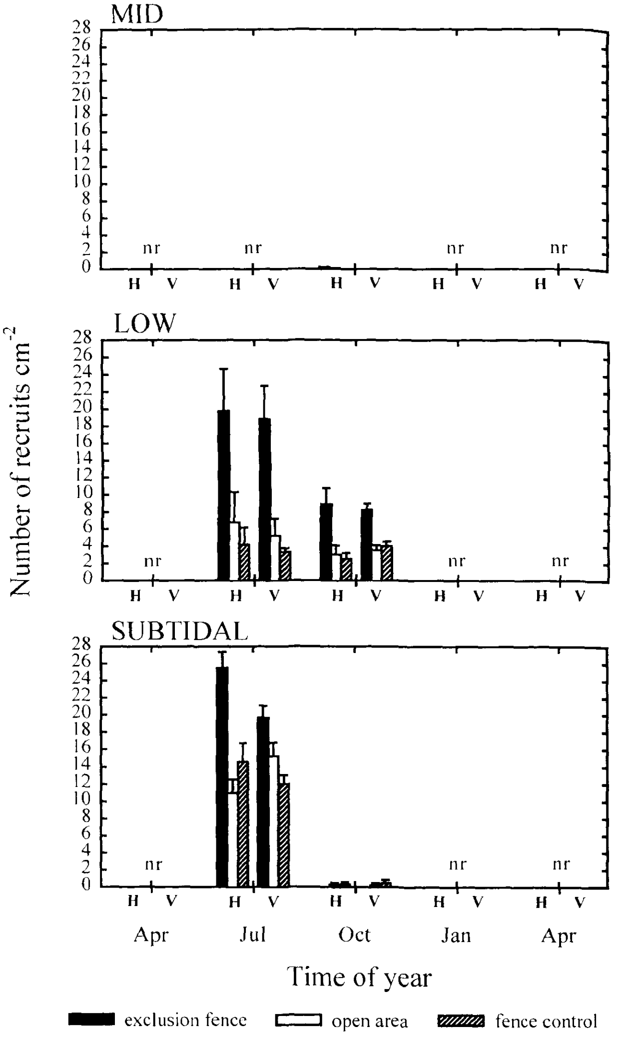

Fig. 3. *Ralfsia expansa*. Effects of herbivory (fence, fence control and open treatments), time and inclination (horizontal vs vertical surfaces) on recruit density (+SE) at 3 tidal heights. nr: no recruits observed at this time; n = 4

The effects of herbivory on algal recruitment have been shown to vary with physical parameters such as tidal height (Underwood 1985), variation in grazer densities and/or colonisation and growth rates of algae (Underwood & Jernakoff 1981). In the present study, however, the density of encrusting algal recruits was reduced by herbivores at all tidal heights. Only for *Ralfsia expansa* in the subtidal did herbivore exclusions not result in significantly increased recruitment. This pattern is likely to be caused by increased densities of highly mobile herbivores (hermit crabs and fish) which, as plates had no roofs, were not effectively excluded from subtidal plates and which preferentially feed on *R. expansa* (Kaehler 1996).

The influence of herbivores also varied with time, although this was not directly related to seasonal changes in herbivore abundance (Kaehler 1996). In Hong Kong, intertidal herbivore densities are reduced each year with the advent of the hot season and are highest during winter (Kaehler & Williams 1996). The temporal effect of herbivory on recruitment, however, varied between algal groups and was greatest during July for *Ralfsia expansa* and, conversely, in January for *Hapalospongidion gelatinosum*. Seasonal variation in molluscan and echinoid density does not, therefore, explain temporal changes in the effect of herbivores on algal recruitment. Of all recruiting species, only *Peyssonnelia* spp. and the structurally defended barnacles and spirorbids were continuously unaffected by herbivory (but see Williams 1994).

Timing of recruitment

All encrusting algae, erect macroalgae and sessile invertebrates exhibited temporal variation in recruitment, the majority recruiting during the cool season. Similar temporal variation in recruitment of other algal species is well documented (e.g. Deysher & Norton 1982, Reed et al. 1988, Flavier & Zingmark 1993,

Table 4. Coralline crusts. Four-way ANOVA of recruit densities (mean number of individuals cm^{-2}) by time, tidal height, herbivory and inclination, followed by SNK multiple comparison tests for significant results. Abbreviations as in Table 2

Source	df	MS	*F*	p	Sign.
Time (T)	4	41.527	140.99	<0.001	**
Height (Ht)	2	123.847	420.48	<0.001	**
Herbivory (Herb)	2	2.837	9.63	<0.001	**
Inclination (Inc)	1	29.589	100.46	<0.001	**
T × Ht	8	14.161	48.08	<0.001	**
T × Herb	8	0.541	1.84	0.070	ns
T × Inc	4	3.705	12.58	<0.001	**
Ht × Herb	4	0.145	0.49	0.740	ns
Ht × Inc	2	4.016	13.64	<0.001	**
Herb × Inc	2	0.325	1.10	0.333	ns
T × Ht × Herb	16	0.424	1.44	0.122	ns
T × Ht × Inc	8	1.672	5.68	<0.001	**
T × Herb × Inc	8	0.0789	0.27	0.976	ns
Ht × Herb × Inc	4	0.0959	0.33	0.861	ns
T × Ht × Herb × Inc	16	0.174	0.59	0.889	ns
Error	270	0.294			

SNK tests

Time	July = April 92 = April 93 < October < January
Height	Mid shore < Low shore < Subtidal
Herbivory	Open = Control < Exclusion
Inclination	Vertical < Horizontal

Time	× Height	× Inclination
April 92	M < L = S	V < H
July 92	M < L < S	V = H
October 92	M < L > S	V = H
January 93	M < L = S	V < H
April 93	M = L < S	V < H

Height	× Inclination
Mid shore	V = H
Low shore	V = H
Subtidal	V < H

Time × Height × Incl	H > V at all heights during January and at all times (except July) in the subtidal; otherwise H = V

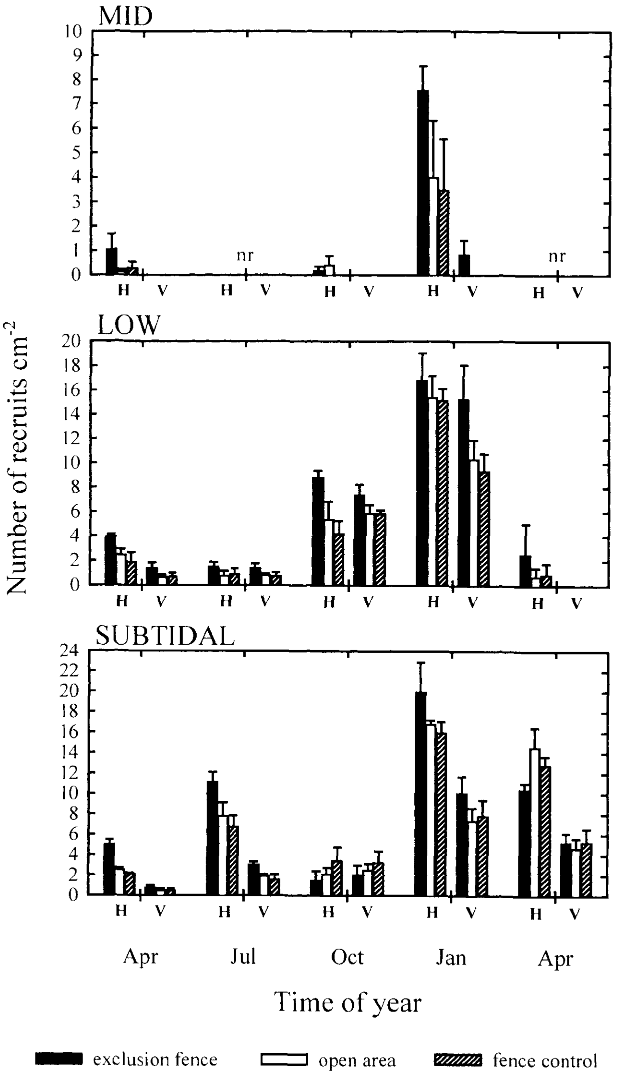

Fig. 4. Coralline crusts. Effects of herbivory (fence, fence control and open treatments), time and inclination (horizontal vs vertical surfaces) on recruit density (+SE) at 3 tidal heights. nr: no recruits observed at this time; n = 4

Kendrick & Walker 1994) and has frequently been related to the timing of reproduction (e.g. Deysher & Norton 1982, Ang 1991). While the local environment may affect propagule release, dispersal, settlement and post-settlement mortality (reviewed by Santelices 1990), the temporal availability of fertile parent plants is in most cases a prerequisite for large scale recruitment (although colonisation through algal fragments is known; Fletcher & Callow 1992).

Reproduction of *Hapalospongidion gelatinosum* and *Ralfsia expansa* is highly seasonal and coincides with periods of high recruitment (Kaehler 1996). In addition to reproductive periods, however, temporal abundance patterns of mature algal populations may also affect the availability of propagules. The abundance of the mid shore *H. gelatinosum* is greatly reduced during the hot season (Kaehler & Williams 1996) and the availability of its propagules is, therefore, likely to be low at this time. In contrast, mature populations of *R. expansa* and the coralline crusts are found lower on the shore and persist in the subtidal throughout the year (Kaehler & Williams 1996), which may account for their ability to recruit in greater numbers during the hot season (see also Underwood & Denley 1984).

Vertical distribution of recruits

All 3 abundant encrusting algal groups recruited in greatest densities on the low shore and/or in the subtidal. Recruitment was reduced on the mid shore and there was no recruitment on the high shore. As most algal spores are non-motile (Fletcher & Callow 1992), environmental conditions are thought to determine their deposition and potential settlement (Santelices 1990). Increased recruitment to lower tidal heights may, therefore, be a function of prolonged submergence (Hruby & Norton 1979, Underwood & Denley 1984, Underwood 1985). Additionally, the close proximity of parent plants (see also Williamson & Creese 1996) may be important, especially for the encrusting algal form group, as their low point of spore release and the reduced water velocities of the boundary layer may increase the probability of settling close to the propagule source (Santelices 1990).

An alternative explanation for increased recruitment towards lower shore levels is an increase in post-settlement mortality at higher shore levels. In Hong Kong, during the hot season (July and October), recruitment was restricted to the low shore and the subtidal, while during the cool season (January and April), species recruited at higher tidal levels (the mid shore), suggesting that the upper limits of recruits are at least partially determined by the physical environment (see also Flavier & Zingmark 1993). *Hapalospongidion gelatinosum* and the coralline crusts which recruit during periods of reduced physical stress extend higher on the shore than *Ralfsia expansa* which recruits only during the hot season. As susceptibility to physical stress is greatest in juvenile stages (Hruby & Norton 1979, Norton 1986, Davison et al. 1993), the potential upper limit of mature encrusting algal populations is probably determined at a very early stage of development and strongly affected by the relative timing of recruitment.

In contrast, the recruitment of other macroalgal species did not always increase down shore. Both *Peyssonnelia* spp. and *Porphyra* sp. were most abundant on the mid shore and unidentified brown spores exhibited a bimodal distribution with peaks on the mid shore and subtidal. Neither physical gradients nor active site selection could account for these patterns.

Distribution of recruits with substratum inclination

Both *Hapalospongidion gelatinosum* and the coralline crusts were more abundant on horizontal as opposed to vertical surfaces at times (January and April) and/or tidal heights (low shore and subtidal) of reduced physical stress. In contrast, during the hot season and at higher shore levels, the abundance of recruits of all 3 encrusting algae did not differ between horizontal and vertical surfaces. Recruitment is, therefore, generally greater on horizontal surfaces, except where physical conditions preclude this pattern from occurring, although the reasons for this pattern are unknown.

Hydrographic conditions may partially account for increased settlement on horizontal surfaces, where the microtopography of the roughened settlement plates may enhance propagule deposition (see Norton & Fetter 1981). Furthermore, overall greater wave impact and turbulence may decrease settlement and increase dislodgement on vertical surfaces. During the hot season and at higher shore levels, however, increased mortality on horizontal surfaces may alter this pattern. Previous studies in the vicinity have shown that horizontal surfaces may reach temperatures of 50°C (Williams 1994) and are hotter (3 to 7°C) than vertical surfaces (Williams & Morritt 1995). This may account for the greater recruitment on horizontal surfaces primarily at low tidal heights and/or during the cool season. Variation in the abundance of

Table 5. Mean recruit densities cm^{-2} (SE in parentheses) of rare or patchily distributed organisms at different tidal heights, herbivore treatments and inclinations. Abbreviations as in Table 2

	Tidal height	Herbivory	Inclination
Crustose algae			
Peyssonnelia spp.	M 0.646 (0.322)	O 0.576 (0.449)	H 0.628 (0.355)
	L 0.489 (0.441)	C 0.334 (0.284)	V 0.151 (0.077)
	S 0.033 (0.008)	E 0.256 (0.130)	
Erect algae			
Gelidium spp.	M <0.001	O 0.005 (0.003)	H 0.009 (0.002)
	L 0.001 (0.001)	C 0.001 (0.001)	V 0.006 (0.003)
	S 0.020 (0.005)	E 0.016 (0.005)	
Porphyra spp.	M 0.386 (0.146)	O 0.108 (0.069)	H 0.066 (0.047)
	L nr	C 0.094 (0.068)	V 0.193 (0.087)
	S nr	E 0.183 (0.075)	
Brown spores	M 0.092 (0.086)	O 0.020 (0.011)	H 0.083 (0.058)
	L nr	C <0.001	V 0.045 (0.003)
	S 0.100 (0.051)	E 0.172 (0.098)	
Green spores	M 0.026 (0.019)	O 0.308 (0.144)	H 0.468 (0.193)
	L 0.014 (0.008)	C 0.235 (0.153)	V 0.535 (0.170)
	S 1.464 (0.371)	E 0.961 (0.321)	
Invertebrates			
Barnacles	M 0.001 (0.001)	O 0.225 (0.092)	H 0.134 (0.038)
	L 0.037 (0.014)	C 0.121 (0.042)	V 0.195 (0.070)
	S 0.456 (0.116)	E 0.148 (0.066)	
Spirorbids	M nr	O 0.476 (0.117)	H 0.202 (0.040)
	L 0.535 (0.125)	C 0.558 (0.131)	V 0.853 (0.145)
	S 1.048 (0.183)	E 0.550 (0.151)	

macroalgae with inclination have been documented (Konno 1985, Sebens 1986, Dethier et al. 1991, Kaehler & Williams 1996) and differences in grazing pressure have been suggested to partially account for these patterns. In the present study, however, recruit densities were greater on horizontal surfaces irrespective of herbivore presence, suggesting that molluscan and echinoid herbivores were not responsible for varying recruitment with inclination. In contrast to the algae, all invertebrates recruited in higher densities on vertical as opposed to horizontal surfaces. The mechanisms generating this pattern are unknown, but the distribution of sessile invertebrate recruits has previously been linked to physical, biotic and/or chemical factors (reviewed by Rodríguez et al. 1993).

Implications for the distribution of encrusting algae

Despite the ability of molluscan and echinoid grazers to reduce the number of encrusting algal recruits, natural grazer densities were not sufficient to directly restrict the distribution of algae during the first month of colonisation. In contrast, the timing of recruitment and the prevailing environmental conditions strongly affected the abundance and distribution of encrusting algae even during the first month of colonisation. Recruit densities generally decreased towards areas of increased physical stress (high shore), and during the hot season recruitment was restricted exclusively to the low shore and subtidal. Species that only recruited during the hot season (*Ralfsia expansa*) were thus not capable of colonising above the low shore, whilst groups that additionally recruited during the cool season (*Hapalospongidion gelatinosum* and the coralline crusts) could colonise higher shore levels (mid shore).

Recruitment never occurred above the natural recorded vertical extent of mature populations (Kaehler & Williams 1996), suggesting that the upper limits of encrusting algal populations are set during the early stages of colonisation (see also Kaehler 1996). In contrast, the lower distribution of adult populations was not always directly related to recruitment patterns. For example, *Hapalospongidion gelatinosum*, which naturally occurs primarily on the mid shore (Kaehler & Williams 1996), recruited far below the vertical extent of adult populations during all study periods. *H. gelatinosum*, however, recruits primarily during the cooler parts of the year, when space is not freely available at lower tidal heights (Kaehler & Williams 1996) and previous space occupants will compete with or directly affect newly arriving recruits (Fletcher 1975, Breitburg 1984, Benedetti-Cecchi & Cinelli 1992). Realised recruitment at lower shore heights is therefore likely to be much reduced when compared to recruitment onto new settlement plates. Even where recruitment does naturally occur to the low shore, however, *H. gelatinosum* is readily overgrown by the competitively superior *Ralfsia expansa* (Kaehler 1996). *R. expansa* recruits only during the hotter parts of the year, when space is more freely available on the low shore (Kaehler & Williams 1996). This suggests that encrusting algae may exhibit dissimilar life-history strategies along the tidal gradient. Species that recruit mainly during the hot season (*R. expansa*) may be adapted to colonise the low shore at a time when space is available and may persist there by means of their superior overgrowth capabilities. In contrast, species that recruit primarily during the physically less stressful cool season have to utilise space at higher shore levels (e.g. mid shore) where bare substratum is available throughout the year and competitive interactions are of reduced importance in determining initial colonisation and subsequent development. The penalty for recruitment at this tidal level is increased physical stress, which during the hot season kills off the majority of adult algae.

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