Early development of algal assemblages under different regimes of physical and biotic factors on a seasonal tropical rocky shore

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ABSTRACT: The roles of physical factors and herbivory in structuring the early development of algal assemblages were investigated on a seasonal, tropical rocky shore in Hong Kong. Physical stress was manipulated by irrigating areas with filtered seawater, whilst herbivore access was controlled using fences. Algal colonisation was monitored at 2 tidal heights (high- and lowshore), once in the cool and dry season and once in the hot and wet season. Dry areas were only colonised in the lowshore and, even when herbivores were excluded, dry highshore areas never developed a macroalgal cover. Algal assemblages did, however, develop in highshore irrigated areas, where, in the presence of herbivores, encrusting algae (e.g. *Hapalospongidion gelatinosum* and coralline crusts) developed. In areas excluding herbivores, ephemeral erect algae (e.g. *Ulva* spp.) developed. All lowshore treatments developed algal assemblages. In the hot season, after an initial phase of erect algae, encrusting algae developed where herbivores had access, whereas, in the cool season, erect *Corallina* spp. dominated these treatments. In herbivore exclusions, erect ephemeral algae developed in the hot season with a sparse cover of encrusting algae (*Ralfsia expansa* and coralline crusts) whilst, in the cool season, a cover of *Corallina* spp. and erect ephemeral algae became abundant. When irrigation was terminated, erect algal cover decreased dramatically in each season in the highshore, although encrusting algae persisted at reduced cover. In lowshore areas, algal cover decreased marginally when irrigation was terminated and only during the hot season. The timing (i.e. hot or cool season) of liberation of rock space was, therefore, important for the development of algal assemblages. In lowshore areas, assemblages dominated by encrusting algae typical of rocky shores in Hong Kong developed only in the presence of herbivores and only during the hot season. During the cool season, *Corallina* spp. became dominant, while exclusion of herbivores (during either season) resulted in the development of ephemeral, erect algal assemblages.

KEY WORDS: Encrusting algae · Assemblage development · Herbivores · Physical stress · Hong Kong · Tropical shores

INTRODUCTION

Investigations of low latitude rocky shores are rare (see review by Brosnan 1992), and experimental studies have, until recently, been restricted to a limited number of localities (mainly Central America; see references below). From these studies it has been concluded that, compared to temperate shores which are grazed principally by molluscs and echinoids, large and highly mobile herbivores (e.g. fish, crabs) are of primary importance in structuring tropical rocky shore communities (Gaines & Lubchenco 1982, Menge 1982, Menge et al. 1986a, b). Furthermore, in contrast to temperate shores, competition is thought to be of importance only between a small number of species that escape consumption (Menge et al. 1986a, b, but see Machado et al. 1996). Consequently, many tropical rocky shores exhibit a high cover of grazer-resistant organisms (e.g. encrusting and turf algae) and lack the proliferation of competitively superior foliose macroal-

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gae commonly found at temperate latitudes (Menge & Lubchenco 1981, Menge et al. 1986a, Brosnan 1992).

Similar to other rocky shores of low latitude (e.g. Loi 1967, Menge & Lubchenco 1981, John & Lawson 1991), many moderately exposed shores in Hong Kong are dominated by encrusting algae (Kaehler & Williams 1996). In Hong Kong, however, the most abundant grazers are molluscs and echinoids, and herbivorous fish and crabs are relatively rare. The impact of these large and highly mobile herbivores on community structure is, therefore, likely to be of little importance in Hong Kong (see also Sutherland & Ortega 1986, Machado et al. 1996).

In addition to grazing, physical stress is also important in structuring communities on tropical rocky shores (Garrity 1984, Brosnan 1992). Physical conditions on some shores of low latitude are seasonally variable and, in these locations, may have a large impact on community dynamics (e.g. Lawson 1966, Hodgkiss 1984, Banaimoon 1988). Organisms inhabiting tropical intertidal shores may experience intense heat, desiccation and radiation stress during emersion (Moore 1972, Levings & Garrity 1984, Williams 1994, Williams & Morritt 1995). Many encrusting algae (with the exception of the coralline crusts) are thought to be comparatively tolerant of physical stress (Lubchenco & Cubit 1980, Littler et al. 1983, Menge et al. 1983, Levings & Garrity 1984, Quinn 1988, Dethier 1994), although there is little direct evidence that, as a group, they are more tolerant of stress than their erect counterparts. During periods of increased physical stress on tropical shores, the abundance and/or upper limits of distribution of erect and encrusting algae have been shown to decrease (Lawson 1966, Hodgkiss 1984, Lubchenco et al. 1984, Williams 1993a). The relative importance of physical stress (as opposed to herbivory) in establishing and maintaining the predominance of the encrusting algal form group on tropical rocky shores has, therefore, yet to be determined.

Hong Kong, unlike Panamanian shores but similar to West African (Lawson 1966) and Indian shores (Banaimoon 1988), experiences a highly seasonal monsoonal climate with annual die-offs of the intertidal epibiota (Williams 1993a). With the advent of the hot season, large areas of bare substratum are liberated in intertidal habitats (Kaehler & Williams 1996). Furthermore, due to the low abundance of herbivorous fish and crabs, molluscan herbivores are thought to be of greater importance in structuring local intertidal communities (Williams 1993a, Williams 1994, Kaehler & Williams 1996). The relative importance of the physical environment and grazing in structuring communities on Hong Kong rocky shores may, therefore, differ from those described from Central America. To investigate these factors, this study assessed the interactive effects

of desiccation and herbivory on the establishment and early development of algal assemblages on cleared rock surfaces on a moderately exposed rocky shore in Hong Kong.

MATERIALS AND METHODS

Study site. Experimental manipulations were conducted on a southwest-facing shore, within Lobster Bay on the Cape d'Aguilar peninsula, Hong Kong (22° 13' N, 114° 12' E). The composition of biota on this shoreline has been studied over a period of years and is typical of local rocky shores of moderate exposure (e.g. Williams 1993a, b, Harper 1996, Morton & Harper 1996, Kaehler 1996, Kaehler & Williams 1996, 1997). Encrusting algae were the most abundant macroalgae, and erect macroalgae and sessile invertebrates were rare (overall <5% cover). A herbivore survey of the study site in July 1993 (1 mo prior to experiment initiation) showed that molluscan herbivores were abundant throughout the shore (Kaehler 1996). Nodilittorinids and the limpet *Cellana grata* dominated the highshore (densities > 100 m^{-2}), while a variety of coiled gastropods (e.g. *Chlorostoma* spp., *Monodonta labio*, *Nerita albicilla*), limpets (e.g. *Cellana toreuma*, *Patelloida saccharina* and *Siphonaria* spp.) and a chiton (*Acanthopleura japonica*) reached peak abundances on the lowshore (densities up to 140 m^{-2}). Small numbers of herbivorous fish (e.g. *Entomacrodus stellifer*) and crabs (*Grapsus albolineatus* and hermit crabs) were also present. Seasonal variation in grazer densities on surrounding shores has previously been described (Harper 1996, Kaehler 1996, Kaehler & Williams 1996, 1997). Hong Kong experiences a strongly seasonal monsoonal climate, with a hot and wet season from approximately May to October (mean monthly air temperature 28°C) and a cool and dry season (mean temperatures can fall to 15°C in January) from November to April (for details see Kaehler & Williams 1996, Morton et al. 1996).

Experimental design. The experiment utilised an orthogonal design to investigate the effects of herbivory and physical stress on early algal assemblage development at 2 tidal heights, once during the hot season (August 1993) and once during the cool season (January 1994). During each study period, algal colonisation and development was monitored in 36 plots of 25 × 25 cm (Σn = 72) which were initially cleared of all organisms by scraping the substratum with a spatula and then a wire brush. Prior to initiation of the experiment, surfaces were burnt with a blowtorch. Half of the plots were located in 6 areas (3 plots per area) in the mid/highshore (the *Kyrtuthrix*-Zone, approximately 1.75 m above Chart Datum) and half in 6 areas (3 plots
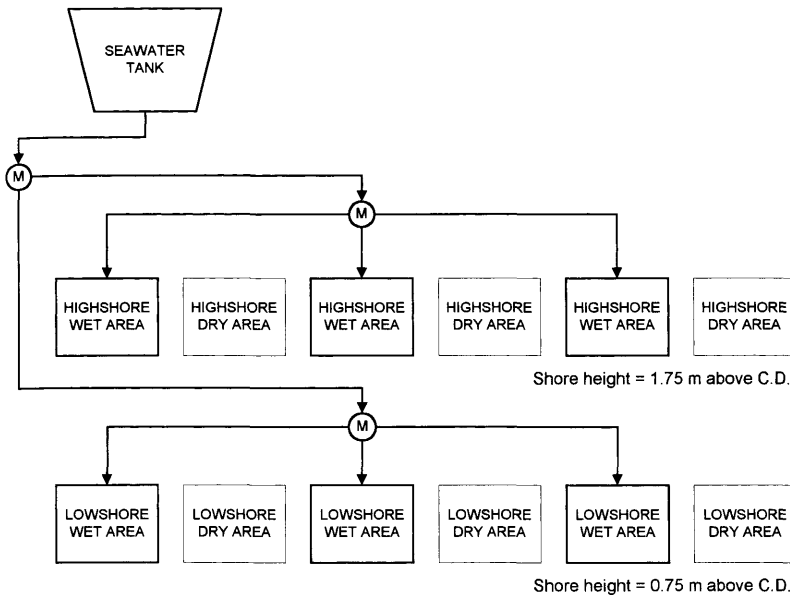
Fig. 1. Schematic representation of the arrangement of dry and wet areas on the shore. Water was drained from a filtered seawater holding tank to 3 experimental areas at each tidal height (C.D.: Chart Datum). The remaining 3 areas were not irrigated. M: manifold to regulate water drainage. Each area contained the 3 randomly allocated herbivore treatments: exclusion (fenced), open (no fence) and control (half-fenced)

per area) in the lowshore (the Mixed-Zone, approx. 0.75 m above Chart Datum, see Kaehler & Williams 1996). The effect of physical stress (e.g. temperature and desiccation stress) on algal assemblage development was assessed by artificially irrigating half of the experimental areas (= wet) for a period of 13 wk. Seawater (filtered through glass wool) was drained from a high-lying, shaded, storage tank via hoses to 3 of the 6 areas at each tidal height (Fig. 1). Taps at each manifold (Fig. 1) controlled the rate of water irrigation and wetting occurred by continuous sprinkling of water onto the areas through perforated PVC pipes. Pipes were elevated ca 10 cm from the plots so as to minimise interference with treatments (e.g. herbivore access, shading). Irrigation of areas was intended to reduce desiccation stress by lowering evaporation rates and also rock temperatures to that of the irrigation water (~25°C in summer and 18°C in winter). Unmanipulated areas (= dry) experienced only natural seawater wetting (tidal and wave induced) throughout the period of the experiments.

Three randomly allocated treatments investigated the effects of molluscan and echinoid herbivores on assemblage development within each wet or dry area. The first treatment excluded herbivores from plots (E = exclusion) using 3 cm high, 26 × 26 cm stainless steel wire fences (4 × 4 mm mesh size). In contrast, both the open treatment (no fence, O = open) and the fence control treatment (half-fenced, C = control) allowed access to herbivores. Half-fenced plots provided a procedural control for possible fence effects and were constructed by erecting 2 half-length fences along opposite corners of cleared plots. Weekly observations showed that exclusion fences were successful at excluding all molluscan and echinoid herbivores but allowed access to fish and crabs.

Scoring and analysis. Algal colonisation and assemblage development was studied by scoring the percentage cover of macroalgae in all plots for a period of 17 wk in each season. A longer study period was avoided, as the investigations would have extended into the subsequent season. The interval between records was variable due to restricted access during times of increased wave-action. Whenever possible, however, algal cover was determined every 2 wk (intervals did not exceed 3 wk) by placing a 100 point double-strung 25 × 25 cm quadrat over the plots and scoring organisms under each intersection point of the strings (Jones et al. 1980).

Four-way ANOVAs were performed on arc-sine transformed percentage cover data of the 4 most abundant algal groups (*Hapalospongidion gelatinosum*, *Ralfsia expansa*, coralline algae and erect macroalgae) and investigated the factors herbivory (exclusion, open and control), tidal height (highshore and lowshore), irrigation (wet and dry) and season (hot season and cool season). The 'coralline algae' combined coralline crusts (encrusting algae belonging to the Corallinaceae) and the erect *Corallina* spp. (i.e. *Corallina sessilis* and *Corallina pilulifera*), as juvenile stages of the 2 form groups could not be distinguished *in situ*. Erect macroalgae included all foliose and filamentous macroalgae, including the non-coralline turfs (e.g. *Ulva* spp., *Enteromorpha* spp., but also *Endarachne binghamiae* and *Scytosiphon lomentaria* during the cool season). Due to temporal non-independence among sequential readings (Underwood 1997), time was not used as a factor in the analysis and data for both seasons were only analysed at Week 13, prior to the irrigation system being turned off.

Due to the low cover of species in the dry highshore treatments, not all variances were homogeneous (Cochran's test). As group sizes were equal, however, ANOVA is thought to be robust against such heterogeneity (Zar 1984). To further investigate significant

differences (after Bonferroni corrections), Student-Neuman-Keuls multiple comparison procedures (SNK tests) were performed.

RESULTS

During both seasons, all treatments, with the exception of dry highshore plots, developed a macroalgal cover (>50%) within 13 wk of the initiation of the experiments. Ephemeral greens (e.g. *Ulva* spp., *Enteromorpha* spp.) were the first macroalgae to colonise (at Week 3), followed by erect *Corallina* spp. and encrusting algal species. The early development and final composition of assemblages, however, was variable and strongly affected by herbivory, irrigation, shore height and season (Tables 1 to 4, Figs. 2 to 5).

Unmanipulated dry plots (dry, +herbivores) were colonised (i.e. > 1% cover) only in the lowshore, where encrusting algal assemblages (dominated by *Ralfsia expansa* and coralline crusts) developed during the hot season and the erect *Corallina* spp. and *R. expansa* dominated during the cool season. While ephemeral, erect macroalgae did initially colonise, they quickly declined in abundance and were almost completely absent by Week 13 (<2% cover).

In dry herbivore exclusion plots (dry, –herbivores), encrusting algae did not dominate (<20% cover), instead, early colonists (ephemeral greens and *Coral-lina* spp. during the cool season) persisted throughout the study periods and developed to cover >80% of the substratum (Figs. 3 & 5). As with the dry herbivore access plots, no species colonised the highshore dry herbivore exclusion plots (<1% cover).

Plots that were irrigated developed macroalgal assemblages at high- and lowshore levels. In the presence of herbivores (wet, +herbivores), encrusting algae or *Corallina* spp. dominated assemblages developed, depending on shore height and time of year (Figs. 2 to 5). In the highshore, *Hapalospongidion gelatinosum* and coralline crusts were most abundant, while in the lowshore *Ralfsia expansa* and coralline crusts dominated during the hot season and *Corallina* spp. during the cool season. In contrast, in herbivore exclusion plots (wet, –herbivores), encrusting algae were less abundant (<15% cover) and erect species (foliose, filamentous and *Corallina* spp.) were dominant (up to 90%).

After the irrigation system was turned off (Week 13), most species in the highshore decreased dramatically in abundance. All erect and coralline algae bleached (turned white and died) and were reduced to <1% cover within 3 wk. In contrast, the 2 non-coralline encrusting algae, *Hapalospongidion gelatinosum* and *Ralfsia expansa*, were less severely affected and persisted in the plots, although reduced to <50% of their original cover. In the lowshore, only erect macroalgae were reduced in cover after the irri-

Table 1. *Hapalospongidion gelatinosum*. Four-way ANOVA of arc-sine transformed algal cover data by herbivory (Exclusion, Control and Open), irrigation (Wet and Dry), tidal height (Highshore and Lowshore) and season (Cool and Hot season). Significance after Bonferroni correction: *p < 0.05 (0.0125); **p < 0.01 (0.0025); ns: not significant. Significant differences were further analysed using SNK multiple comparison tests

Source	df	MS	F	p	Significance
Herbivory (Herb)	2	0.027	4.003	0.025	ns
Irrigation (Irrig)	1	0.334	49.197	<0.001	**
Height (Ht)	1	0.222	32.717	<0.001	**
Season (Seas)	1	0.001	0.001	0.997	ns
Herb × Irrig	2	0.014	2.023	0.143	ns
Herb × Ht	2	0.006	0.914	0.408	ns
Herb × Seas	2	0.008	1.214	0.306	ns
Irrig × Ht	1	0.353	51.947	<0.001	**
Irrig × Seas	1	0.015	2.225	0.142	ns
Ht × Seas	1	0.053	7.760	0.008	*
Herb × Irrig × Ht	2	0.021	3.036	0.057	ns
Herb × Irrig × Seas	2	0.007	1.063	0.354	ns
Irrig × Ht × Seas	1	0.011	1.685	0.200	ns
Herb × Irrig × Ht × Seas	2	0.002	0.344	0.711	ns
Error	48	0.007			

SNK tests

Irrigation × Height	Wet > Dry on Highshore, Wet = Dry on Lowshore
	High > Low in Wet treatments, High = Low in Dry treatments
Height × Season	High > Low during both Seasons
	Cool > Hot on Highshore, Cool = Hot on Lowshore

Table 2. *Ralfsia expansa*. Four-way ANOVA of arc-sine transformed algal cover data by herbivory, irrigation, tidal height and season. E: exclusion, C: control, O: open. Significance values as in Table 1. Significant differences were further analysed using SNK multiple comparison tests

Source	df	MS	F	p	Significance
Herbivory (Herb)	2	0.171	12.886	<0.001	**
Irrigation (Irrig)	1	0.082	6.159	0.017	ns
Height (Ht)	1	2.780	209.277	<0.001	**
Season (Seas)	1	0.234	17.610	<0.001	**
Herb × Irrig	2	0.025	1.890	0.162	ns
Herb × Ht	2	0.072	5.443	0.007	*
Herb × Seas	2	0.040	3.024	0.058	ns
Irrig × Ht	1	0.052	3.938	0.053	ns
Irrig × Seas	1	0.073	5.525	0.023	ns
Ht × Seas	1	0.198	14.903	<0.001	**
Herb × Irrig × Ht	2	0.001	0.009	0.991	ns
Herb × Irrig × Seas	2	0.031	2.358	0.105	ns
Herb × Ht × Seas	2	0.025	1.911	0.159	ns
Irrig × Ht × Seas	1	0.054	4.058	0.050	ns
Herb × Irrig × Ht × Seas	2	0.023	1.720	0.190	ns
Error	48	0.013			

SNK tests

Herb × Height	E < C = O on Lowshore, E = C = O on Highshore
	Low > High in all Herbivore treatments
Height × Season	Low > High during both seasons
	Hot > Cool on Lowshore, Hot = Cool on Highshore

Table 3. Erect macroalgae. Four-way ANOVA of arc-sine transformed algal cover data by herbivory, irrigation, tidal height and season. Significance values as in Table 1. Significant differences were further analysed using SNK multiple comparison tests

Source	df	MS	F	p	Significance
Herbivory (Herb)	2	2.839	131.365	<0.001	**
Irrigation (Irrig)	1	0.246	11.375	0.001	**
Height (Ht)	1	0.564	26.095	<0.001	**
Season (Seas)	1	0.001	0.008	0.931	ns
Herb × Irrig	2	0.274	12.694	<0.001	**
Herb × Ht	2	0.498	23.046	<0.001	**
Herb × Seas	2	0.003	0.136	0.873	ns
Irrig × Ht	1	0.321	14.860	<0.001	**
Irrig × Seas	1	0.059	2.735	0.105	ns
Ht × Seas	1	0.210	9.716	0.003	*
Herb × Irrig × Ht	2	0.208	9.635	<0.001	**
Herb × Irrig × Seas	2	0.038	1.742	0.186	ns
Herb × Ht × Seas	2	0.153	7.085	0.002	**
Irrig × Ht × Seas	1	0.041	1.895	0.175	ns
Herb × Irrig × Ht × Seas	2	0.031	1.448	0.245	ns
Error	48				

SNK tests

Herb × Irrig × Ht	E > C = O in all treatments except HighDry, where E = C = O
	Wet > Dry in all HighE treatments, otherwise Wet = Dry
	Low > High in all DryE treatments, otherwise Low = High
Herb × Ht × Seas	E > C = O in all treatments except HotHigh, where E = C = O
	Low > High in Exclusion treatments, otherwise Low = High
	Hot > Cool in LowE treatments, otherwise Hot = Cool

Table 4. Coralline algae. Four-way ANOVA of arc-sine transformed algal cover data by herbivory, irrigation, tidal height and season. Significance values as in Table 1. Significant differences were further analysed using SNK multiple comparison tests

Source	df	MS	F	p	Significance
Herbivory (Herb)	2	0.433	16.086	<0.001	••
Irrigation (Irrig)	1	0.870	32.367	<0.001	••
Height (Ht)	1	3.548	131.938	<0.001	••
Season (Seas)	1	0.899	33.442	<0.001	••
Herb × Irrig	2	0.044	1.639	0.205	ns
Herb × Ht	2	0.106	3.942	0.026	ns
Herb × Seas	2	0.006	0.227	0.798	ns
Irrig × Ht	1	0.327	12.160	0.001	••
Irrig × Seas	1	0.001	0.003	0.954	ns
Ht × Seas	1	0.930	34.591	<0.001	••
Herb × Irrig × Ht	2	0.025	0.926	0.403	ns
Herb × Irrig × Seas	2	0.001	0.041	0.959	ns
Herb × Ht × Seas	2	0.020	0.748	0.479	ns
Irrig × Ht × Seas	1	0.001	0.024	0.877	ns
Herb × Irrig × Ht × Seas	2	0.037	1.392	0.258	ns
Error	48	0.027			

SNK tests

Herbivory	E < O = C
Irrig × Height	Wet > Dry on Highshore, Dry = Wet on Lowshore
	Low > High in both Irrigation treatments
Height × Season	Low > High during both seasons
	Cool > Hot on Lowshore, Cool = Hot on Highshore

gation system was turned off, and only during the hot season (Fig. 3).

Molluscan and echinoid herbivores significantly reduced the abundance of erect macroalgae in all but the most physically stressful plots (i.e. highshore dry and highshore hot season treatments; Table 3), and their presence resulted in assemblages with a significantly greater abundance of the encrusting alga *Ralfsia expansa* and the coralline algae (Tables 2 to 4). For *R. expansa*, however, herbivory had a significant effect only on the lowshore (Table 2). No significant differences were exhibited between control plots (half-fenced) and open plots throughout the experiment (Tables 1 to 4), suggesting that fences successfully excluded herbivores, but did not otherwise affect algal abundance.

With the exception of *Ralfsia expansa*, all species were affected by irrigation and were more abundant on wet compared to dry plots (Tables 1 to 4). This pattern, however, was always restricted to the highshore, and in the case of the erect macroalgae to exclusion treatments. All species, with the exception of *Hapalospongidion gelatinosum*, were more abundant in the lowshore than in the highshore.

The abundance of *Ralfsia expansa* and the coralline algae varied with season. *R. expansa* was more abundant during the hot season while the coralline algae were more abundant during the cool season. In both groups, significant seasonal abundance patterns were

restricted to the lowshore (Tables 2 & 4). No significant difference in final cover was recorded between the seasons for *Hapalospongidion gelatinosum* or erect macroalgae.

DISCUSSION

The development of algal assemblages was greatly influenced by herbivory, physical stress, tidal height and the season when rock space was liberated. In unmanipulated treatments (dry, +herbivores), during the hot season, encrusting algal assemblages developed that were similar to those found in surrounding natural habitats. Most other treatments, however, affected algal colonisation and development and resulted in a number of contrasting assemblages that are usually only found in small patches on Hong Kong shores of moderate exposure (Kaehler & Williams 1996).

Physical stress

On the highshore, physical stress prevented the establishment of all macroalgal species (<1% cover after 17 wk), while in plots of reduced physical stress (i.e. lowshore and highshore irrigated plots) macroalgae colonised within 3 wk of experiment initiation. An

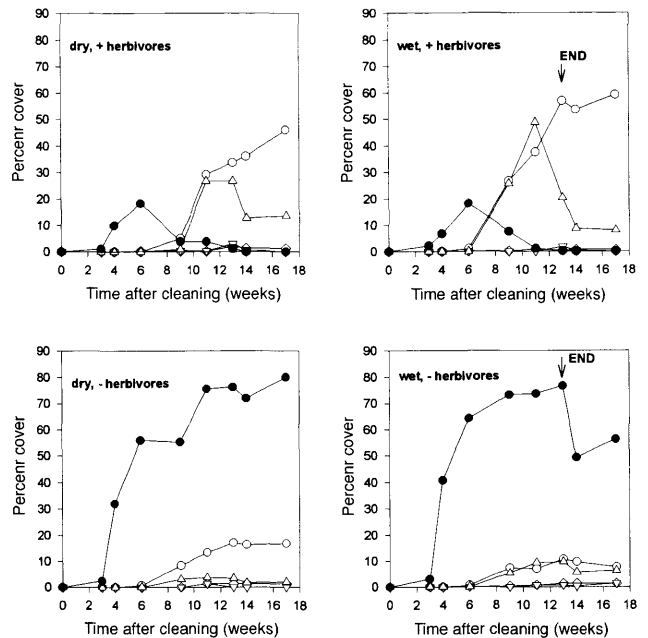## HOT SEASON - HIGHSHORE
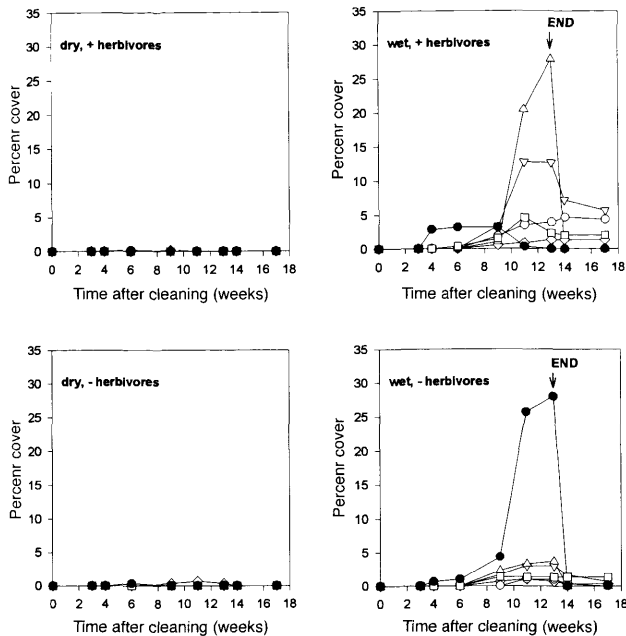
HOT SEASON - LOWSHORE

Fig. 2. Development of highshore macroalgal assemblages (1.75 m above C.D.) during the hot season (initiated August 1993) under different physical (dry: natural condition; wet: surfaces irrigated) and biological (−herbivores: fenced exclusions; +herbivores: open and half-fenced control plots) regimes. Herbivore access plots (+herbivores) contain pooled data from open and control plots as the 2 treatments were not significantly different. (△) Coralline crusts, (▽) *Hapalospongidion gelatinosum*, (○) *Ralfsia expansa*, (□) *Kyrtuthrix maculans*, (◇) *Hildenbrandia rubra*, (●) erect algae (mostly Ulvales, but some *Endarachne binghamiae* and *Scytosiphon lomentaria* during the cool season), (▲) *Corallina* spp. END: time at which irrigation was stopped. Error bars have been omitted for clarity. Note smaller scale in Fig. 2 as compared to Figs. 3 to 5

Fig. 3. Development of lowshore macroalgal assemblages (0.75 m above C.D.) during the hot season (initiated August 1993) under different physical (dry: natural condition; wet: surfaces irrigated) and biological (−herbivores: fenced exclusions; +herbivores: open and half-fenced control plots) regimes. Herbivore access plots (+herbivores) contain pooled data from open and control plots as the 2 treatments were not significantly different. Symbols as in Fig. 2. Error bars have been omitted for clarity

increased supply of propagules to irrigated highshore areas may have confounded the present experimental design; however, filtering of the seawater through glass wool is likely to have minimised the density of propagules arriving on the shore via the irrigation system. Physical stress appears to be the main factor restricting the establishment of macroalgal assemblages on the highshore, as at no time did colonisation to dry areas occur. In contrast, on the lowshore, irrigation had no effect on the establishment and abundance of algal species, suggesting that, at this tidal height, physical stress is of reduced importance.

Physical stress has been widely reported to influence the distribution of intertidal algae (e.g. Zanefeld 1937, Moore 1939, Doty 1946, Lewis 1964, Frank 1965, Dayton 1971, Connell 1972, Schonbeck & Norton 1978,

Buschmann 1990) and it has been implied that, towards their upper vertical limits, macroalgae are restricted by physiological intolerances during low tide (reviewed by Norton 1985, Underwood 1985, 1991, but see Underwood 1980). Physiological tolerances, however, may vary between algal functional groups (Dethier 1994), and between individual species (Schonbeck & Norton 1978, Dethier 1994), as well as ontogenetically with the size and developmental stage of the macroalgae (Hruby & Norton 1979, Norton 1986, Davison et al. 1993).

In the present study, on the highshore, macroalgal colonisation was completely prevented unless physical stress was reduced (i.e. wet treatments). Once established, however, several encrusting species were able to persist in this physically stressful habitat for several months after irrigation was stopped (Kaehler pers. obs.), suggesting that juvenile algal colonists are more susceptible to physical stress than older and larger individuals (Hruby & Norton 1979, Norton 1986, Davison et al. 1993). Furthermore, while all erect algae and the coralline crusts totally disappeared within a few
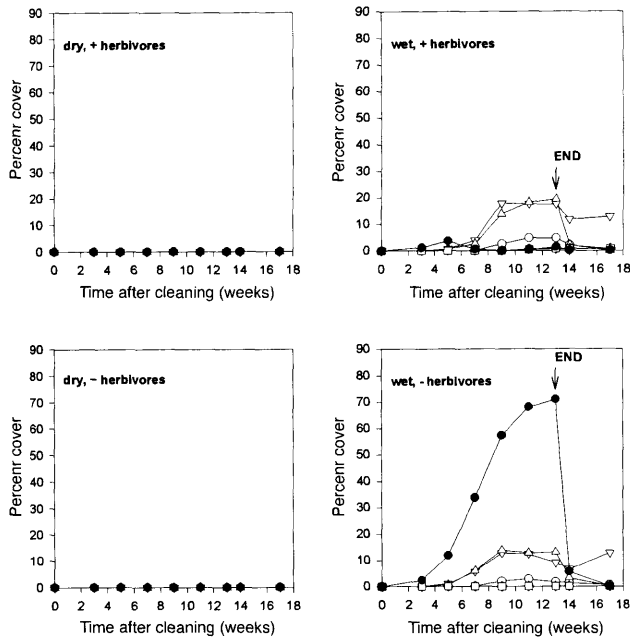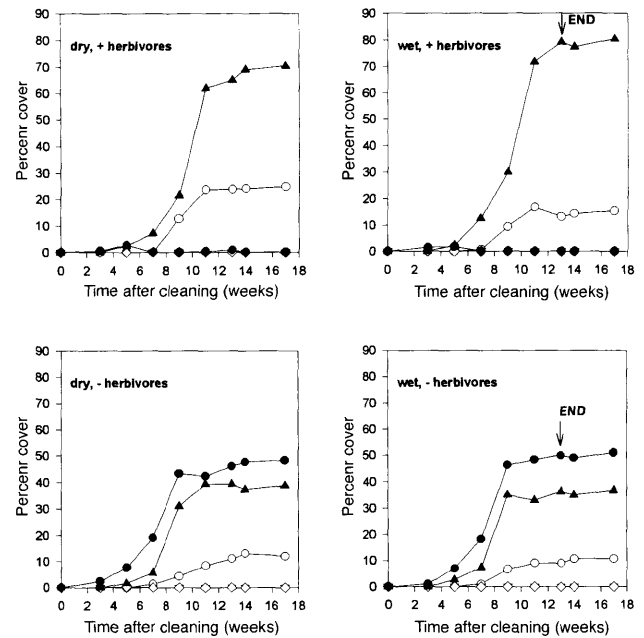
COOL SEASON - HIGHSHORE

Fig. 4. Development of highshore macroalgal assemblages (1.75 m above C.D.) during the cool season (initiated January 1994) under different physical (dry: natural condition; wet: surfaces irrigated) and biological (–herbivores: fenced exclusions; +herbivores: open and half-fenced control plots) regimes. Herbivore access plots (+herbivores) contain pooled data from open and control plots as the 2 treatments were not significantly different. Symbols as in Fig. 2. Error bars have been omitted for clarity

COOL SEASON - LOWSHORE

Fig. 5. Development of lowshore macroalgal assemblages (0.75 m above C.D.) during the cool season (initiated January 1994) under different physical (dry: natural condition; wet: surfaces irrigated) and biological (–herbivores: fenced exclusions; +herbivores: open and half-fenced control plots) regimes. Herbivore access plots (+herbivores) contain pooled data from open and control plots as the 2 treatments were not significantly different. Symbols as in Fig. 2. Error bars have been omitted for clarity

weeks, several fleshy, encrusting algae (e.g. *Hapalospongidion gelatinosum, Ralfsia expansa*) and the encrusting cyanobacterium *Kyrtuthrix maculans* persisted at reduced abundance for several months. Encrusting algae, therefore, appear to be more resistant to physical stress than erect species (but see Buschmann 1990). The greater desiccation tolerance of fleshy encrusting algae may be partially due to their low exposed surface area (see also Dromgoole 1980, Dethier 1994). Coralline crusts share the low specific surface of other encrusting algae, but under natural conditions have a very low water content (Dethier 1994, Kaehler 1996) and may subsequently be more susceptible to desiccation stress.

Tidal height

In dry plots, physical stress totally prevented colonisation of the highshore and macroalgae were restricted to the lowshore. The distribution of some species, however, could not be explained by gradients in physical

stress. *Hapalospongidion gelatinosum* was almost completely restricted to the highshore, although sparse numbers of individuals can recruit to the lowshore (Kaehler & Williams 1997). Neither a reduction in physical stress (wet treatments) nor the absence of herbivores promoted the establishment of this species on the lowshore. It is likely, therefore, that the colonisation and/or development of *H. gelatinosum* was inhibited by other space occupying species, either by space preemption (see also Dungan 1986) or by lateral overgrowth (erect macroalgae, *Ralfsia expansa* and *Corallina* spp. all overgrow *H. gelatinosum*; Kaehler 1996).

In contrast, *Corallina* spp. became established on the lowshore in the presence of all potential competitors as well as herbivores, and at no time, even in wet treatments, did these species develop in the highshore. This restricted distribution pattern may be a result of the limited dispersal of non-motile *Corallina* spp. propagules confining them to short distances from their primarily subtidal source of origin (see also Deysher & Norton 1982, Kendrick & Walker 1991). Alternatively, it is possible that *Corallina* spp. propagules did recruit

to the highshore but did not develop into erect articulated individuals. This would not have been detected because, in the present study, the basal crusts of juvenile *Corallina* spp. and non-articulated coralline crusts were not distinguished.

Season of substratum clearance

Clearings initiated during the cool season resulted in different assemblages as compared to during the hot season. While ephemeral green species (e.g. *Ulva* spp. and *Enteromorpha* spp.) and most encrusting algae colonised throughout the year, some erect macroalgae (e.g. *Corallina* spp., *Endarachne binghamiae* and *Scytosiphon lomentaria*) established only during the cool season and were abundant until the end of the experiment. As a result, assemblages dominated by encrusting algae, similar to those found in natural habitats, developed only during the hot season. The timing of substratum clearance, therefore, seems to be of primary importance in determining the composition of colonists and subsequent assemblage development.

Several studies have shown that the colonisation, succession and abundance of algal species can be affected by temporal patterns in species recruitment (e.g. Niell 1979, Sousa 1979a, Breitburg 1985, Benedetti-Cecchi & Cinelli 1993a, b, Lively et al. 1993). In the present study, temporal variation in assemblage development was most pronounced in the lowshore. During the cool season, *Corallina* spp. were one of the first species to colonise (shortly after the ephemeral greens), and wherever they became established the development of encrusting algae (e.g. *Ralfsia expansa*, coralline crusts) was inhibited, possibly due to interspecific competition (see also Machado et al. 1996). On Hong Kong shores, *Corallina* spp. always overgrow all encrusting algae (Kaehler 1996).

The abundance of individual species was also effected by the timing of substratum clearance. *Ralfsia expansa*, for example, was overall more abundant during the hot season than the cool season, while, conversely, *Hapalospongidion gelatinosum* and the erect macroalgae were more abundant during the cool season. For these species, increased abundance coincided with periods of reproduction (Kaehler & Williams 1997).

Herbivory

The greatest overall effect on algal assemblage development was produced by herbivores on the lowshore. Both a decrease in the densities of herbivores and a reduction in available feeding time during high-

tide may account for the lessened effectiveness of herbivores at higher shore levels (e.g. Hartnoll & Wright 1977, Hawkins 1981, Williams 1993a).

In all plots in which algae became established, ephemeral green algae were the first to colonise. In the absence of herbivores, these fast growing species dominated the substratum. In the presence of natural grazer densities, however, the majority of erect macroalgae were removed from the plots within a few weeks of colonisation and encrusting algae dominated or *Corallina* spp. dominated assemblages became established. In Hong Kong, shores of moderate exposure are frequently dominated by encrusting algae; herbivory must therefore be important in mediating encrusting algal establishment and subsequent development (Williams 1993a, b, Kaehler & Williams 1996). Herbivores drive succession (increase species replacement) by preferentially removing early successional species (ephemeral greens) which can inhibit the development of encrusting algae (see also Lubchenco & Menge 1978, Sousa 1979b, Robles & Cubit 1981, Lubchenco 1983, Buschmann 1990, Benedetti & Cinelli 1993b).

Development of encrusting algal assemblages on seasonal tropical shores

Similar to studies from Panama (e.g. Menge et al. 1986a, b), herbivory was found to be of primary importance in determining the abundance of encrusting algae. In Hong Kong, however, molluscan and echinoid herbivores (fishes and crabs were not excluded by the fences), as opposed to large and highly mobile consumers in Panama, were sufficient for the exclusion of superior algal competitors. Furthermore, the physical environment in Hong Kong is more strongly seasonal than in Central America and affected assemblage composition on the lowshore by liberating bare substratum only during the hot season, when the herbivore-resistant and competitively superior species (e.g. *Corallina* spp.) did not recruit. All foliose and filamentous erect macroalgae became established and remained abundant only in the absence of herbivores. In contrast, the abundance of grazer-resistant species was likely related to their competitive abilities (e.g. *Corallina* spp., *Ralfsia expansa*). This observation agrees with models of community dynamics (Connell 1975, Menge & Sutherland 1976) which predict that competitive interactions in natural communities are important only between species that escape consumption.

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