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Distribution of algae on tropical rocky shores: spatial and temporal patterns of non-coralline encrusting algae in Hong Kong

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Abstract Encrusting algae have been described as dominant space occupying species on rocky shores around the world. Despite their abundance, however, most studies classify species under generic names (e.g. *Ralfsia* sp.) or as a functional group (e.g. encrusting algae), thereby underestimating the number of species present and their ecological importance. Studies on six rocky shores of varying exposure, in Hong Kong, recorded eight common species of encrusting algae. The greatest abundance of encrusting algae was recorded on shores of intermediate exposure, where four distinct zonation bands could be identified; a cyanobacterial "*Kyrtuthrix*-Zone" in the upper midlittoral, a "Bare-Zone" below this, a "Mixed-Zone" in the lower midlittoral and a "Coralline-Zone" in the infralittoral fringe. Abundance declined on shores of greater and lower exposure to wave action, where bivalves and barnacles were competitively dominant. Certain species were found in greater abundance on exposed shores (e.g. *Dermocarpa* sp. and *Hildenbrandia occidentalis*), while others preferred more sheltered shores (e.g. *Hildenbrandia prototypus* and *Kyrtuthrix maculans*). With the exception of some cyanobacterial crusts, the abundance of encrusting algae was always greatest towards the low shore, an area of decreased physical stress and increased herbivore density. Zonation patterns showed seasonal variation associated with the monsoonal climate of Hong Kong. Most species increased in abundance during the cool season, while during the summer months the cover and vertical extent of encrusting algae decreased in relation to summer temperatures, although *K. maculans* increased in abundance during the summer. On Hong Kong shores, encrusting algae have a high species richness and exhibit within-functional group spatial and temporal variation which is mediated by herbivory and seasonal, physical stresses.

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Introduction

Unlike their temperate counterparts, most tropical intertidal rocky shores appear, superficially, to be barren due to a lack of foliose macroalgae and a low abundance of sessile invertebrates (Lubchenco et al. 1984; Brosnan 1992). Instead, the dominant space occupying species on many tropical shores are low-lying forms such as encrusting algae and turf algae (Menge and Farrell 1989; Brosnan 1992). Studies from central America (e.g. Brattström 1980; Lubchenco et al. 1984), tropical Africa (e.g. Plante 1964; John and Lawson 1991) and from the tropical western Pacific (e.g. Loi 1967; Kamura and Choonhabandit 1986; Williams 1993a) have all highlighted the importance of encrusting algae as abundant, or even dominant, space occupants. Despite this apparent abundance, however, there is very little quantitative information available on their distribution patterns on tropical intertidal shores.

The principal reason for the lack of information on encrusting algae is the difficulty with which they are identified in the field (Dethier 1994). The scarcity of taxonomic literature, together with their superficially similar morphologies, tends to result in investigations acknowledging the presence of "encrusting algae" on certain parts of the shore, but ignoring species identification. Instead, species are often pooled into colour classes (e.g. Lewis 1960; Levings and Garrity 1984), combined under one generic or specific name (e.g. Plante 1964; Brattström 1980; Kamura and Choonhabandit 1986; Liu 1993; Williams 1993a, b), or simply classed as "encrusting algae" without any further distinction (e.g. Hodgkin and Michel 1962; Hartnoll 1976). Although this functional grouping is often sufficient in terms of general ecological descriptions, it can also be misleading. The perception that many tropical shores are depauperate of sessile species, for example, is furthered by this trend since in many cases one group of encrusting algae may consist of several only distantly related species (Kaehler 1994). Due to the inherent difficulties involved with the identification of encrusting species, the encrusting growth form has been described as "probably the least well understood but most widespread functional group" of all macroalgae (Dethier 1994).

In addition to difficulties arising from the lack of information at the species level, the scarcity of large scale quantitative studies in the tropics makes an understanding of even broad distribution patterns very difficult. Descriptive accounts of vertical zonation patterns of the tropical flora and fauna exist from several longitudes (see references above). In most cases, however, individual studies were conducted over a short time period and/or at a very local scale, which makes comparisons between localities very difficult (Underwood and Petraitis 1993). Brosnan (1992) reviewed "typical" zonation patterns for tropical rocky shores along a wave exposure gradient based on descriptive accounts from several longitudes. As she acknowledged, however, the relative abundance and distributions of individual species and groups of organisms varied greatly between localities. To understand better the distribution of sessile organisms and their relationship to factors such as exposure, seasonality and locality, studies that integrate both a series of shores in one region and multiple observations over a period of time are necessary.

The present paper investigates the spatial and temporal distributions of intertidal encrusting algae on seasonal, tropical, rocky shores in Hong Kong. Broad patterns of the abundance and distribution of sessile organisms were quantified in wet and dry monsoon periods on six shores of varying exposure. More detailed spatial and temporal distributions of individual species of encrusting algae (abundance in relation to tidal height, inclination and season) were studied on a shore of intermediate exposure, at monthly intervals, for 17 months.

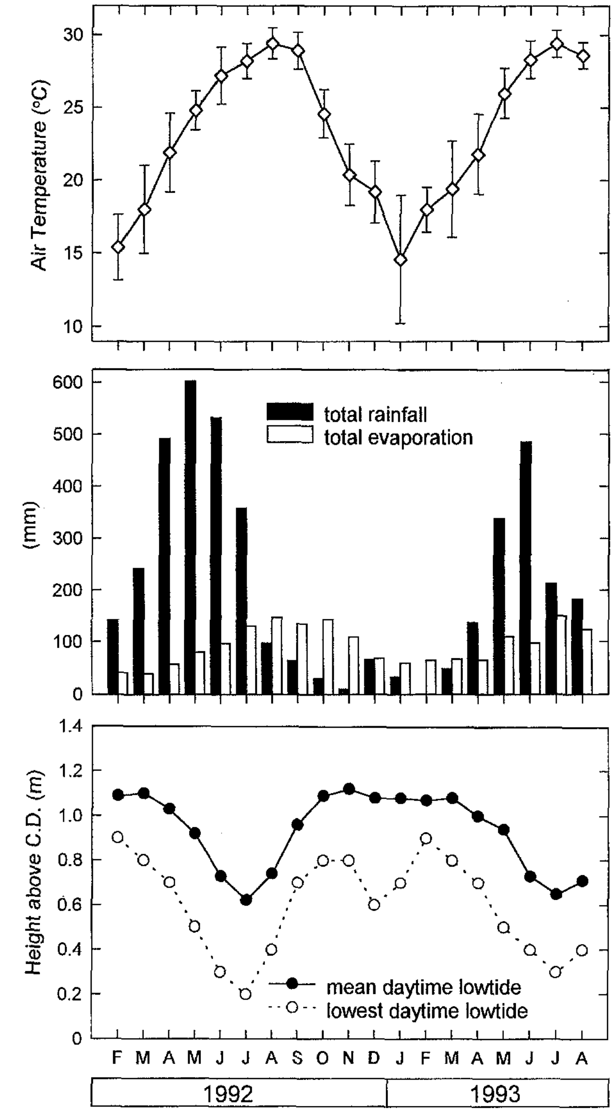

Fig. 1 Seasonal physical parameters during the time of study. Air temperature (± SD), total rainfall, total evaporation (as an indicator of desiccation stress), and tidal data provided by the H.K. Royal Observatory

Materials and methods

The climate of Hong Kong

Hong Kong has a tropical monsoonal climate with a cool and dry season from November to March and a hot and wet season during the summer and autumn months (for summary see Morton and Morton 1983). The period from July to September is generally the most physically stressful (sensu Moore 1972) for sessile intertidal organisms due mainly to increased desiccation stress. During this time of the year, maximum air temperatures (max. = 36 °C, monthly mean = 28 °C) and sea surface temperatures (monthly mean = 27 °C) as well as highest evaporation rates coincide with extreme low tides during daytime hours (Fig. 1). The winter months, in comparison, are cooler with mean air and sea temperatures falling to 15 and 17 °C, respectively. During this period of reduced temperature stress and high wave-action, extreme low tides occur during the night, and daytime low tides can be 55 cm (monthly mean) higher than during the hot summer months (Fig. 1).

The strong seasonality of Hong Kong's climate produces a distinct seasonal variation in the composition of intertidal communities. While during the hot summer months shores have been described as devoid of all macroalgae except encrusting algae, shores in winter may support large patches of foliose and other erect macroalgae (Hodgkiss 1984; Williams 1993b). The distribution of a great variety and density of herbivores (mainly molluscs and urchins) also varies seasonally due to migrations up and down the shore and summer die-offs (Williams and Morritt 1995).

Distribution of sessile biota in relation to shore exposure

Six rocky shores of 10 to 15 m horizontal length were chosen for their homogeneity (few crevices and only small cracks) at and

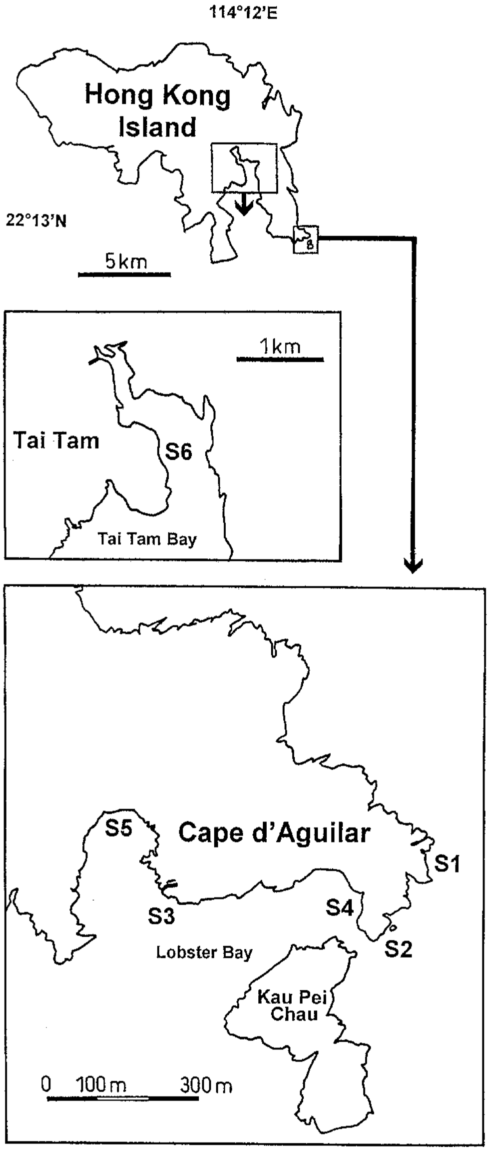

Fig. 2 Location of the six sampling sites at Cape d'Aguilar and Tai Tam Bay. Sites ranked in order of exposure. S1 and S2 are exposed to the South China Sea, S3 to S5 are inside Lobster Bay and sheltered to varying degrees by Kau Pei Chau Island, while S6 is deep within the very sheltered Tai Tam Bay

around the Cape d'Aguilar peninsula, Hong Kong Island (Fig. 2). The relative exposures of the shores were ranked, first subjectively by visually comparing wave heights on the shores and then by measuring white "splash zones" from aerial photographs. The exposure of the sites ranked from very exposed, with an oceanic windfetch (S1 and S2), to very sheltered inside Tai Tam Bay (S6). Shores of intermediate exposure (S3 to S5) were sheltered to different degrees by Kau Pei Chau Island (Fig. 2).

The shores were surveyed to establish identical tidal heights and sampled once in February 1993 (cool/dry season) and once in July 1993 (hot/wet season). Shores were sampled along horizontal belts at 50 cm vertical height intervals with a 100 point, double-strung, 50 × 50 cm quadrat. Ten quadrats were located along a meter band on each belt, using a random number table, and percent cover of sessile organisms determined. Percent cover was often greater than 100% due to the scoring of organisms both on primary and secondary substratum as well as determining understorey and canopy cover. Although the above sampling design did not always describe the exact distribution limits of each species, larger scale patterns could be determined. The two lower heights at the exposed Shores 1 and 2 were never quantitatively sampled due to heavy wave action.

Species distribution in relation to tidal height, seasonality and substratum inclination

The more detailed vertical distribution and temporal variation of the intertidal flora was investigated on a shore of intermediate exposure (S4). This shore was chosen as representative of shores of moderate exposure, having easy access and being relatively safe to work on during all times of the year.

The shore was divided into 12 horizontal belts at 25 cm vertical height increments. At each height eight quadrats were scored on horizontal surfaces (<45° slope) and eight quadrats on vertical surfaces (45° to 90° slope). A 100 point double-strung 25 × 40 cm (height × length) quadrat was located along each belt, using a random number table, until all eight samples of each orientation were taken. Percentage cover was estimated by, wherever possible, identifying species and scoring organisms under each intersection point of the strung quadrat on a monthly basis from April 1992 to July 1993.

Two-way analysis of variance (ANOVA) was applied to the data from the heights of maximum species cover (see Table 2) of each of the six most common encrusting algae, to investigate the effects of the factors "time" and "substratum inclination" on the abundance of encrusting algae. Other heights were excluded from the analysis as the preponderance of zero values violated the assumptions of homogeneity and normality required for ANOVA (Zar 1984). Bonferroni corrections were applied to maintain the probability of a Type-I overall experimental error at 5%. Student–Neuman–Keuls (SNK) multiple comparison procedures were carried out to further investigate significant factors. Spearman rank order correlations were also carried out to test for relationships between changes in algal cover and temperature, which was used as the most important indicator of seasonality (Fig. 1).

Results

Seasonal distribution of sessile biota in relation to shore exposure

Species composition varied not only between the six shores but also with tidal height and the time of the survey (Table 1). During both the cold season and hot season, encrusting algae were the dominant space occupants at all tidal heights on the moderately exposed shores (S4 and S5, Fig. 3). On all other shores, encrusting algae were common (occurring in ≥ 50% of quadrats), but their relative abundance decreased towards both extremes of exposure. On shores of extremely high exposure (S1, S2) barnacles such as *Tetraclita squamosa*, *Megabalanus volcano* and the mussel *Septifer virgatus* predominated, while on the extremely sheltered shore (S6) the oyster *Saccostrea cucullata* and the barnacle *Euraphia withersi* were dominant (Table 1). Apart from differences in total abundance, the species composition of encrusting algae also varied between shores. *Kyrtuthrix maculans* and *Hildenbrandia prototypus* (= *rubra*), for example, occurred only on the four most

Table 1 Common (occurring in ≥ 50% of quadrats) sessile rocky shore organisms along an exposure gradient in Hong Kong

Location, Type	Exposed	Intermediate	Sheltered
Supralittoral fringe			
Erect algae	*Porphyra suborbiculata*[a]	*Porphyra suborbiculata*[a]	
Upper midlittoral			
Sessile inverts	*Capitulum mitella* *Chthamalus malayensis*	*Capitulum mitella*	
Erect algae	*Endarachne binghamiae*[a] *Porphyra suborbiculata*[a] *Ulva* spp.[a]	*Porphyra suborbiculata*[a]	
Encrusting algae		*Dermocarpa* sp.[a] *Hildenbrandia prototypus* *Kyrtuthrix maculans*	*Hildenbrandia prototypus* *Kyrtuthrix maculans*
Lower midlittoral			
Sessile inverts	*Capitulum mitella* *Megabalanus* sp. *Septifer virgatus* *Tetraclita squamosa*	*Tetraclita squamosa*	*Euraphia withersi* *Saccostrea cucullata* *Tetraclita squamosa*
Erect algae	*Chaetomorpha antennina*[a] *Dermonema frappieri*[a] *Endarachne binghamiae*[a] *Gelidium pusillum* *Hincksia mitchelliae*[a] *Corallina pilulifera* *Polysiphonia* spp.[a] *Pterocladia tenuis*[a] *Ulva* spp.[a]	*Corallina sessilis* *Endarachne binghamiae*[a] *Gelidium pusillum* *Hincksia mitchelliae*[a] *Ulva* spp.[a]	*Gelidium pusillum* *Ulva* spp.[a]
Encrusting algae	coralline crusts *Dermocarpa* sp. *Hildenbrandia occidentalis* *Ralfsia expansa*	coralline crusts *Endoplura aurea* *Hapalospongidion gelatinosum* *Hildenbrandia prototypus* *Ralfsia expansa*	coralline crusts *Hapalospongidion gelatinosum* *Hildenbrandia prototypus* *Ralfsia expansa*
Infralittoral fringe			
Sessile inverts	*Megabalanus* sp.		*Saccostrea cucullata*
Erect algae	*Corallina pilulifera*	*Colpomenia sinuosa*[a] *Gelidium pusillum* *Sargassum hemiphyllum*[a]	*Colpomenia sinuosa*[a] *Gelidium pusillum* *Sargassum hemiphyllum*[a]
Encrusting algae	coralline crusts	coralline crusts *Hildenbrandia prototypus* *Ralfsia expansa*	coralline crusts

[a] Strongly seasonal species completely absent during summer months

sheltered shores, while *Dermocarpa* sp. and *Hildenbrandia occidentalis* were most common on exposed shores (Table 1). On all shores, encrusting algal cover and species richness were greatest in the lower midlittoral and the infralittoral fringe (sensu Stephenson and Stephenson 1972). Although no quantitative data were taken for the lower two heights at S1 and S2, a qualitative assessment of these parts of the shores revealed a high cover of coralline crusts.

Erect macroalgae showed great temporal variation in abundance and species richness (Fig. 3). The number of species was reduced from 13 common erect macroalgae during the cool season to four turf forming species during the hot season. All supralittoral fringe and upper midlittoral species were lost (<1% cover), with only small patches of turf algae (*Gelidium pusillum*, *Corallina* spp. and an unidentified brown turf) surviving on the lower shore during the hot season. In contrast, during the cool season, erect species exhibited a high percentage cover, especially on the more exposed shores (up to 60%) where foliose macroalgae such as *Porphyra suborbiculata*, *Ulva* spp. and *Endarachne binghamiae* were commonly found in the supralittoral fringe and upper midlittoral (Table 1). Seasonal variation was also found in the encrusting algae which exhibited a reduced cover during the hot season. The cyanobacterial crust *Dermocarpa* sp. died off completely during the summer, while other species

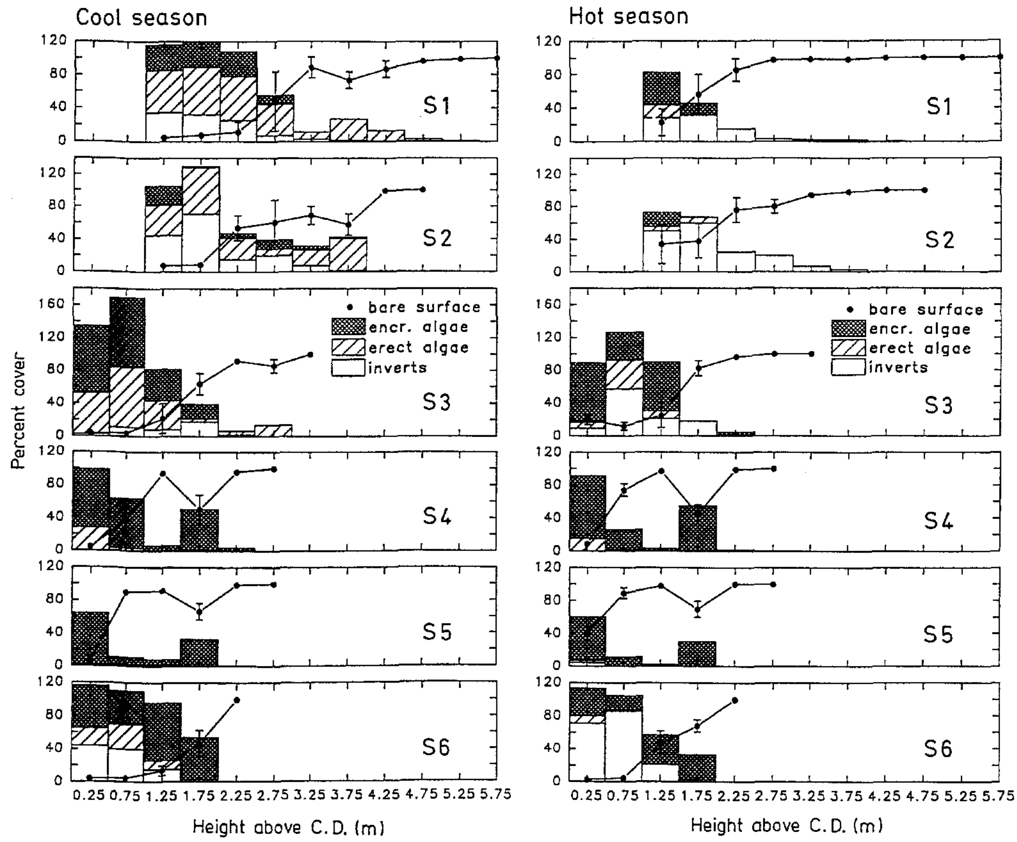

Fig. 3 Vertical distribution of three sessile form groups on six shores of varying exposure (S1 = most exposed to S6 = most sheltered). Data taken in February 1993 (cool season) and August 1993 (hot season)

such as *Hapalospongidion gelatinosum* and *Ralfsia expansa* became less abundant (Fig. 3). The seasonality of sessile invertebrate species was less uniform. The overall cover of invertebrates was higher during the hot season than during the cool season (Fig. 3), due mainly to an increase in the cover of the barnacle *Tetraclita squamosa*. Species such as *Septifer virgatus*, however, had a lower abundance during the hot season.

Species distribution in relation to tidal height, seasonality and substrate inclination

Throughout the period of study, four distinct zones were apparent on S4 (Fig. 4). The upper midlittoral was dominated by a zone of the cyanobacterial crust *Kyrtuthrix maculans* at its upper reaches (the "*Kyrtuthrix*-*Zone*"; 1.75 to 2.25 m above Chart datum, C.D.) and by a zone of reduced cover (the "Bare-Zone") below. *K. maculans* only occurred at this height of the shore, and was the only common species, apart from a very low cover of *Hildenbrandia prototypus* and patches of foliose macroalgae during the cool season (Fig. 5). The Bare-Zone generally contained a macroalgal cover of less than 15%, and a high abundance and variety of microscopic cyanobacteria. The lower midlittoral (the "Mixed-Zone") exhibited a high number of species, with up to seven encrusting species and a variety of erect macroalgae during the cooler winter months.

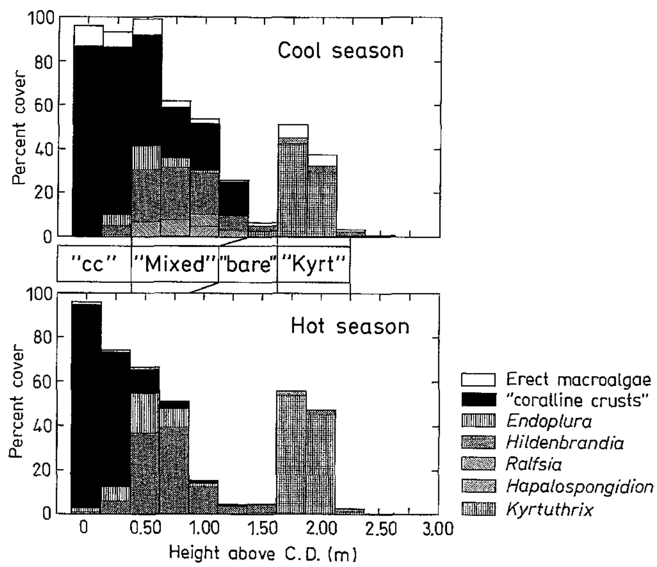

Fig. 4 Vertical distribution of "fleshy" encrusting algal species, the coralline crusts and erect macroalgae. A four banded zonation pattern is apparent throughout the period of study, with a "*Kyrtuthrix*-Zone", a "Bare-Zone" of reduced cover, a "Mixed-Zone" and a "Coralline-Zone" in the infralittoral fringe. Data taken in March 1992 (cool season) and August 1992 (hot season) on Shore 4

Three species of common brown encrusting algae (*Hapalospongidion gelatinosum, Ralfsia expansa* and *Endoplura aurea*), one "fleshy" encrusting red algae (*Hildenbrandia prototypus*) and coralline crusts were

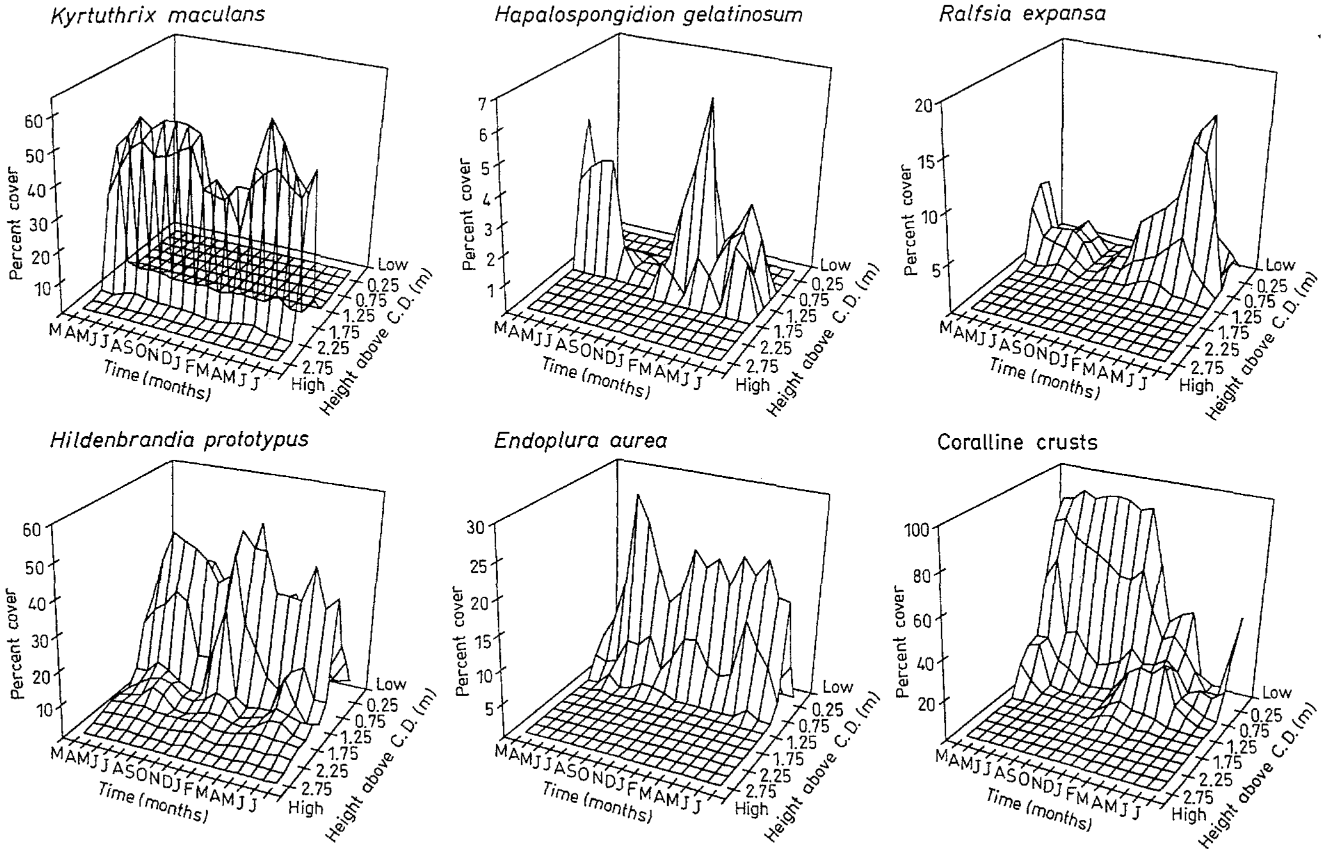

Fig. 5 Temporal changes in the vertical distribution and abundance (% cover) of encrusting algal species during the 17 mo study. Pooled data from both horizontal and vertical surfaces were used (Shore 4)

common at this height of the shore. *H. gelatinosum* inhabited a distinct band from 0.75 to 1.5 m above C.D., and was never found above or below this height. All other species in this zone exhibited heights of peak abundance but no distinct lower limits (Fig. 5). Upper limits varied between species and were seasonally variable in some encrusting algae. The lowest zone, in the infralittoral fringe, was dominated by coralline crusts (the "Coralline-Zone"). Although other species were present at this height, the coralline encrusting algae initially covered over 90% of the substratum.

Although the four-banded zonation pattern was apparent throughout the period of study, the abundance of individual species varied greatly with time (Table 2). In the midlittoral, the cover of *Hapalospongidion gelatinosum*, *Ralfsia expansa*, coralline crusts and the erect macroalgae exhibited an inverse relationship to air temperature (Spearman's correlation coefficient $r_S = -0.664$, $P = 0.004$; $r_S = -0.552$, $P = 0.023$; $r_S = -0.849$, $P < 0.005$ and $r_S = -0.772$, $P < 0.005$ for the above species, respectively). The abundance of these species peaked in the cool season while, during the hot summer months, their cover was greatly reduced (Fig. 5). Unlike any other species, *Kyrtuthrix maculans* exhibited a significantly higher percentage cover during the hot seasons than during the cool season (Fig. 5, SNK-test). The abundance of this species was closely related to variations in temperature ($r_S = 0.716$, $P = 0.002$). *Hildenbrandia prototypus* and *Endoplura aurea* exhibited slight decreases in cover during the winter months, although their abundance was bimodal, with an additional reduction in abundance during the hottest months of the year (Fig. 5). It was during the transition periods (i.e. April–June and November) that the abundance of these species was greatest (Fig. 5). The coralline crusts, with peak abundance in the infralittoral fringe, exhibited high variation in their upper limits. While coralline crusts extended to a height of 2 m above C.D. during the cooler months (December–April), they were limited to a height of 1.25 m above C.D. during the hot season (June–October). In contrast to the midlittoral, no relationships between temperature and abundance were apparent in the infralittoral fringe. In October 1992 most of the coralline crusts were smothered by sediments, and, subsequently, erect macroalgae became predominant and remained abundant until July 1993 (Fig. 6).

All of the encrusting algal species, except for *Hapalospongidion gelatinosum*, exhibited significant differences in cover between vertical and horizontal

Table 2 Two-way ANOVAs of encrusting algal abundance data (% cover) by time and inclination, for common species collected on Shore 4. Belt height on shore (m above C.D.) from which data for ANOVA was taken. Significance after Bonferroni correction, *ns* not significant; $*P < 0.05$ (0.0084); $**P < 0.01$ (0.0016)

Classification (Belt height)	Source	*df*	MS	*F*-ratio	*P*	Significance
Kyrtuthrix maculans						
(1.75 m)	Time	16	799.0	2.53	0.001	**
	Inclination	1	33797.9	106.82	0.000	**
	Interaction	16	682.0	2.16	0.007	*
	Error	238	316.4			
Hapalospongidion gelatinosum						
(1.00 m)[a]	Time	15	2.886	6.09	0.000	**
	Inclination	1	0.779	1.64	0.201	ns
	Interaction	15	0.325	0.69	0.796	ns
	Error	224	0.474			
Ralfsia expansa						
(0.75 m)[a]	Time	16	9.943	20.89	0.000	**
	Inclination	1	20.290	42.63	0.000	**
	Interaction	16	0.137	0.29	0.997	ns
	Error	238	0.476			
Hildenbrandia prototypus						
(0.75 m)	Time	16	723.2	2.42	0.002	*
	Inclination	1	10650.0	35.57	0.000	**
	Interaction	16	346.4	1.16	0.304	ns
	Error	238	299.4			
Endoplura aurea						
(0.75 m)[a]	Time	16	2.987	4.57	0.000	**
	Inclination	1	15.04	22.99	0.000	**
	Interaction	16	1.034	1.58	0.075	ns
	Error	238	0.654			
coralline crusts						
(0.75 m)[a]	Time	15	11.045	29.32	0.000	**
	Inclination	1	8.053	21.37	0.000	**
	Interaction	15	1.226	3.25	0.000	**
	Error	224	0.376			

[a] Data ln transformed to normalise distributions and/or homogenise variances

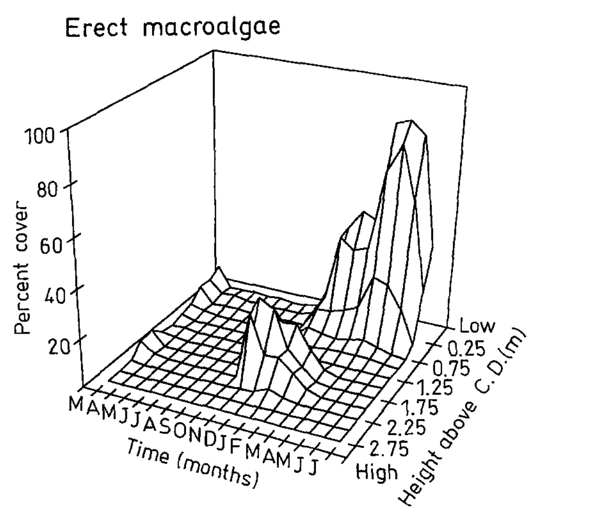

Fig. 6 Temporal changes in the abundance of erect macroalgae. Pooled data from both horizontal and vertical surfaces were used (Shore 4)

surfaces (Table 2). While *Ralfsia expansa* and *Endoplura aurea* were always more abundant on horizontal surfaces, *Kyrtuthrix maculans* and the coralline crusts were only more abundant on horizontal surfaces during some of the hotter months of the year (Table 3). In complete contrast, *Hildenbrandia prototypus* was most abundant on vertical surfaces throughout the year.

Discussion

Horizontal distribution

As previously described from Hong Kong (Williams 1993b), when viewed as a functional group (sensu Steneck and Watling 1982), encrusting algae are the dominant intertidal space occupants at sites of intermediate exposure (S4 and S5). Although they are also present on all other shores, their relative abundance decreased towards shores both of extremely high exposure (S1 and S2) and extreme shelter (S6). These shores are instead dominated by sessile invertebrates or seasonally by erect macroalgae. Studies from Barbados and tropical western Africa (Lewis 1960; John and Lawson 1991) have both indicated a greater cover of encrusting algae on shores of intermediate exposure, while others have demonstrated an increase of certain invertebrate species towards either extreme

Table 3 Effects of inclination on the abundance (% cover) of the six most common encrusting algae over 17 mo. Significant differences (Student–Neuman–Keuls at $P < 0.05$) shown as *H* greater cover on horizontal surfaces and *V* greater cover on vertical surfaces. – indicates no significant difference between horizontal and vertical surfaces

	1992										1993						
	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J
Kyrtuthrix maculans	–	–	H	–	H	H	H	H	–	–	–	–	–	–	–	–	–
Hapalospongidion gelatinosum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ralfsia expansa	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H
Hildenbrandia prototypus	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V
Endoplura aurea	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H
coralline crusts	–	–	–	–	H	H	–	–	–	–	–	–	–	–	H	–	–

of exposure (e.g. Endean et al. 1956; Rodriguez 1959; Ho 1962; Menge and Lubchenco 1981; John and Lawson 1991; Lipkin 1991). Although in Hong Kong encrusting algae occur on all shores, they are dominant only where erect macroalgae and sessile invertebrates are absent. Their predominance on these shores may therefore be related to the absence of superior competitors (Menge et al. 1986) rather than directly to shore exposure.

In Hong Kong, molluscan grazers can successfully exclude sessile invertebrates and erect macroalgae (Williams 1993b, 1994) and may subsequently promote the predominance of encrusting algae. The density of molluscan herbivores was much greater on a shore of intermediate exposure (S4) than on the sheltered S6 and the very exposed S1 (mean densities 103 m^{-2}, 48 m^{-2} and 42.8 m^{-2}, respectively; March 1993, Kaehler unpublished data). Increased grazing pressure and the subsequent removal of invertebrate and macroalgal competitors, therefore, could be responsible for the predominance of the more grazer-resistant encrusting algae on these shores. The importance of consumer pressure on the distribution patterns of encrusting algae has previously been demonstrated in Panama, where encrusting algae were most abundant in areas of highest grazing pressure (Menge et al. 1983) and exclusion of consumers increased the cover of erect macroalgae and sessile invertebrates (Menge et al. 1985).

At the species level, horizontal distributions exhibited little uniformity, and patterns of species abundance were not predictable (see also Steneck and Dethier 1994). Species such as *Hildenbrandia occidentalis* and *Dermocarpa* sp. were most abundant on exposed shores. *Kyrtuthrix maculans* and *Hildenbrandia prototypus* occurred on all shores apart from those of very high exposure in Hong Kong as well as in Vietnam (Ho 1962). Conversely, unidentified *Ralfsia* spp. in Madagascar are most abundant on sheltered shores (Plante 1964), while other species, such as *Ralfsia expansa* from Hong Kong and *Mesospora schmidtii* from Vietnam (Ho 1962), occur throughout the full range of exposures.

Vertical distribution

Independent of shore exposure, encrusting algae (with the exception of cyanobacterial crusts) were always most abundant in the lower midlittoral and/or the infralittoral fringe. While in the lower midlittoral fleshy brown and red encrusting algae as well as some coralline crusts occurred, the infralittoral fringe was usually dominated by coralline crusts. Encrusting algae on shores of intermediate exposure exhibited distinct vertical zonation patterns. Although the abundance and upper limits of individual species varied with time, four zones were evident throughout the period of study. At the upper-most extent of the upper midlittoral, the *Kyrtuthrix*-Zone occurred, followed below by a Bare-Zone (zone of reduced cover), a lower midlittoral Mixed-Zone and in the infralittoral fringe a Coralline-Zone.

Although care should be taken when comparing shores from different regions (Underwood and Petraitis 1993), certain basic distribution patterns appear to be pan-tropical. Where cyanobacterial crusts occur, for example, they always inhabit the highest vertical zone. Although their lower limits vary between localities, high littoral *Kyrtuthrix*-Zones are known from Vietnam (Ho 1962; Loi 1967), Thailand (Kamura and Choonhabandit 1986), Indonesia (Kaehler personal observations) and Australia (Cribb 1966), while similar cyanobacterial crust zones have been described from the Caribbean (Dawes et al. 1991), Mauritius (Stephenson and Stephenson 1972), the Red Sea (Lipkin 1991) and tropical western Africa (John and Lawson 1991). In contrast, due to their poor desiccation tolerance and poor competitive abilities, the coralline crusts are restricted to the lower-most parts of the intertidal or to slightly higher regions during times of reduced physical stress. A few hours of sunshine, while exposed at the start of the hot season, can bleach and kill almost the entire midlittoral population of coralline crusts (Williams 1993b). Finally, between the cyanobacterial crusts and the Coralline-Zone, the fleshy encrusting algae achieve their greatest abundance. While, depending on the physical and biological constraints of individual species, the upper and lower limits of these zones may vary, Mixed-Zones of encrusting algae from the mid and lower intertidal have been described from the tropical west and east Pacific (e.g. Loi 1967; Lubchenco et al. 1984) and Atlantic (e.g. Brattström 1980; John and Lawson 1991). Thus, in terms of their vertical distribution, encrusting algae (with the exception of some cyanobacteria) tend to be most abundant on the lower shore, an area of high grazing intensity, high potential productivity (sensu Steneck and Dethier 1994) and reduced desiccation stress.

Temporal distribution

In Hong Kong, algal species vary in abundance temporally as well as spatially (Kennish et al. 1996). When examined at the functional group level, several patterns can be discerned. Encrusting algae persist on all shores throughout the year, although overall, their abundance is reduced during the hot season. Most supralittoral fringe and midlittoral erect macroalgae were opportunists and consisted of filamentous and foliose species. During the cool season they were abundant on exposed shores but they died-back to $<1\%$ cover, on most shores, during the hotter parts of the year. Corticated macroalgae and articulated corallines mostly inhabited the infralittoral fringe and were less affected by seasonal changes. Leathery macroalgae such as *Sargassum* spp. were strongly seasonal, occurred only in the infralittoral fringe and subtidal, and persisted only for a few of the cooler months. Sessile invertebrates occurred throughout the intertidal, did not exhibit any overall decrease in abundance during the hot season, and appeared to be least affected by the associated increase in physical stress (but see Liu and Morton 1994). Temporal variation in macroalgal composition has been described from several other tropical longitudes (e.g. Lawson 1956; Loi 1967; Murthy et al. 1989; Sheppard et al. 1992), but can not always be related directly to seasonality of the physical environment (Lubchenco et al. 1984).

At the species-level, a variety of strategies were observed that allow the encrusting algae to persist in an environment of fluctuating physical stress and grazing pressure. Species, such as *Hapalospongidion gelatinosum*, *Ralfsia expansa*, and the midlittoral coralline crusts and macroalgae were opportunistic in character, and changes in their abundance could be related directly to the seasonal climate. The abundance and vertical extent of these species were greatest during the cooler months of the year and were much reduced during the hot season. They died-back almost completely during times of elevated physical stress, but immediately recolonised available substratum when temperatures decreased. The ephemeral character of *Ralfsia californica* has previously been recorded from temperate America (Dethier 1981).

Other species were perennial. The cyanobacterial crust *Kyrtuthrix maculans*, for example, was not affected by an increase in temperature during the hot season (see also Loi 1967), but had a reduced cover during the cooler months, when erect macroalgae invaded the upper midlittoral and *K. maculans* was overgrown by foliose species. In addition, during the cooler months, the density of grazing littorinids increased from 230 to 368 ind m^{-2} (Kaehler unpublished data). In Vietnam, a similar increase in the number of littorinids greatly decreased the cover of *K. maculans* (Loi 1967) during the winter months. While individual littorinids were shown to be able to denude large areas of this crust, *K. maculans* was found to be very resistant to desiccation. It was able to survive out of water for periods of up to 12 d at temperatures of 50 °C (Loi 1967). *K. maculans* therefore appears to be affected more by grazing intensity than by physical seasonality. Similarly, both *Hildenbrandia prototypus* and *Endoplura aurea* were not greatly affected by seasonal fluctuations. Only in their upper reaches was cover reduced, once during the hottest months and then again from January to March, which are times of increased grazing pressure. Both *H. prototypus* and *E. aurea* peaked in abundance in the lower midlittoral, where they were protected to some extent from physical extremes but also exposed to increased molluscan grazing. *H. prototypus* thrives at this height as it is resistant to grazing (Underwood 1980; Bertness et al. 1983) and dependent on a high consumer intensity, due to its competitive subordinance to all other sessile invertebrate and algal species (Kaehler unpublished data). Where other species are excluded, *H. prototypus* may survive extreme herbivory, reduced in thickness to a "film" only a few cell layers thick. Visually "bare-surfaces" in the lower midlittoral revealed a high cover of *H. prototypus* when viewed under the scanning electron microscope.

Similar to the sublittoral "urchin barren grounds" that have been described world-wide (Russell 1991), the lower most part of the intertidal in Hong Kong was dominated by coralline crusts. Coralline crusts are very susceptible to desiccation, and are competitively subordinate to most other macroalgae. They are, however, very grazer resistant and, thus, the only group of algae that can withstand urchin grazing. Apart from cases where massive urchin loss occurs, "barren grounds" are generally perceived as temporally stable and predictable. While in Hong Kong this was initially the case, towards the end of 1992 the coralline crusts on S4 were covered in sediments from nearby dredging works, and the red turf *Gelidium pusillum* overgrew the encrusting algae and became the most abundant species. Simultaneously, a dramatic loss in urchin numbers was also noted. Although no quantitative information is available, urchins decreased in abundance from several m^{-2} to only occasional individuals. A tropical storm in late May removed most of the sediments, renewed the access of benthic herbivores (urchins and molluscs), and coralline crusts once more became abundant. In the infralittoral fringe of very exposed shores, coralline crusts were abundant throughout the period of study as water-movement kept the encrusting algae clear of sediments. On the most sheltered shore, S6, sedimentation was continuously high and coralline crust cover was low.

Inclination

Most encrusting algal species in Hong Kong reached maximum abundance on horizontal surfaces, although *Hapalospongidion gelatinosum* showed no preference and *Hildenbrandia prototypus* exhibited a higher cover on vertical surfaces. In subtidal studies of encrusting algae from temperate environments, partially similar patterns have been described (Sebens 1986; Dethier et al. 1991). "Fleshy" red encrusting algae, including a species of *Hildenbrandia*, were more abundant on vertical surfaces, while coralline crusts exhibited a higher cover on horizontal surfaces. Increased urchin grazing pressure on horizontal surfaces was indicated as a possible cause for this pattern (Sebens 1986). In the Panamanian intertidal, molluscan herbivores tend to aggregate (Garrity 1984) and feed predominantly on vertical surfaces (Levings and Garrity 1984). Likewise, in the intertidal zone of Hong Kong, some herbivores have been shown to prevail on vertical surfaces and in cracks and crevices (Williams and Morritt 1995). It is in such shaded areas that *H. prototypus* is most abundant (Williams 1994). Due to being highly grazer resistant (Underwood 1980; Bertness et al. 1983), this species may, on vertical surfaces, gain a competitive advantage over other encrusting algae that would otherwise overgrow it. The prevalence of the majority of encrusting species on horizontal surfaces indicates a high resistance to physical stress, as horizontal rock surfaces may reach temperatures of up to 50 °C during the hot season (Williams 1994).

Tropical distribution patterns

Spatial distribution patterns of sessile organisms in Hong Kong mirror those described from other tropical shores. However, due to a lack of information on spatial, temporal and within functional group variation, these distributions could previously not be related to environmental gradients. This study shows that the abundance of encrusting algae may vary greatly between shores only a few hundred meters apart or temporally, even within one shore. In Hong Kong, encrusting algae were dominant on shores of intermediate exposure, where disturbance from grazers was high and competitively superior sessile invertebrates and erect macroalgae were absent. At a smaller scale, their abundance (with the exception of cyanobacterial crusts) was greatest towards the low shore, an area of increased grazing pressure, potential productivity and decreased physical stress. At the species-level, the distribution of encrusting algae was more variable and less predictable. While all encrusting species were dependent to some degree on the exclusion of competitors, the encrusting algae varied in their resistance to herbivory and physical stress, thus resulting in the broad zonation bands previously recorded from other shores of low latitude. Overall, the distribution of encrusting algae in the tropics seems to agree with the model proposed by Steneck and Dethier (1994) which predicts that crustose algae often dominate in areas of high disturbance (grazing pressure) and high productivity potential (low shore). In the tropics, however, the importance of potential productivity is unknown. Instead, physical stress appears to be a determining factor in limiting encrusting algae to the lower shore.

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