Grazing Drives Spatial Variation in the Abundance and Distribution Patterns of Autotrophs in Tropical Rocky Shore

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Grazing is known as a fundamental process that shapes the community structure of many rocky shores. In this study, the impact of molluscan grazing on autotroph assemblage at different scales in Hong Kong rocky shores were assessed to test whether grazing have different impacts at different spatial scales. The recruitment of various autotrophs in the grazer manipulation experiments were monitored regularly. Most of the treatment plots were colonized by various macroalgae with ephemeral erect algae increasing in abundance in various mollusc exclusion plots throughout the study period. Erect algal cover increased abundantly in shores during the coldest month of winter. The most conspicuous effect of grazing was at the two Stanley sites and to a lesser degree at the Cape d’Aguilar that were reflected in the low values of chlorophyll a and autotroph covers in the control and grazer access plots. Complete exclusion was not possible in the two Stanley sites because of the high number of grazer intruders that entered the plots. This strong grazing pressure kept the algal cover in the exclusion and control treatments similar and dominated by encrusting algae throughout the experimental period. Because of this, it appears that the observed growth of erect algae in the mollusc exclusion plots and its patchy distribution near the sites and in rock pools support the hypothesis that molluscan grazers are the major causes of low settlement and recruitment of erect algae in these shores during winter.

INTRODUCTION

Rocky shores have long been the favorite study site of many experimental ecologists understanding intertidal habitats for their presence along coastlines, ease of access to rock platforms, beaches, and organisms with short generational times, and ease of manipulation (Roughgarden et al. 1988; Farrell et al. 1991; Deepananda & Macusi 2012). Manipulative experiments done in intertidal shores are crucial tools for investigating and testing the various concepts of ecology. The majority of intertidal research has been carried out in temperate areas while in the tropics, these are mostly confined to Central America, Hong Kong, and Australia, which are all relatively distant from the equator (Macusi 2010; Deepananda & Macusi 2012).

The Hong Kong rocky shore is characterized by a diverse assemblage of macroalgae, cyanobacteria, and diatoms that support a dense population of consumers (Hodgkiss 1984; Williams 1993a, b; Kaehler & Williams 1996). It experiences strong seasonal variation in its climate and this is reflected by changes in community structure (Williams 1993a; Williams et al. 2000) resulting in the increase of
macroalgal cover during winter, which also decreases as
the summer approach and algal diebacks occur (Kaehler
& Williams 1997). Although recurrent diebacks happen,
some autotroph species survive all year round like the
epilithic cyanobacterium, *Kyrstuherix maculans* and the
encrusting algae such as *Hildenbrandia rubra*, *Ralfsia
expanse*, *Hapalospondyion gelatinosum* and *Endopleura
aurea* while some are also more ephemeral such as *Ulva
sp.*, *Enteromorpha* sp. and *Porphyra suborbiculata*.

These ephemeral erect algae recruit onto the shores
during the cool and dry winter season which offers relief
from physical stress to many sessile prey species such as
barnacles and algae (Williams 1993b, 1994). A recent study
performed by the author (Macusi 2010) also confirmed
that Hong Kong shores are mainly dominated by molluscs.
In contrast, non-seasonal tropical rocky shores like those
in Panama experience diffuse predation, where no fish,
mollusc, or crab predators are observed to dominate or
control the abundance and distribution patterns of algal and
invertebrate communities (Menge et al. 1986). Other studies
though suggest that the presence of a guild of shell crushing
fishes may play a critical role in controlling the foraging
behavior and numbers of predatory and herbivorous
gastropods in the area (Bertness et al. 1981; Menge &
Lubchenco 1981; Garrity et al. 1986). Nonetheless, this
tropical intertidal area experiences harsh physical condition
during daytime exposures with significantly less desiccation
in crevices than in exposed vertical or horizontal surfaces
at any tidal height (Garrity 1984).

There is no canopy of macroalgae or abundant sessile
invertebrates to provide shelter or to modify the
environment for mobile gastropods. To adapt to this
physically stressful conditions, gastropods modify their
foraging behavior through limited periods of activity such
as moving away from their refuges only for a limited
period and during minimal abiotic stress (Garrity &
Levings 1981, 1983; Garrity 1984). Herbivory in these
shores are therefore constrained by physical factors,
mainly heat and desiccation, and predation during a
limited time window for foraging activities of gastropods
(Garrity 1984; Garrity et al. 1986).

Although there were previous grazer and consumer studies
conducted in tropical rocky shores, most of these studies
dealt with the impact of oceanographic forcing such as
ENSO (El Niño Southern Oscillation) cycles (Vinuza et al.
2006), seasonal variation (Williams 1993a), number of
recruits (Kaehler & Williams 1997), predation and
herbivory (Garrity & Levings 1981, 1983; Garrity 1984;
Menge et al. 1986) and to complex interactions (Sauer
Machado et al. 1996) and effects of different consumer
guilds on distribution patterns of autotrophs (Macusi
2010). Less studies paid attention on spatial variation as
caused by grazing in tropical rocky shores. In particular,
the study of Hutchinson and Williams (2001) provides
evidence that local algal recruits grow and colonize a bare
space excluded from grazers during the winter but is then
constrained by physical stress during summer and dies
back. Growth and recruitment of algal species become
negligible during the summer as high temperature prevents
the establishment of recruits. Given the recent literature
reports that grazing, organisms and processes are mostly
variable in space and time (Lawton 1999; Underwood
2000), repeated experiments at various geographical
locations and scales are necessary to test the generality
of our theory and hypotheses (Anderson & Underwood

Previous reports on the settlement and recruitment of
sessile species such as algae on Hong Kong shores
were shown to vary seasonally, and survival of recruits
were low during summer due in part to higher levels of
physical stress (Williams 1993b; Kaehler & Williams
1996; Hutchinson & Williams 2001). In addition, limpet
grazing in Hong Kong shores has been known to control
algal biomass in the mid- and low shore especially during
winter. Algal species richness and abundance follow a
markedly seasonal pattern, peaking during the winter
months and decreasing in the summer in both the mid- and
low shores (Williams 1993b).

These studies also indicate that at higher shore levels
physical factors influence algal abundance to a greater
extent than on the lower shore where herbivory is deemed
to be more important (Williams 1994). Most of the studies
were, however, limited with spatial replication and did
not focus on quantifying the variability of grazing on the
autotroph assemblage at different scales. The present study
examines the impact of grazing on autotroph abundance
and distribution in the mid shore and how this process
may vary at different scales during winter.

**MATERIALS AND METHODS**

**Study sites and conditions during set-up**

Experiments were performed on two rocky shore platforms
at two localities in Hong Kong Island: Cape d’ Aguilar
marine reserve (site 1: 22°12′25.89″N, 114°15′37.32″E and
site 2: 22°12′27.33″N, 114°15′33.02″E) and Stanley (site 1:
22°12′59.61″N, 114°13′12.30″E and site 2: 22°12′59.15″N,
114°13′13.73″E) (see map at Figure 1). Sites were all semi-
exposed based on Kaehler & Williams (1996). The mid
shore level was chosen for experiments based on previous
studies which show greater abundance and diversity of
herbivores at this level (Hutchinson & Williams 2003).
The two sites in Cape d’Aguilar were separated by ~100m
distance while the two sites in Stanley by ~40m from each
other. All sites chosen have similar species composition, located on gently sloping rock platforms (substrate angle at 0-30°), and aspect at 1.5 m above Chart Datum. During the initial set-up (October 2007), no visible erect macroalgal cover was observed at the Cape d’Aguilar sites although some patches of green turfs were observed near tide pools found in Stanley. A band of *K. maculans* visibly separates the midshore level from the low shore level at the two sites in Cape d’Aguilar and Stanley shores.

**Exclusion experiments**

A nested experimental design was used to examine spatial variation in recruitment of autotrophs and grazing pressure at four study sites located on two shores either with or without grazer access. Two study sites were nested within shores and thereafter referred to as Cape d’Aguilar 1 and 2 and Stanley 1 and 2 with the experiments conducted during the cool and dry winter season of Hong Kong (October 2007 to March 2008). At each site, 15 plots measuring 22 x 22cm were haphazardly marked and assigned randomly to three different treatments: fence (F) exclusion plot, partial fence (P) as a procedural control and open (O) marked plot or about 60 plots in total spread in the four study sites (see Figure 2 for illustration of experimental set-ups). Treatment plots used were randomly chosen on area of the shore with similar slope (< 30°), with no rock pools or deep cracks and crevices. The fence treatment has all sides closed (5 cm high) and with 2 cm out-turned lip at the top to exclude all molluscan grazers that would

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**Figure 1.** Detailed map of the study area showing the four study sites located on the shores of Cape d’Aguilar and Stanley at Hong Kong Island.

**Figure 2.** Fence experimental set ups used to exclude grazers in the study (a), partial fence as a procedural control to avoid fence effects (b) and open plots marked with rawl plugs at each opposite corner as control (c). All experimental set ups (*n* = 5) were established on the midshore level of gently sloping rock bench found at the semi-exposed sites of Cape d’Aguilar and Stanley shores.
Variation in chlorophyll $a$

During the initial stage of the experiment, measured chlorophyll $a$ values were taken as a means to indirectly estimate microalgal abundance and standing stock in each study site. This was done due to difficulties of scoring the biofilm cover in the field during the initial months of the study. The sampling period for chlorophyll $a$ lasted until the first visible and scorable appearance of macroalgal cover in the exclusion treatments. For the Cape sites this was assessed until day 46 and for the Stanley sites, this was until day 62 because of the scorable visible macroalgae already present in the exclusion plots. Rock chips were randomly taken from the internal 20 x 20 cm of each treatment plot at time zero (during set-up) using hammer and chisel and regularly after every 10 to 15 days until day 46 (all sites). Because rock chips removed may have varying sizes, an approximate size of about ~3 cm$^2$ was collected from every treatment plot, extra ones were taken for SEM visual plot cover count. Rock chips were rinsed in seawater and transported to the laboratory damp, where chlorophyll $a$ was estimated within 24 h of collection by cold methanol extraction (see Nagarkar & Williams 1997).

Variation in autotroph cover determined from rock chips using SEM and visual plot cover

A different set of rock chips were collected (~3 cm$^2$) to investigate changes in species composition from counts made using scanning electron micrographs. The rock chips were fixed in 2.5% glutaraldehyde for 1-2 hours, air dried overnight and stored in a vacuum desiccator. These were then coated with a gold/palladium mixture for 30min and then viewed under fix magnification (500x) using a Cambridge S440 Scanning Electron Microscope. Three random fields were photographed from each rock chip and three replicates were randomly chosen from each treatment. In total, there were 3 random field views x 1 rock chip x 3 replicates x 3 treatments x 5 sampling dates x 4 sites = 540 fields of views. Cover was scored from the digital photographs (~8” x 6” image size) on a notebook screen by overlaying a 50 point uniform grid over each photograph using Coral Point Count with Excel extensions software (CPCe, copyrighted freeware by the National Coral Reef Institute at the Nova Southeastern University Oceanographic Center, Dania Beach, Florida; see Kohler & Gill 2006). Percentage autotroph cover from rock chip SEMs was plotted onto graphs to show temporal changes in algal cover during the first 50 days of the experiment.

Visual percentage cover of treatment plots was estimated as above by using digital photographs (taken with Fuji fine pix A610, 6.1 MP) during regular sampling intervals (~15days). These photographs were later scored on a notebook computer screen where 50 points of a uniform grid were overlaid on each digital photograph using the CPCe software. Species were identified and scored in broad categorical groupings (Littler & Litter 1980, 1984; Steneck & Watling 1982). In this study the following morphological groups were designated: cyanobacteria, encrusting algae and erect algae; for herbivore groups these were grouped into chiton, limpets, coiled gastropods, and total grazers. (Details of individual species are presented in the paper Macusi 2010, particularly, Table 1 and 2).

Transect surveys

On a regular basis during the initial months of experiments (October-December 2007), grazer abundance surveys were conducted at each site to determine possible differences in grazer pressure. All grazer surveys on the four sites were performed during visits using ten 25 x 25 cm quadrats along a 10 m transect located in the midshore.

Data analysis

Spatial variation between shores, sites and treatments were examined using nested ANOVA model and multivariate techniques. For comparison of herbivore abundance and grazer pressure at the four sites, abundance data was analyzed separately for each morphological group. For comparison in chlorophyll $a$ variation between sites and treatments, only the initial (Day 0) and final (Day 46) dates were analysed for temporal non-independence of repeatedly sampled plots. Data was checked for homogeneity of variances (Cochran’s C-test) and transformations were performed when necessary to satisfy this assumption. When variances remained heterogeneous after transformation, significant results were still discussed but should be regarded with some caution (Underwood 1997; Williams et al. 2000; Quinn & Keough 2002; Benedetti-Cecchi et al. 2003). Significant differences were further examined using S.N.K. (Student–Newman–Keuls) multiple comparison tests.

To examine spatial variation and differences between treatments and sites, a non-parametric multivariate technique was used. Non-metric multidimensional scaling (nMDS) can be used to visualize treatment differences by producing two-dimensional ordinations of the rank orders of similarities of samples in the various treatments; for nMDS ordinations, stress levels with values less than < 0.2 were considered to give an interpretable nMDS
The null hypotheses that (1) there were no differences between the effects of the various treatments and (2) there was no difference in abundance among autotrophs within treatments were tested using ANOSIM (analysis of similarities) and SIMPER (similar percentage) analyses (Clarke 1993). The Global R values from tests across time and across treatments were tabulated. Significant factors were further analyzed by pair-wise comparisons between treatments using ANOSIM. All multivariate analyses were performed with Primer-E (ver. 6, Plymouth Marine Laboratory, UK).

RESULTS

The autotroph cover during the beginning of the experiment consists mostly of the cyanobacterium *Kyrtuthrix maculans* on the high-shore and by *Hildenbrandia rubra* on the low to mid-shore at the study sites. There were patches of crustose corallines occurring mostly in rockpools near the study sites and these were free from foliose green algae. Autotrophs in the treatments were classified into different morphological groups during surveys on the shore. *Ralfsia expansa*, *H. rubra* and *K. maculans* were the dominant autotrophs in all the treatment plots during the initial period. But visible macroalgae started to appear in the exclusion plots (fence treatments) after two weeks. A variety of mobile grazers were found on the shores, including coiled gastropods (*Lunella coronata, Chlororosta argyrostroma, Monodonta labio, Nerita albicila, Planaxis sulcatus*), six species of limpets (*Cellana toreuma, C. grata, Siphonaria laciniosa, S. japonica, Patelloidea pygmea, P. saccharina*) and a chiton (*Acanthopleura japonica*). Limpets were the most abundant morphological herbivore group recorded at the study sites, followed by coiled gastropods and littorinids (Figures 3 and 4).

**Grazer abundance and variation in chlorophyll a**

There were significant differences in the abundance of limpets, coiled gastropods and the total number of grazers across sites (Table 1). The Stanley shore has more abundant total grazers compared to the Cape d’Aguilar shore (Table 1; Fig. 4). Limpets were most abundant in Stanley 1 and 2, followed by Cape d’Aguilar 1 and 2 (Fig. 3), while littorinids were also abundant in the Stanley sites but few were found in the Cape d’Aguilar sites (Fig. 3). Coiled gastropods were however more abundant in the Cape d’Aguilar sites and significantly different (Table 1; Fig. 3) while the total grazer counts also showed that it was significantly different with higher abundance in the two Stanley sites compared to the other sites (Table 1). Comparison of change in the abundance of grazers through time (Fig. 4) indicated higher abundance of molluscan herbivores present in the Stanley shore compared to the Cape d’Aguilar shore (Fig.

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Table 1. ANOVA of grazer abundance as recorded in the four study sites during winter 2007. Significant differences are shown in bold (*P* < 0.05) and were examined further using SNK tests. Data transformed by *X*^{0.015} except for total grazers which was transformed by *X*^{0.15} to homogenize variance. (Sh= shore, Si= site, ns = not significant).

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<td>0.0121</td>
<td>0.9133</td>
<td>23.7517</td>
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<td>C = 0.5959 ns</td>
<td>C = 0.5803 ns</td>
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<tr>
<td>SNK tests</td>
<td></td>
<td>Cape &lt; Stanley</td>
<td>Cape &lt; Stanley</td>
<td>Cape &lt; Stanley</td>
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Table 2. ANOVA of grazer abundance recorded within fence treatments at the four study sites during winter 2007. Significant differences are shown in bold (*p* < 0.05) and were examined further using SNK tests. Data transformed by *ln(X+1)* except for total grazers which was transformed by *ln(X+3)* to homogenize variance. (Sh= shore, Si= site, ns = not significant).

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<th>p</th>
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<td>Sh</td>
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<td>74.4503</td>
<td>&lt; 0.0001</td>
<td>44.1065</td>
<td>94.1681</td>
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<td>Si (Sh)</td>
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<td>1.4400</td>
<td>2.4085</td>
<td>0.1114</td>
<td>3.9775</td>
<td>8.4919</td>
<td>0.0016</td>
<td>0.3192</td>
<td>1.7684</td>
<td>0.1921</td>
</tr>
<tr>
<td>Error</td>
<td>24</td>
<td>0.5979</td>
<td>0.4684</td>
<td>0.1805</td>
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<tr>
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<td>C = 0.7906, p &lt; 0.05</td>
<td>C = 0.6912 ns</td>
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<td>SNK tests</td>
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Limpets were most abundant compared to other groups of molluscan herbivores, followed by littorinids, coiled gastropods and some chitons found in the two shores. It appears that the abundance of the limpet *C. toreuma* in most sites also indicate higher grazing pressure from this group (Fig. 3 and 4). There were significantly more grazer-intruders that entered the exclusion treatment plots at Stanley site compared to those in the Cape site (see grazer intruders, Fig. 3; Table 2).

Further, the range of increase in terms of the amount of chlorophyll *a* present in the treatment plots showed that, the fence treatments have higher level than those found in the control or open treatments (Figure 5). In addition, there was
higher amount of chlorophyll *a* found at the Cape d’Aguilar shore compared to the Stanley shore. Consequently, the amount of chlorophyll *a* present at the two Cape sites also reveal a higher level than those found at the two Stanley sites. Significant differences in chlorophyll *a* were detected in the

shores, sites, and treatments by the end of the sampling period for chlorophyll *a* (Day 46, see Table 3). But further differences between sites and treatments were not testable (Underwood 1997) although plots of the different treatments appear to indicate that there was higher level of chlorophyll *a* found in the fence treatments than in other treatments (Figure 5).

**Variation in algal groups through time (SEM and visible algal cover observations)**

Direct assessment of autotrophs using SEM showed some significant differences in cyanobacteria, encrusting, and erect algae in the shores and sites (Table 4). There was a significantly higher percentage cover of cyanobacteria found at Stanley than at the Cape d’Aguilar shore (20.5% vs 0.64% *p* < 0.05; Day 46) while the percentage cover of diatom did not show any significant variation between shores or sites at any period during sampling. However, there were some significant variations in the total encrusting algal cover for the site (shore) interaction even during the start of the experiment (Day 0) but not by the end of sampling period (Day 46) (Table 4). Thus, it appears that a greater algal cover of encrusting algae could be found primarily in Cape d’Aguilar than in Stanley (Fig. 4). In addition, there were significant differences between the two shores in terms of erect algal cover (Day 46). In general, there were no significant differences between the cyanobacteria, diatom, erect, and encrusting covers in the three treatments found in Stanley compared to that in Cape d’Aguilar (Table 4).

On the other hand, plots of autotrophs in the SEM reflect the trend in chlorophyll *a* values seen earlier in Fig. 2 for the different sites (Figure 6). For instance, there was general increase in erect algal cover found in the fence treatments as early as two weeks after the set-up and this continued for both the two Cape d’Aguilar sites. The erect algal cover for the two Stanley sites was however more variable. There was also a more reduced erect algal cover found in both the open and control treatments in all the sites. Relatively, the encrusting algal cover remained

![Figure 5](image)

**Figure 5.** Mean (±S.E., *n* = 5) variation of chlorophyll *a* concentration for the experimental treatments during the first two months of study to estimate the microalgal standing stock. (Legend is common to all charts; experiments were started on October 11, 2007). Note change in scale.

**Table 3.** ANOVA of Chlorophyll *a* variation in the four study sites in response to grazer exclusion during winter 2007. Significant differences are shown in bold (*P* < 0.05). Data transformed by *ln*(X+0.1) to homogenize variance. (Sh= shore, Si= site, Tr= treatment, ns = not significant).

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<td>Error</td>
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<td>0.4665</td>
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147
high throughout the sampling dates in the control and open treatments though fairly reduced also in the fenced treatments in all the sites (Fig. 4).

The visual plot cover of autotrophs showed a clearer trend than the SEM covers. For instance, the erect algal cover found in the fence treatments had a higher percentage cover through time. This can be seen with the fence treatments having a higher erect algal cover at the two Cape sites (40-100%) than those at the two Stanley sites (~40%) (Figure 7). In contrast, the erect algal cover found in the control and open treatments of all the sites remained very low, although Cape d’ Aguilar site 2 reached up to more than 40% cover in January and February (Figure 7). There was also a higher percentage cover of encrusting algae in the control and open treatments in the two Cape sites than at the two Stanley sites. Clearly, there was more free space available in the control and open treatments of the two Stanley sites compared to the other sites (Fig. 7). Generally, the encrusting algal cover in the fence treatments declined greatly as the erect algal cover increased through time in the two Cape sites while it was more variable in the two Stanley sites.

Species assemblage differences with treatments and sites
The nMDS ordinations of species assemblages showed distinct, identifiable clusters in all the months (Figure 8). During the set-up month (October), most of the different treatments and sites were mixed together although Stanley site 2 already separated from the rest of the group. In November, the control and open treatments of Stanley 2 and Cape d’ Aguilar 1 also separated from the groups but by December and January, the control and open treatments of Stanley 1 separated from the main group. And by February, the control, open and some fence treatments of Cape d’ Aguilar 1 and 2 and Stanley 1 also separated from the homogeneous grouping.

Analysis of monthly variation across sites showed significant differences in assemblages in all the dates examined from October 2007 to February 2008 with a peak global $R$ value in December ($R$ value = 0.612, $p < 0.05$; Table 5) which also gradually decreased. Monthly variation across treatments

### Table 4

Summary ANOVA of various autotroph covers from SEM of rock chips in the four study sites in response to grazer exclusion during winter 2007. Significant differences are shown in bold. Data transformed by arcsin(%) to homogenize variance. (Sh = shore, Si = site, Tr = treatment, ns = not significant).

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<th>MS</th>
<th>$F$</th>
<th>$p$</th>
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<tbody>
<tr>
<td>Sh</td>
<td>1</td>
<td>77.3643</td>
<td>0.1672</td>
<td>0.6862</td>
<td>3556.0107</td>
<td>13.5058</td>
<td>0.0012</td>
<td>25.4819</td>
<td>0.2123</td>
<td>0.6491</td>
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<tr>
<td>Si (Sh)</td>
<td>2</td>
<td>472.1548</td>
<td>1.0205</td>
<td>0.3755</td>
<td>95.7162</td>
<td>0.3635</td>
<td>0.6990</td>
<td>208.2130</td>
<td>1.7350</td>
<td>0.1978</td>
</tr>
<tr>
<td>Tr(Sh x Si)</td>
<td>8</td>
<td>391.7898</td>
<td>0.8468</td>
<td>0.5721</td>
<td>318.7079</td>
<td>1.2105</td>
<td>0.3346</td>
<td>73.6044</td>
<td>0.6133</td>
<td>0.7579</td>
</tr>
<tr>
<td>Error</td>
<td>24</td>
<td>462.6646</td>
<td>263.2946</td>
<td>120.0054</td>
<td>380.8556</td>
<td>180.8556</td>
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<tr>
<td>Cochran's test</td>
<td>0.6266</td>
<td>ns</td>
<td>0.7626</td>
<td>p &lt; 0.01</td>
<td>0.7525</td>
<td>p &lt; 0.05</td>
<td>0.8772</td>
<td>p &lt; 0.01</td>
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<td>SNK tests</td>
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<table>
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<th>$F$</th>
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<th>MS</th>
<th>$F$</th>
<th>$p$</th>
<th>MS</th>
<th>$F$</th>
<th>$p$</th>
</tr>
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<tbody>
<tr>
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<td>1.5822</td>
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<td>0.0959</td>
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<tr>
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<td>4.8243</td>
<td>0.0173</td>
<td>206.1736</td>
<td>0.4283</td>
<td>0.6565</td>
<td>389.8421</td>
<td>2.8922</td>
<td>0.0749</td>
</tr>
<tr>
<td>Tr(Sh x Si)</td>
<td>8</td>
<td>514.8677</td>
<td>0.5943</td>
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<tr>
<td>Error</td>
<td>24</td>
<td>866.3946</td>
<td>481.3679</td>
<td>134.7888</td>
<td>296.6888</td>
<td>0.6869</td>
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<td>Cochran's test</td>
<td>0.5849</td>
<td>ns</td>
<td>0.5391 ns</td>
<td>0.8524</td>
<td>p &lt; 0.01</td>
<td>0.5937 ns</td>
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</table>

### Table 5

Monthly variation in global $R$ values across sites and treatments from a two-factor ANOSIM. Significant differences are shown in bold ($p < 0.05$).

<table>
<thead>
<tr>
<th>Month</th>
<th>Differences between sites (µ across treatments)</th>
<th>Differences between treatments (µ across sites)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oct-2007</td>
<td>0.508</td>
<td>0.012</td>
</tr>
<tr>
<td>Nov-2007</td>
<td>0.484</td>
<td>0.213</td>
</tr>
<tr>
<td>Dec-2007</td>
<td>0.612</td>
<td>0.225</td>
</tr>
<tr>
<td>Jan-2008</td>
<td>0.47</td>
<td>0.104</td>
</tr>
<tr>
<td>Feb-2008</td>
<td>0.42</td>
<td>0.146</td>
</tr>
</tbody>
</table>
also showed a peak value in December that declined after, but still significant ($R$ value = 0.225, $p<0.05$; Table 5). This variation across treatments was largely contributed to by the fence treatments which was significantly different from the control or open (see Dec., treatments, in Table 6).

The frequency of differences in assemblages between treatments showed that 100% of the comparisons between the fence and the control or open treatments differed significantly while there was no significant differences

### Table 5. Monthly variation in global $R$ values across sites and treatments from a two-factor ANOSIM. Significant differences are shown in bold ($p < 0.05$).

<table>
<thead>
<tr>
<th>Month</th>
<th>Differences between sites ($µ$ across treatments)</th>
<th>Differences between treatments ($µ$ across sites)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oct-2007</td>
<td>0.508</td>
<td>0.012</td>
</tr>
<tr>
<td>Nov-2007</td>
<td>0.484</td>
<td>0.213</td>
</tr>
<tr>
<td>Dec-2007</td>
<td>0.612</td>
<td>0.225</td>
</tr>
<tr>
<td>Jan-2008</td>
<td>0.47</td>
<td>0.104</td>
</tr>
<tr>
<td>Feb-2008</td>
<td>0.42</td>
<td>0.146</td>
</tr>
</tbody>
</table>
between the control and open treatments in all the months examined (Table 6). This indicates that the assemblages found at the control and open treatments were similar for most of the duration of the experimental period. The high $R$ value for the month of December coincided with the general increase of erect algal cover across sites (Fig. 7). This signifies the magnitude of variation between treatments (Clarke 1993), which also indicates the increase in the settlement and recruitment of erect algae in the fence treatments during this period.

Thus, we have more confidence in the separation of treatments when these are examined by pair-wise comparisons as shown in Table 6. The general slight decrease in $R$ values during January and February could be an indication of the increased amount of erect algal...
cover that recruited in the control and open treatments during this period, making them more similar so that the $R$ value declined slightly, although still significantly different. The ANOSIM between sites also reflect this variation with 67% of peak $R$ values occurring in the month of December comparisons that gradually declined. This peak differences between sites during December may also reflect the increased settlement and recruitment of erect algae in the fence treatments as well as in the control and open treatments. Although all the $R$ values are significant across sites, which shows high variability between assemblages, the high $R$ values between Cape d’Aguilar 1 (C1) vs Stanley 2 (S2) and Cape d’Aguilar 2 (C2) vs Stanley 2 (S2) and Stanley 1 (S1) vs Stanley 2 (S2) indicates the reduced erect and encrusting algal cover found in the Stanley 2 (see Figs. 5, 6 & 7; see also S2 in Table 6).

Analysis of autotroph contribution using SIMPER reveals that green turfs (erect algae) contributed $\sim23\%$ and $\sim22\%$ to the average dissimilarities between fence and control and fence and open treatments (Table 7). The high dissimilarities between these treatments ($\sim82\%$) were mainly caused by the erect algal cover. The main differences between the control and open treatments were mainly due to the encrusting algae ($\sim48\%$), and cyanobacteria ($\sim22\%$). For the overall differences in treatments, about $44.44\%$ were contributed by the encrusting algae, $33.33\%$ by cyanobacteria and $22.22\%$ by erect algae. For site differences, cyanobacteria appear to predominate in the Cape sites while encrusting algae primarily covers the Stanley sites. For instance C1 and C2 differs primarily due to the high cyanobacteria cover in C2 (ave. diss. = 80.24; contrib. of main species= 34.43%; Table 7) while S1 and S2 differs primarily due to the encrusting alga, $R$. expansa (ave. diss. = 89.76; contrib.of main species= 34.88%; Table 7). The highest dissimilarities were recorded for C1 and S2 (95.6) and S2 and S2 (94.11) of which, $R$. expansa contributed $\sim22\%$ for the first pair and $H$. rubra contributed $\sim30\%$ for the second pair. Results for the overall differences in sites reveal that about 50% of site differences are contributed by encrusting algae, 28% by cyanobacteria and 22% by erect algae.

**DISCUSSION**

Ecologists are primarily preoccupied with the question whether patterns and processes that govern a single locale occur similarly in other areas. Often, the observed generalities found by several studies are used to confirm principles or theories in the field. For example, the re-occurring studies on the effects of herbivores on algal communities could facilitate acceptance of commonly observed phenomena on intertidal assemblages or reject generally accepted patterns of assemblage structure based on new or persistent experimental data (Foster 1990). This study compared the results found in an earlier investigation whether the patterns found previously (Williams 1993a, b) are also reflected in the present grazer-alga study.
Table 7. Summary of average dissimilarity between treatments and sites based on autotroph group contributions from two way analysis using SIMPER. Only the top three autotroph groups with greater than ~10% contributions are listed (F = fence, P = partial, O = open; C1 = Cape d’Aguilar 1, C2 = Cape d’Aguilar 2, S1 = Stanley 1, S2 = Stanley 2).

<table>
<thead>
<tr>
<th>Treatments/Sites</th>
<th>Average diss.</th>
<th>Autotrophs</th>
<th>(%) Contrib.</th>
<th>Average abund.</th>
</tr>
</thead>
<tbody>
<tr>
<td>F &amp; P</td>
<td>81.95</td>
<td>Green turf</td>
<td>22.77</td>
<td>2.61</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Hildenbrandia rubra</em></td>
<td>18.62</td>
<td>2.12</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Cyanobacteria</td>
<td>16.22</td>
<td>0.63</td>
</tr>
<tr>
<td>F &amp; O</td>
<td>82.14</td>
<td>Green turf</td>
<td>21.59</td>
<td>2.61</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Hildenbrandia rubra</em></td>
<td>18.47</td>
<td>2.12</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Cyanobacteria</td>
<td>17.02</td>
<td>1.18</td>
</tr>
<tr>
<td>P &amp; O</td>
<td>76.96</td>
<td><em>Ralfsia expansa</em></td>
<td>26.28</td>
<td>1.00</td>
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<tr>
<td></td>
<td></td>
<td>Cyanobacteria</td>
<td>22.42</td>
<td>1.30</td>
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<tr>
<td></td>
<td></td>
<td><em>Hildenbrandia rubra</em></td>
<td>21.44</td>
<td>2.03</td>
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<tr>
<td>C1 &amp; C2</td>
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<td>Cyanobacteria</td>
<td>34.43</td>
<td>1.48</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Hildenbrandia rubra</em></td>
<td>29.56</td>
<td>1.79</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Green turf</td>
<td>9.76</td>
<td>0.73</td>
</tr>
<tr>
<td>C1 &amp; S1</td>
<td>89.34</td>
<td><em>Hildenbrandia rubra</em></td>
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<td>1.79</td>
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<tr>
<td></td>
<td></td>
<td>Cyanobacteria</td>
<td>19.08</td>
<td>1.48</td>
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<tr>
<td></td>
<td></td>
<td>Green turf</td>
<td>14.61</td>
<td>0.73</td>
</tr>
<tr>
<td>C2 &amp; S1</td>
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<td>30.09</td>
<td>4.65</td>
</tr>
<tr>
<td></td>
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<td>Cyanobacteria</td>
<td>23.10</td>
<td>3.15</td>
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<td></td>
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<td>Green turf</td>
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<tr>
<td>C1 &amp; S2</td>
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<td><em>Hildenbrandia rubra</em></td>
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<td>1.79</td>
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<td>C2 &amp; S2</td>
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<td>29.91</td>
<td>4.65</td>
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<td>Cyanobacteria</td>
<td>21.45</td>
<td>3.15</td>
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<tr>
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<td><em>Ralfsia expansa</em></td>
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<td>0.00</td>
</tr>
<tr>
<td>S1 &amp; S2</td>
<td>89.76</td>
<td><em>Ralfsia expansa</em></td>
<td>34.88</td>
<td>0.95</td>
</tr>
<tr>
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<td></td>
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<td>20.67</td>
<td>1.97</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Green turf</td>
<td>18.78</td>
<td>1.69</td>
</tr>
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</table>

with more replicated sites. Comparison between the two studies showed similar results with molluscs causing a high grazing pressure on various autotrophs as found earlier by Williams (1993a, b) in a single locale. There was high grazing pressure found in the four study sites with observed variations that occur from the very small (microns; SEM) to the medium scale (meters; sites) and attributed primarily to molluscan grazing (Macusi 2010). For example, measured chlorophyll $a$ values, percent cover of autotrophs from rock chips (SEM) and visual plot covers were all much reduced in the control and open treatments but high in the mollusc exclusion treatments in all the sites examined.

The transect surveys of grazer abundance and the reduction of autotroph covers found in the control and grazer access in the various sites indicate the high grazing pressure encountered but more especially in the two Stanley sites. Limpets are invariably the most abundant
among all grazer groups and also the most persistent among all grazer intruders. Given the abundance of grazer intruders found in the fence treatments at the two Stanley sites, this severely affected the amount of chlorophyll \( a \) concentration and later the autotroph cover in the rock chips and the visual counts of the plots. The measured chlorophyll \( a \) concentration represents the microalgal standing stock found in the rocky shore (Nicotri 1977; Nagarkar & Williams 1997; Jenkins et al. 2001) which is primarily represented by the epilithic algal biofilm that covers most rock surfaces. The biofilm represents a major part in the energy base of food web in marine benthic intertidal shores because it nourishes most grazers living in the shores (Underwood 1984; Hutchinson et al. 2006). Previous investigations in temperate (MacLulich 1987) and tropical (Williams 1993a; Nagarkar & Williams 1997) shores show that chlorophyll \( a \) is highly variable in space and time.

Measurements of chlorophyll \( a \) are very important as it represents the amount of algal sporelings, new recruits, and settled algae (Underwood 1984). Other investigations of epilithic microalgae and the effects of grazing in Hong Kong rocky shores indicate that grazers can limit the abundance of this food supply (Nagarkar & Williams 1997; Williams et al. 2000). The significant differences in chlorophyll \( a \) concentration between shores, sites, and treatments (Day 46) were probably caused by the variable amount of chlorophyll \( a \) in mollusc exclusion treatments in the two Stanley sites and the increasing trend found in the two Cape d’Aguilar sites. This trend of increase in chlorophyll \( a \) concentration was also reflected in the plots of erect and encrusting algae in the SEM, with the two Stanley sites having a highly variable erect algal cover and an increasing trend for the two Cape d’Aguilar sites. In general, the control and grazer access treatments for all the sites showed an almost flat erect algal cover and a higher cover of encrusting algae. Interestingly, at a higher spatial scale (with the visual plot covers) the same trend that was observed in the chlorophyll \( a \) concentration and in the SEM becomes more distinct with the erect algal cover found in the two Cape d’Aguilar sites showing an increase through time while the two Stanley sites fluctuated in algal cover.

The impact of grazing becomes more apparent when the control and grazer access plots are compared together with the mollusc exclusion. Erect algae were unable to recruit successfully as compared to encrusting algae but were successful in the mollusc exclusion treatments in the two Cape d’Aguilar sites. Although a modest growth can also be observed in the two Stanley sites, evidently, the higher abundance of grazers found in Stanley sites reduced the chances for higher recruitment of this algae onto the plots.

Williams (1993a, b) found that grazing is a strong factor during winter in dictating community dynamics in the Hong Kong shores while Hutchinson and Williams (2001) further examined the impact of grazing and recruitment on three shores at different spatial and temporal scales suggesting that grazing appears to be secondary only to seasonal variation. It is apparent that grazing and many other ecological processes in different geographical locations are context dependent and scale dependent in many rocky shore communities (Underwood et al. 2000; Benedetti-Cecchi et al. 2001). This study demonstrates that grazing in winter is highly variable in space and time from the very small (microns), small (centimeters to meters), and medium (tens of meters) scales of spatial variability.

Observed variations between treatments, sites and shores mainly arise from fluctuations of abundance of encrusting and erect algae throughout the sampling period. It is generally held that once an algal sporeling finds a size refuge, this would eventually grow and mature (Underwood 1980; Underwood et al. 1983; Menge et al. 1986). Simple escapes and recruitment differences of microalgae and macroalgae in each treatment plots may later drive the large scale patterns observed as differences between sites and shores. Other studies (Underwood & Petratis 1993; Archambault & Bourget 1996; Coleman 2002) show that some processes that work at very small scales can actually drive observed patterns that occur in larger scales. An example of this pattern is recruitment where dispersed sessile algal propagules and juveniles of sessile invertebrates can travel in very distant localities as carried by ocean currents (Deysher & Norton 1982; Hoffmann & Ugarte 1985).

There are cases however when this pattern appears secondary to another stronger controlling factor such as seasonal (Williams 1993a) and oceanographic differences (Vinueza et al. 2006), supply of recruits and physical stress (Hutchinson & Williams 2001). When a local process such as grazing controls the assemblage in the winter, this control can be released and becomes secondary when a large swarm of algal recruits occur in the shore or when physical stress bakes the rocks causing algal diebacks. Thus, macroalgal settlement and recruitment in the mollusc exclusions are successful only to the degree that they attain a size refuge and are free from the influence of molluscan grazers. The favorable condition during winter for both macroalgae and grazers suggests that when the number of molluscan grazers are high, they can control the assemblage structure in the shore but once the algae attains a size refuge, this allows them to get established on the shore (Macusi 2010). This is, however, dependent on the number of grazers and the availability of algal recruits.
CONCLUSION
This study contributes to the mounting evidence that grazing drives shifts in overall assemblage cover from a largely encrusting to erect algal cover in many rocky shore communities. The most conspicuous effect of grazing can be found in Stanley sites, and to a lesser degree, in Cape d’Aguilar which are reflected in the low values of chlorophyll \(a\) and autotroph covers found in the control and grazer access plots. Complete exclusion was not possible in the two Stanley sites because of the persistent high number of grazer intruders that entered the plots. This strong grazing pressure kept the algal cover in the exclusion and control treatments similar and dominated by encrusting algae throughout the period of the study. Further, the high percentage cover of encrusting algae found in the control and open treatments in all the sites indicates the strong impact of grazing. In association with this, the observed growth of erect algae in the mollusc exclusion and its patchy distribution near the sites and in rock pools supports the hypothesis that molluscan grazers are a major cause of low settlement and recruitment of erect algae in these shores.

ACKNOWLEDGMENTS
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