

Factors that structure algal communities in tropical rocky shores: what have we learned?

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Abstract- Experiments in tropical rocky intertidal habitats across the globe have identified various effects of biological and physical factors on algal assemblage. High- and mid-intertidal rocky shores in tropical areas are exposed, with varying degrees, to the same physical factors such as temperature, heat, desiccation, shore height, supply of sediment and nutrients that affects temperate rocky shores. The degree of exposure to physical extremes however determines the structure of assemblage in most tropical rocky shores. The low shore is often controlled by biological factors, i.e., grazing and predation by mollusks, fishes, amphipods, crabs, and iguanas, while the high shore is mainly controlled by physical factors. It appears that the keystone species concept may not apply to tropical rocky shore communities. Reasons for this include indirect effects, overlapping food requirements and a diffuse predation due to a diverse set of assemblage that may mask the effect of one species. Present paper compare the several studies carried out in Hong Kong and Panama on tropical rocky shore consumer interactions. Studies on the effects of physical disturbances in coastal areas such as storms or typhoons are rare and there were little studies dealing with interactions of the sub tidal coralline algae and the low shore algae in tropical areas. More experimental work across a variety of spatial and temporal scales are therefore needed to determine significant biological and physical processes affecting the structure of algal assemblage across broad areas in the tropics.

Index Terms- algae, physical factors, grazers, community structure, tropical rocky shores

INTRODUCTION

Tropical rocky shores are diverse and species rich but hides the fact that it is one of the most neglected study areas in community ecology. Basic studies of tropical rocky shores have not been considered until recently by many countries and territories which have understood the importance of these systems in maintaining diversity and richness of adjacent communities (Gray 1997; Huang et al. 2006; Uy et al. 2008). John Done wrote that “no man is an island”, but even this maxim is proving futile in the light of present researches uncovering significant relationships between different systems. For instance, a mangrove community is not an isolated system but subsidizes the near shore systems by its rich humic and organic substances that are exchanged as tides move in and out of estuaries (Primavera 1998; Dittmar & Lara 2001; Jennerjahn et al. 2004). In addition to its protective role (Danielsen et al. 2005), it acts as

a nursery ground for many planktonic larvae not just to fish but to other marine invertebrates (Primavera 1995 & 2005)

The connectivity of different systems is being subjected to studies in many interdisciplinary projects carried out in various parts of the world (Liu et al. 2007). These studies do not only consider the human or the ecological points of view, but the two systems as connected together. One of these studies includes the topic on climate change. Nevertheless, focus on basic research should not be neglected, including the subject of tropical rocky shore ecology which is long neglected by countries that needed the information derived from them. In the light of climate change, increasing anthropogenic impact and global warming, the rate of biotic extinction has reached a record of as much as 100 to 1000 times before the existence of humans (Vitousek et al. 1997; Liu et al. 2007). Most of the remaining unsurveyed coastlines are concentrated in tropical countries that are vulnerable to global warming and may potentially lose valuable resources for new crops, medicine, vaccines and even for oil. Studies of coastal ecosystems around the world should be given the attention and importance it needs. This should stem from testing theories and hypotheses developed from higher latitudes that remain untested in many tropical systems, and the fact that these remain uncontested truths (Gray 1997; Hutchinson & Williams 2001). Tropical rocky shores can be distinguished by their seemingly barren and free space from the abundant foliose macro algal cover that characterizes most temperate rocky shores. It is often covered by bands of encrusting algae in both low- and mid-shore and, in addition the biofilm cover can also be distinguished at a closer glance (Williams 1993b & 1994). The encrusting algae and the ubiquitous biofilm cover in these shores nourish the herbivores present (Nicotri 1977; Garrity & Levings 1981, 1983; Menge et al. 1986; Kaehler & Williams 1998; Williams et al. 2000; Macusi 2010). However, most of these algal assemblages are not fully characterized nor studied (Brosnan 1992).

At present there are few studies that describe the roles these algae play in structuring the benthic invertebrates living in tropical rocky shores (Kaehler & Williams 1997). Most often, studies which have been done on encrusting algae, have been carried out basically on functional groups (Littler & Littler 1983) probably due to difficulties of examining the morphology and reproductive biology of their life history (Paine et al. 1979; Kaehler & Williams 1996). This could be a new avenue for research on taxonomy and surveys of encrusting algae considering the dearth of studies on tropical rocky shores (Kaehler & Williams 1996). Present review on tropical rocky shores, results from previous studies conducted in tropical rocky

shores are compared and presented to examine areas where further studies can be carried out. We limited our comparison to experimental manipulations and characterization surveys done in five countries, those previously conducted in Panama and Hong Kong shores as well as those recently conducted in Brazil, the Galapagos and Sri Lanka. Apparently, some of our comparisons may differ in many respects since data from these areas have different experimental designs. Other than that, survey protocols were much in the same way such as using quadrat counts and/or recording vertical and horizontal zonation patterns. In addition to these, the study sites in Hong Kong are typical of tropical seasonal shores and those in Panama as typical of tropical rocky shores with no seasonal variations. Further, the Hong Kong area can represent a typical biogeographic boundary region between East and South East Asia which shares a lot of characteristics to that of subtropical shores. A second aim was to characterize these systems, what factors affect them? What have we learned from these factors? How do algal communities react with these factors? A third and last aim was to provide the reader with the current trends and patterns in most tropical rocky shore systems, where are we at this time?

Most of the recent concepts of community ecology; keystone species concept (Paine 1966), intermediate disturbance hypothesis (Connell 1978), marine protected reserves (Castilla & Bustamante 1989; Castilla 1999), environmental stress models and community regulation (Menge & Sutherland 1976, 1987) have been derived from basic and applied rocky shore studies. This contribution from rocky shore ecology reflects the advancement of community ecology not just in theoretical aspects but also in the experimental aspects to mainstream ecology (the larger body of knowledge of ecology). Presently, most concepts applied in tropical rocky shores have been developed in temperate shores and have not been well tested in tropical rocky shores. This dearth of experiments can lead us to assume that many uncharacterized communities of organisms in tropical shores have the same characteristics as the temperate shores do. The recognition of this disparity of research between temperate and tropical rocky shores have led the groups of Bertness, Garrity and Menge in the early to mid 1980's to conduct what possibly the first large scale experimental ecology done in tropical rocky shores (Bertness et al. 1981; Garrity & Levings 1981, Garrity 1984, Garrity et al. 1986; Menge et al. 1986). At present these efforts have spread to Brazil (Sauer Machado et al 1996), Galapagos (Witman & Smith, 2003; Vinuela et al 2006) and Hong Kong (Williams 1993a,1994); while we do not want to think that advancements of ecology comes from experiments done in rocky shores, the relative ease of access, the exposure of fauna and flora to harsh elements when emersed and immersed in the water and the short generational times of the organisms in these habitats have made rocky shores a haven for manipulative experiments. Basic research using experimental manipulations have probably uncovered and tested many hypotheses that work and does not work in many temperate shores. Many of these concepts therefore may not apply strictly to tropical rocky shores compared to other temperate rocky shores. Even then, temperate versus temperate rocky shore comparisons may still yield significant differences between each other (see Menge et al. 2002) making it a necessity that processes and principles that apply in one locality may not do so in others.

This paper will focus on the discussion of the roles of the encrusting intertidal algae on the distribution of benthic invertebrates, mechanisms of structuring factors for the encrusting algae, the effect of herbivory on the algae, presence or absence of competition among encrusting algal species, and the potential effect of sub tidal predators in structuring the algae. The literature used in this brief essay mainly comes from published papers of the Swire Institute of Marine Science, The Hong Kong University, and where appropriate compared to studies from other parts of the world. Most of our discussions are from the works of Williams (1993a and b and 1994), Kaehler and Williams (1996, 1997 & 1998), Hutchinson and Williams (2001 & 2003), Menge and Lubchenco (1981), and Menge et al. (1985 & 1986) and partly on our work (Macusi 2010; Deepananda 2008).

General description of algal communities

The encrusting algal community structures in most tropical rocky shores are described to be intensely grazed by fishes (Menge & Lubchenco 1981; Menge et al. 1983, 1986) and molluscan grazers (Williams 1993b; Williams 1994; Macusi 2008) so that only a limited cover of macroalgae are able to colonize in open spaces. These community structures are however not consistent throughout all the tropics and zonation patterns varies per region (Sauer Machado et al. 1996). In the case of the Hong Kong shores which are mostly moderately exposed to waves, it experiences a seasonal growth of algae in both the mid- and low-intertidal zone and distinct zonation of encrusting cyanobacteria with a *Kyrthuthrix* zone is visible compared to the Panamanian shores (Williams 1994, Hutchinson & Williams 2001 and 2003, Kennish et al. 1996). Macro-algae are restricted in crevices or rock pools with sparse banding of *Kyrthuthrix maculans* in the midshore and encrusting coralline algae are low on the shore (Williams 1994). In contrast, the Panamanian rocky shore experiences little disturbance as the climate pattern shows no seasonality. This has a great significance in terms of the number of species living in the area. Experiments on the effect of refuges (Menge et al. 1983 & 1985) as well as observed shading effects (Menge et al. 1983 & 1986) encouraged appearance and growth of macroalgae not present when the artificial refuges were not yet installed. Other tropical rocky shore zonation patterns seem to be dependent on both of these models, the tropical rocky shore with and without clear seasonal patterns.

The Costa Rican rocky shores for example have a near patchy distribution of organisms but with greater diversity and abundance of organisms compared to that of Panama (Sutherland 1987). Moreover it has been observed that, in comparison with Panama, the rate of recruitment of algae and barnacles are greater in these shores (Sutherland & Ortega 1986; Sutherland 1987). Macroalgae seems to grow larger and play a more dominant role as latitudes increases below or upwards of the tropical latitudinal zone. For example Bustamante and Branch (1996) have found that sub tidal kelp forests in the cape of South Western South Africa play a key role by enriching organic nutrients to the near shore environment. This was also observed to be the same with the rocky shores found at the Island of Helgoland in North Germany where decomposing kelps return nutrients to the near shore communities for recycling and usage by consumers in the area (author's pers. obs.). Diversity may not be as abundant per

species when compared to tropical shores but macroalgal size, distribution and abundance increases with increasing latitude (Santileces 1990; Meneses & Santelices 2000); and with this increase in abundance, the macroalgae's key role in the system also increases. This is illustrated by kelp bed forests which play an important role in the subtidal habitat but the same can be said of their role in providing nutrient subsidy and food resource to grazers in the rocky shore (Bustamante et al. 1995a, 1995b; Bustamante & Branch 1996; Duggins & Eckman 1997). The temperate rocky shores are well known for the great abundance and diversity of foliose macroalgae that inhabit the wave exposed as well as the moderately and sheltered rocky shores. Patterns of zonation are common but not strictly the same. Figure 1 illustrates the distinct vertical zonation pattern in a temperate rocky shore in Chile. Even in temperate to subtropical areas, some algal species are present and are widely distributed in both areas. Distribution patterns and factors that affect such

distribution of algae are not yet clearly understood. It has been postulated by Meneses and Santelices (2000) that these are due to temperature and latitudinal gradients that are affecting the germination of sporelings of macroalgae. Surveys detailing the biogeographic regions of South America have been started out but inter-country comparison and studies are yet to be carried out. Other popular study areas from temperate rocky shores include those in the Oregon coasts, California, New England as well as the South African coasts, Helgoland in Germany, New Zealand and the UK, Italy and Portugal. The most common characteristics that these shores exhibit are the abundance of foliose macroalgae (brown algae and green algae), a distinct littorinid and barnacle zone, urchins and sea stars and mussel beds which are non-existent in most tropical rocky shores if not very patchily distributed.

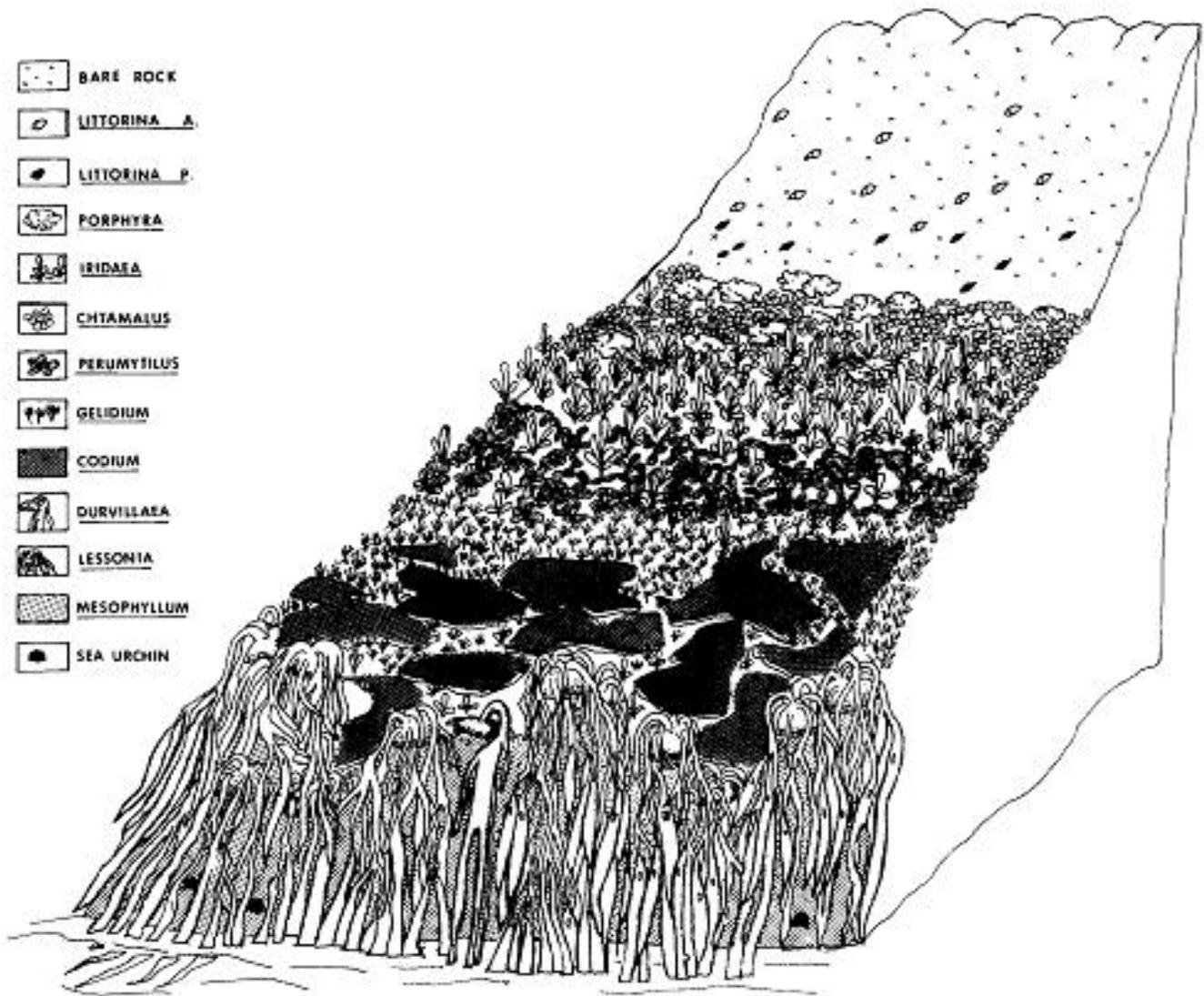


Figure 1: The pattern of vertical zonation commonly characterizing a typical rocky shore found in Chile which is an example of a temperate rocky shore. The upper shore is bare rock and the mid shore is populated by patchily scattered littorinid grazers and

barnacles. Both the mid- and low-shores are comprised of a mixture of mostly brown foliose macroalgae (adapted from Santelices 1990).

Distribution and abundance of encrusting algae in tropical rocky shores

The rocky shores found in Panama can be typical of tropical rocky shores which experiences no distinct seasonal changes or having constant temperature and season year round (Menge and Lubchenco 1981; Lubchenco et al. 1984; Menge et al. 1986). While this provides a familiar environment, it does not allow other preys to establish themselves on the shore due to dominance of constant predators found in the area. Table 1 shows a list of common encrusting and non-encrusting algae found in Panama, Hong Kong and Sri Lanka. The “bare” rocks are often dominated by the encrusting algae (Menge et al. 1985,

1986) in these shores. While in Hong Kong, the encrusting algae and biofilm covers most of the spaces in the shore with patches of green turfs in the mid-shore and tide pools. The distribution of algae in the rocky intertidal shores of Hong Kong is governed by seasons and physical conditions and much less by predation. Effects of seasonal patterns as discussed above shows a cycle of summer die out of several algal species and a winter regrowth for most of the ephemeral macroalgae that thrives in the shore. Physical stress was suggested to limit algal abundance and diversity during the summer months from May to September in Hong Kong (see Hodgkiss 1984; Williams 1994).

Table 1: Comparison of common grazers and consumers found in tropical rocky intertidal shores of Panama, Hong Kong, Brazil and Sri Lanka.

	Panama (Garrity & Levings 1981, 1984; Menge et al 1986)	Hong Kong (Williams 1993b, 1994; Macusi 2008)	Brazil (Sauer Machado et al . 1996)	Sri Lanka (Deepananda 2008)
Fish	<i>Ophioblennius sreindachner</i> <i>Kyphosus elegans</i> <i>Scarus perrico</i> <i>Holacanthus passer</i> <i>Bodianus diplotaenia</i> <i>Eupomacentrus acapulcoensis</i>	<i>Entomacrodus stellifer</i>	<i>Caranx latus</i> <i>Trachinotus carolinus</i> <i>Trachillotus falcatus</i> <i>Trachinotus goodei</i> <i>Conodon nobilis</i> <i>Hyporhamphus unifasciatus</i> <i>Sphoeroides testudineus</i> <i>Umbrina coroides</i>	
Gastropod	<i>Fissurella virescens</i> <i>F. longifissa</i> <i>Acanthochitona</i> <i>Ceratozona angusta</i> <i>Chiton stokesi</i> <i>Littorina aspera</i> <i>L. modesta</i> <i>Nerita scrabicosta</i> <i>Scurria stipulata</i> <i>Siphonaria maura</i> <i>S. palmata</i> <i>S. gigas</i> <i>Acanthina brevidentata</i> <i>Thais melones</i> <i>Purpura pansa</i> <i>P. paura</i>	<i>Acanthopleura japonica</i> <i>Cellana toreuma</i> <i>C. grata</i> <i>Siphonaria laciniosa</i> <i>S. japonica</i> <i>Patelloida pygmaea</i> <i>P. saccharina</i> <i>Lumella coronata</i> <i>Chlorostoma argyrostoma</i> <i>Monodonta labio</i> <i>M.neritoides</i> <i>Nerita albicila</i> <i>Planaxis sulcatus</i> <i>Echinolittorina radiata</i> <i>E. trochoides</i> <i>E. vidua</i> <i>Thais clavigera</i> <i>Morula musiva</i>	<i>Anachis lyrata</i> <i>Leucozonia nassa</i> <i>Pilsbryspira albomaculata</i> <i>Pisania auritula</i> <i>Tegula vindula</i> <i>Thais haemastoma</i>	<i>Trochus radiatus</i> <i>Trochus tentorium</i> <i>Clypidina notata</i> <i>Cellana radiata</i> <i>Nerita costata</i> <i>Nerita plicata</i> <i>Littoraria undulate</i> <i>L. scabra</i> <i>Nodilittorina granularis</i> <i>N. pyramidalis</i> <i>Thais alveolata</i> <i>T. rudolphi</i> <i>Drupa granulata</i> <i>D. margariticola</i>
Sea urchins	<i>Echinometra vanbrunti</i>	<i>Anthocnidaris crasspina</i> <i>Diadema sp.</i>	<i>Paracentrotus gaimardii</i>	<i>Tripneustes sp.</i> <i>Diadema sp.</i>
Crabs	<i>Pachygrapsus transversus</i> <i>Grapsus grapsus</i>	<i>Grapsus albolineatus</i> <i>Eriphia sp.</i>	<i>Epialtus brasiJiensis</i> <i>Eriphia gonagra</i> <i>Pachygrapsus transversus</i>	<i>Percnon sp.</i> <i>Dardanus sp.</i>

General factors

Studies on the effects of temperature on many invertebrates have been inconclusive and rather this is an area where a needed focus can be done on many other tropical rocky shores. While sedimentation can be a problem in many coastal areas under development and encroachment of human habitat, studies on

those have not been widely conducted in many tropical rocky shores (Huang et al. 2006). Whenever possible we compared different tropical systems such as Panama, Hong Kong, Brazil and the Galapagos. This is when we are focusing on the subject of the encrusting algae and herbivory in the tropical rocky shores. Experiments carried out in Panama were different in

experimental designs compared to those in Hong Kong. Nevertheless, some of the findings were similar and a comparison between the results of these studies will sum up the knowledge on these tropical rocky shores.

Physical factors (temperature, desiccation and seasonality)

Moore (1972) has published that environmental stresses in the tropics are greater compared to temperate shores. Aside from this, the effects of season can also vary between two different tropical rocky shores, depending on the locality. Tropical countries which are directly above the equator experiences a constant radiation from the Sun (e.g. Sri Lanka and Panama) but other areas such as Hong Kong or those directly adjacent to tropical countries can experience both summer and winter conditions. This has an effect on the abundance and distribution of flora and fauna in these areas. The Hong Kong shores appear to be largely controlled by the strong seasonality present which affects the abundance and distribution of marine algae (Williams 1993a; Kennish et al. 1996). A high temperature that rises up to 50 °C during summer causes algal die-offs in the shores in both the wave exposed and sheltered sites (Williams 1993b & 1994; Hutchinson and Williams 2001 & 2003). A study on the effects of physical disturbances was conducted by Kaehler and Williams (1998) using artificial drip irrigation set-ups on study plots during summer and winter. The results suggest that physical stress structures the assemblage of algae in the high shore but there are no significant differences in the low shore set-up even with the drip irrigation. In the irrigated set-ups high on the shore, fleshy macroalgae settled and colonized empty plots and subsequently the encrusting algae also settled and recruited into the plots. When the irrigation was stopped, macroalgal settlement and colonization stopped except for several encrusting species like *Hapalospodidion gelatinosum* and *Ralfsia expansa* and the cyanobacteria *Kyrtuthrix maculans* that persisted for several months though in much reduced cover. These results suggest that in the high shore level, the physical stress is predominant not just in temperate areas but even in tropical rocky shores where heat and desiccation can be several times harsher than those experienced in a temperate shores. In contrast to these, observations in the Mediterranean shores demonstrate that recovery from disturbances changes the structure of the community including the rate of succession (Benedetti-Cecchi and Cinelli 1993; Dye 1993). While in Panama, the shores do not exhibit seasonal variations and no distinct zonation patterns appear in the sense as those of temperate shores.

Tidal height

The tidal height of the rocky shore can also be one factor in structuring the assemblage of encrusting algae. The study of Kaehler and Williams (1998) provides insight with respect to tropical rocky shores that there are species of algae which prefer to grow in the high shores compared to growing in the low shore areas. Some of these low shore species can also be found in the high shore areas when reduced physical stress occurs during seasonal changes, e.g. from summer to winter. The alga *Hapalospodidion gelatinosum* was almost completely restricted to the high shores although some individuals recruited to the low shores (Kaehler and Williams 1997). However, in this study, the wet treatments (irrigated) did not develop or allow this encrusting alga to be established in the low shore abundantly.

The authors postulated that competition from overgrowth of other algae such as *Ralfsia expansa* and *Corallina spp* can be one of the main reasons (Kaehler and Williams 1996, 1998). Restriction to low shore areas of other species such as *Corallina spp* can be due to desiccation stress in the high shore areas (Kaehler and Williams 1998). Whereas in temperate areas, the brown alga *Pelvetia canaliculata* which is called Channel wrack by the British, was thought before to be restricted only in the upper shores (Wilson 1951), recent removal and succession experiments however proved this assumption untrue (Little & Kitching 1996). In Panama, foliose algae outcompetes the crustose algae even in the upper shores when shading experiments were conducted (Menge & Lubchenco 1981; Menge et al. 1985 & 1986). It was also observed that in upper shores, these foliose algae are restricted to cracks and crevices. The usually barren looking areas were observed to be mostly colonized by encrusting algae and corallines (Navarrete & Menge 1997).

Sediment supply

Though the effects of sediments on algal assemblage and its associated organisms are essential to understand the impact of coastal structures built in urban and recreational facilities. Those studies in tropical rocky shores have not been covered in most experiments. This area is important as the effects of anthropogenic dredging, bottom trawl fisheries, modern coastal infrastructures as well as strong typhoons and storms can have an indirect effect on re-suspension of sediment particles (Ruffin 1998; Hutchinson & Williams 2003) that can scour or remove encrusting algae (McQuaid & Dower 1990; McCook & Chapman 1991, 1997). This too can affect new recruits and early propagules of algae and invertebrates colonizing the substrate. The smothering of algae results from abrasion but can also be due to light attenuation (Airoldi & Cinneli 1997; Airoldi & Virgilio 1998). The effects of sedimentation may vary when other biological and physical factors are present; at small scales, it decreases the abundance and biomass of turf forming algae but at larger scales, the effects were variable or unclear (Airoldi and Virgilio 1998). Irving and Connell (2002) also suggested that sedimentation could further reduce the survivorship of algae on shaded subtidal rocky reefs.

In another study, violent episodic disturbances caused by wave action and sediment scouring revealed differences between how algal turfs, erect and encrusting algae colonize a bare substratum (Airoldi 2000). The turf forming algae spreads through vegetative reproduction while the encrusting and erect algae by dispersal of its propagules. This means that in the event of short pulse disturbances of substratum colonization, the most effective colonizers would be turf formers while the encrusting and erect algae would be dependent on reseeding to colonize the bare area. Further studies remain to be seen whether encrusting algae can overgrow or colonize dumped sediment loads in cases of reclamation, change of direction of water flow and sediment deposition in cases of barriers built on the shore e.g. groins or banks. These artificial structures may influence species settlement and colonization and affect the abundance and distribution patterns of algae and other epibiotic organisms (McGuinness & Underwood 1986; Olalia et al. 2009). In the Daya Bay coastal region of China, human activities and nutrient

loading has been positively related to the occurrence of harmful algal blooms in the area (Yu et al. 2007). This was often the case in many embayment areas where there is high primary productivity, intense human activities and the system receives both intense and short pulses of dissolved and particulate materials from the land (Cembela et al. 2005). Land and ocean interaction is not new science but the intense and increasing activities of humans in the coastal zones have particularly impacted most marine systems.

Nutrient supply

Most studies in nutrient enrichment focused on its impact on sub tidal areas such as in rocky and coral reefs and the plankton. Studies on direct impacts of eutrophication to algal assemblage in tropical rocky shores are still scant and needs to be quantified to have an idea of its effects and the extent of its occurrence. In addition, fertilization studies in the context of induced algal species succession have yet to be started in tropical rocky shores. An upstart project would be to assess nutrient enriched sub-tidal waters such as those near the mangrove areas or estuaries. It is probable that the rocky shore near this system benefits from exports of nutrients coming from these systems (Primavera 1998; Ditmar & Lara 2001; Nordhaus et al. 2006). The study of Bustamante et al. (1995a & 1995b) in South African rocky shores showed that kelp beds near the colonies of limpets are found to nourish and enhance the abundance and biomass of the limpets. Their study also showed that where dense aggregates of limpets are found, no foliose macroalgal beds develop as a result of intense herbivory on macroalgal sporelings. This was confirmed by previous experimental removals (Branch 1981; Eekhout et al. 1992) as well as removal of grazers due to natural catastrophe (Branch et al. 1990; McQuaid & Dower 1990), where foliose macroalgae developed quickly in the absence of the grazers. Recently the authors have observed this occurrence in their field study sites in Sri-Lanka and in Hong Kong where areas of high grazer density are mainly dominated by encrusting algae but areas of low grazing intensity allow the establishments of turf forming algae. Comparison of areas of high and low disturbances showed that macroalgal growth is stunted in less disturbed areas than in areas of high disturbance and this can be attributed to the presence of a number of grazers (Deepananda 2008; Deepananda & Macusi 2012).

Worm and Sommer (2000) postulates that even a single nutrient pulse can have direct and indirect effects such as on the increase of the number of grazers on seaweeds exposed to high nutrients compared to those which were unexposed. They also suggested that the length of time of duration or exposure to nutrients is a more decisive factor compared to frequency of nutrient pulses (Worm & Sommer 2000). A recent field manipulation study by Nielsen (2003) with nutrient additions in tide pools in rocky shores of Oregon (which experiences intermittent upwelling) showed that macrophyte abundance and biomass increases with increased nutrient loading. These nutrient pulse studies can be conducted in tropical rocky shores to determine the effects of high nutrient input in algal assemblage found in the coastal zone.

Complex habitat structure

The complexity of habitat structures found in many tropical rocky shores adds another advantage to consumers from constant

predation and physical stress (Menge & Lubchenco 1981; Menge et al. 1985 & 1986). Substrate heterogeneity adds variation and increase in surface area of many rock platforms enabling animals and plants to live astride together whether as cryptic species hiding from the harsh exposure to desiccation or to the beating of waves and persistent herbivory (Menge 1983; Raimondi 1988; Blanchete et al. 2000). During the last Asian tsunami in 2004 in the Indian Ocean, villages with remaining plantations of *Casuarina* and mangroves were left unscathed by the deluge of strong waves compared to areas in other parts of Tamil Nadu where there were no barriers, the damages were much lesser (Danielsen et al. 2005). Authors have observed the similar result from Sri Lanka after the same tsunami event in 2004. In the Wadden Sea, the complex habitat structures such as eelgrass bed can prevent overexploitation by predators as well as competitive exclusion, allowing a diversification of assemblage (Reise 1978). In the case of the tropical rocky shores, the availability of refuges for predator avoidance and refuge from desiccation and physical stress seems to increase diversity in the community (Garrity 1984; Menge et al. 1985, 1986). Similar observations were recorded in Hong Kong rocky shores where most animals were found hiding in cracks and crevices including some foliose algae concentrated in various patches to avoid physical stress during the summer period (Williams 1993a, Williams 1994). This highly stressful condition leads to release of prey from predation and increase effect of competition among basal species e.g. encrusting algae. Similarly if this condition is reversed, e.g. physical stress is much reduced, predation or herbivory affects sessile prey species in greater magnitude than competition between the basal species as predicted by the environmental stress models.

This model which suggest that species of high trophic status (e.g. predators) would be regulated primarily by competition while species of low trophic status (basal species e.g. algae and barnacles) should be regulated primarily by predation (Menge & Sutherland 1976; Menge et al. 1986; Menge & Olson 1990) predicts that in benign areas, the effect of competition is not clear or present at all. In the Hong Kong rocky shores, we tested whether the predictions of the environmental stress model holds true when different herbivores are present and the conditions are benign. Using manipulation experiments, our results show that molluscan herbivores primarily controls the algal assemblage in this area when they are present in high number (Deepananda & Macusi 2012), while the fish and crabs do contribute in reducing algal cover but only those which attain escape sizes from molluscan herbivores (Macusi 2010).

Biological factors (recruitment, settlement, herbivory and predation)

Algal standing crop increases from the high-shore to the low-shore; herbivore distribution pattern also shows similar pattern, i.e., increases from the high-shore to the low-shore. During summer, most of the ephemeral green algae that were able to grow during the winter die off leaving the encrusting algae to be the most dominant cover during the season (Williams 1993a & 1993b; Williams 1994). Grazing is mostly concentrated down on the low shore during these months to avoid heat stress and gain moist algae found growing on the low shore. Grazing is presumably much reduced during these summer months because

most gastropods and algae die out of desiccation, heat stress while the remaining ones can be found concentrated in crevices and pools.

A different condition occurs in Panama where a continuous grazing pressure by fish and gastropods are present on the shores (Garrity & Levings 1981, 1983; Levings & Garrity 1983; Garrity 1984; Menge et al. 1986). Because fishes are abundant in these shores, and prey on the sessile algae and the gastropods. This predation by fishes have restricted the grazing behavior of herbivorous gastropods (Garrity & Levings 1981, 1983) which now keeps a predator avoidance mechanism, leaving patches of grazed and ungrazed areas in the mid- and low-shore especially when the tides are moving in. For instance, the herbivorous gastropods, *Nerita scabricosta*, *N. funiulata* and *Siphonaria gigas* were observed to scurrying back to their holes and home scars to avoid predation by damsel and parrot fishes as the tide rushes back in (Levings & Garrity 1983 & 1984). In effect, patches of algae are grazed near the home zones of these gastropods but far where they are not found, patches of ungrazed crustose algae can be observed including some erect algae (Levings & Garrity 1984). In comparison to these observations, study on the Brazilian shores (Sauer Machado et al. 1996) have shown that erect macroalgae outcompetes most of crustose algae during removal experiments but predation by fishes or gastropods or predatory avoidance mechanisms of gastropods in the area do not exist. These contrasting observations in the presence of predators have led one of the authors (EDM) to conduct exclusion experiments in Hong Kong shores and find out if fish dominates in every tropical rocky shore just as have been suggested earlier by Brosnan (1992). Our findings are in line with the findings of Sauer Machado and others (1996) in which they have found the effects of predation by fishes on grazers are not the major features of these shores nor does the benign environment automatically favors the grazers (Macusi 2010). Top-down grazing has been observed in these shores (Williams 1994; Hutchinson and Williams 2001), although fishes are present, they do not dominate other consumers there. But the higher abundance of molluscan grazers largely controls the abundance of sessile preys. It is also possible that indirect effects can be the major character occurring in many of these shores as a secondary effect of the interactions happening in the community (Guidetti & Dulcic 2007).

Petratis (1983) has pointed out that in temperate rocky shores, the movement of littorinid grazers are also important in structuring rocky shores. In his experiments, the recruitment of *Balanus sp.* has been directly related to the grazing density of littorinids. At lower density, the littorinids can help *Balanus spp.* settle but at a higher density, this becomes detrimental. This is presumably due to the bulldozing effect of these grazers (Denley & Underwood 1979). The effect on *Enteromorpha* has been to eliminate patches at high grazing densities but at lower grazing intensity the patches of algae remain resistant (Petratis 1983). Other grazing investigations done in temperate areas have found that the territorial patelid limpet, *Patella longicosta* has been responsible to increase the productivity of a crustose alga, *Ralfsia verrucosa* (McQuaid & Froneman 1993; Kaehler & Froneman 1999). It was postulated that physical disturbance through its grazing enhances the productivity of the algae by providing spaces for its margins to extend. Another is that the molluscs can

leave nutrient rich mucus and excretion behind the patches of grazed crustose algae. These limpets rarely leave their territories and remove other competitors of *R. verrucosa* by completely grazing on sporelings as well as foliose algae that finds its way in its territory. Studies on the effects of mucus on patches of algae in Hong Kong show that it has limited effects on stimulating production of algae as heat and desiccation can easily dry them out (Williams et al. 2000).

Several studies on grazing in Hong Kong (Williams 1993b; Williams et al. 2000; Hutchinson and Williams 2001; Macusi 2010) have shown that whether in the low shore or in the high shore, grazers can remove erect macroalgae in experimental plots within a few weeks. This favors to establish the grazer resistant assemblages such as corallines and other encrusting algae (Kaehler & Williams 1998). Herbivores can preferentially remove species of ephemeral green algae and allow the encrusting algae to develop (Lubchenco & Menge 1978; Benedetti-Cechi & Cinelli 1993). If molluscs predominate in Hong Kong, fish tends to graze and predate on sessile algal preys including some gastropods in Panama (Menge & Lubchenco 1981; Menge et al. 1986). The presence of the herbivorous and omnivorous fishes such as damsel fishes-*Eupomacentrus acapulcoensis*, the chub-*Kyphosus elegans*, the parrot fish-*Scarus perri*, the wrasse-*Bodianus diplotaenia*, and the porcupine fish-*Diodon hystrix* in the subtidal area which forages in the low- and mid-intertidal zone during high tide has been one of the distinguish characteristic of this tropical rocky shore community (Menge et al, 1986; Garrity & Levings 1981 & 1983). While in the Galapagos, climate perturbations such as the El Niño effect have a detrimental and large scale effects on the intertidal community (Vinueza et al. 2006). Continued evaluation of the effects of herbivory is important in identifying major groups of consumers and species that can directly or indirectly influence the settlement, growth and distribution of algae in tropical rocky shores. Fish grazing studies in other tropical rocky shores are needed to confirm the studies done by Menge and others (1986) where studies were unreplicated owing to shortage of funds and manpower. It is presently postulated that just as the molluscs play a dominant role in structuring the algal assemblage, fish dominated systems are also thought to do the same (Randall 1961 & 1965). Common grazers found in Panama, Hong Kong, Brazil and Sri Lanka are listed in Table 2.

Effects of herbivory/ predation

The effects of mobile subtidal predators such as fish and crabs have been intensively studied on subtidal areas of rocky reefs; temperate rocky shores and tropical coral reefs. Presence of sub tidal predators such as fish and crabs are not new but very few studies have been done on their contribution for structuring of the near shore systems such as the tropical rocky coasts. Most of the studies on fish grazing have been confined to the sub tidal areas such as in coral reefs (Randall 1961; 1965), in tropical freshwater streams (Power 1983; Power et al. 1989) and in general coastal areas like near breakwaters (John and Pople 1973). One of the most extensive studies done of this kind was by Menge and others (1986), who examined the interactions of varied consumers in the rocky intertidal shores of Taboguila island in Panama. The observed patchiness of the area led them to postulate that this patchiness may be attributed to a large mobile

predator like fish. Findings of a previous study (John & Pople 1973) off the Ghanaian coasts have also confirmed the grazing effect of fishes. Choat and Kingett (1982) however preclude the results of such studies as they were not able to find the relationship of amphipod seasonal decline in abundance with the sparid fishes they studied. Although they were not able to quantify the direct effect of predation by fishes on amphipods, it is possible that the abundant fishes they have studied would also be preying on other sessile forms such as macro- and micro-algae as those cases discussed above. Moreover, the experimental design of the study which was only done in less than a year of observation and focused on invertebrate predation but not on

herbivory. Some fishes are omnivorous but there are quite few accounts on fish nutritional ecology and Choat and Clements (1998) recounts even further the scarcity of biogeographical studies on this aspect. A recent studies by Rilov and Schiel (2006a, 2006b) in New Zealand examined if fish predation was seascape dependent or not (that is, the adjoining topography of the land affects the way the assemblages are structured) and how it affects mussel mortality in the mid- and low-intertidal zones. The study provided evidence that in the presence of rocky reef systems mussel mortality was lesser compared when there were none.

Table 2: Lists of common rocky intertidal algae from Panama, Hong Kong and Sri Lanka

Panama (adapted from Lubchenco 1984)	Hong Kong (adapted from Kaehler and Williams 1996)	Sri Lanka (Deepananda 2008)
<i>Lobophora sp</i>	<i>Ralfsia expansa</i>	<i>Acanthopora sp.</i>
<i>Mesospora sp</i>	<i>Hapalospongidion gelatinosum</i>	<i>Asporagopsis sp.</i>
<i>Ralfsia sp</i>	<i>Hildenbrandia prototypus</i>	<i>Caulerpa racemosa</i>
<i>Hildenbrandia sp</i>	<i>H. occidentalis</i>	<i>C. sertulariodes</i>
<i>Schizothrix calcicola</i>	<i>Dermocarpa sp.</i> ^a	<i>Centroceras clavulatum</i>
<i>Bryopsis spp</i>	<i>Kyrtuthrix maculans</i>	<i>Gracilaria cassa</i>
<i>Caulerpa botryoides</i>	<i>Chaetomorpha antennina</i> ^a	<i>Hypnea pannosa</i>
<i>C. peltata</i>	<i>Ulva sp.</i> ^a	<i>Padina boergesenii</i>
<i>Chaetomorpha sp</i>	<i>Corallina sessilis</i>	<i>Valonia fastigiata</i>
<i>Chladophoropsis sp</i>	<i>C. pilulifera</i>	<i>Ahnjeltiopsis pygmaea</i>
<i>Cladophora sp</i>	<i>Dermonema frappieri</i> ^a	<i>Chaetomorpha antennina</i>
<i>Enteromorpha sp</i>	<i>Gelidium pusillum</i>	<i>C. gracilis</i>
<i>Ulva sp</i>	<i>Hincksia mitchelliae</i> ^a	<i>Chnoospora minima</i>
<i>Amphiroa sp</i>	<i>Polysiphonia sp.</i> ^a	<i>Enteromorpha intestinalis</i>
<i>Cenfroceros clavulatum</i>	<i>Porphyra suborbiculata</i> ^a	<i>Euryomma platycarpa</i>
<i>Corallina spp</i>	<i>Pterocladia tenuis</i> ^a	<i>Sarcodia montagneana</i>
<i>Gelidiella sp</i>	<i>Endarachne binghamiae</i> ^a	<i>Sargassum cristaefolium</i>
<i>Gelidium pusillum</i>		<i>S. wightii</i>
<i>Hypnea sp</i>		<i>Ulva fasciata</i>
<i>Jania sp</i>		<i>U. lactuca</i>
<i>Laurencia sp</i>		<i>U. rigida</i>
<i>Polysiphonia sp</i>		
<i>P. pacifica</i>		
<i>Spyridium sp</i>		
<i>Microcoleus lyngbyaceae</i>		

a=strongly seasonal

This shows that fishes can exert strong effects to their immediate community. Trophic linkage is usually described as the transfer of energy from organisms of one trophic level to the other through different interactions. We depicted a hypothetical food web interaction links for the rocky shore algal communities of Panama and Hong Kong (Figure 2). Predation and herbivory are

examples of trophic linkage where producers transfer their accumulated energy to the consumer. In Hong Kong, the rare predatory crab *Eriphia sp* can predate on other crabs such as the herbivorous grapsid crabs usually found foraging on the shore. But its gut content can also include other invertebrates like mussels and limpets as well. While in Panama, fish usually

includes in their meals the herbivorous gastropods as well as the predatory ones such as *Purpura paura* and *P. pansa* (Garrity & Levings 1981; Garrity 1984). This trophic linkage in the rocky shores can occur fast through subtidal predators like fishes and crabs that usually forage only during high tides. Current trends

seem to suggest that the lack of single dominant key species in tropical rocky shore systems can be a reflection of the complex interactions of various consumers present. This brings us the next topic, the keystone species concept.

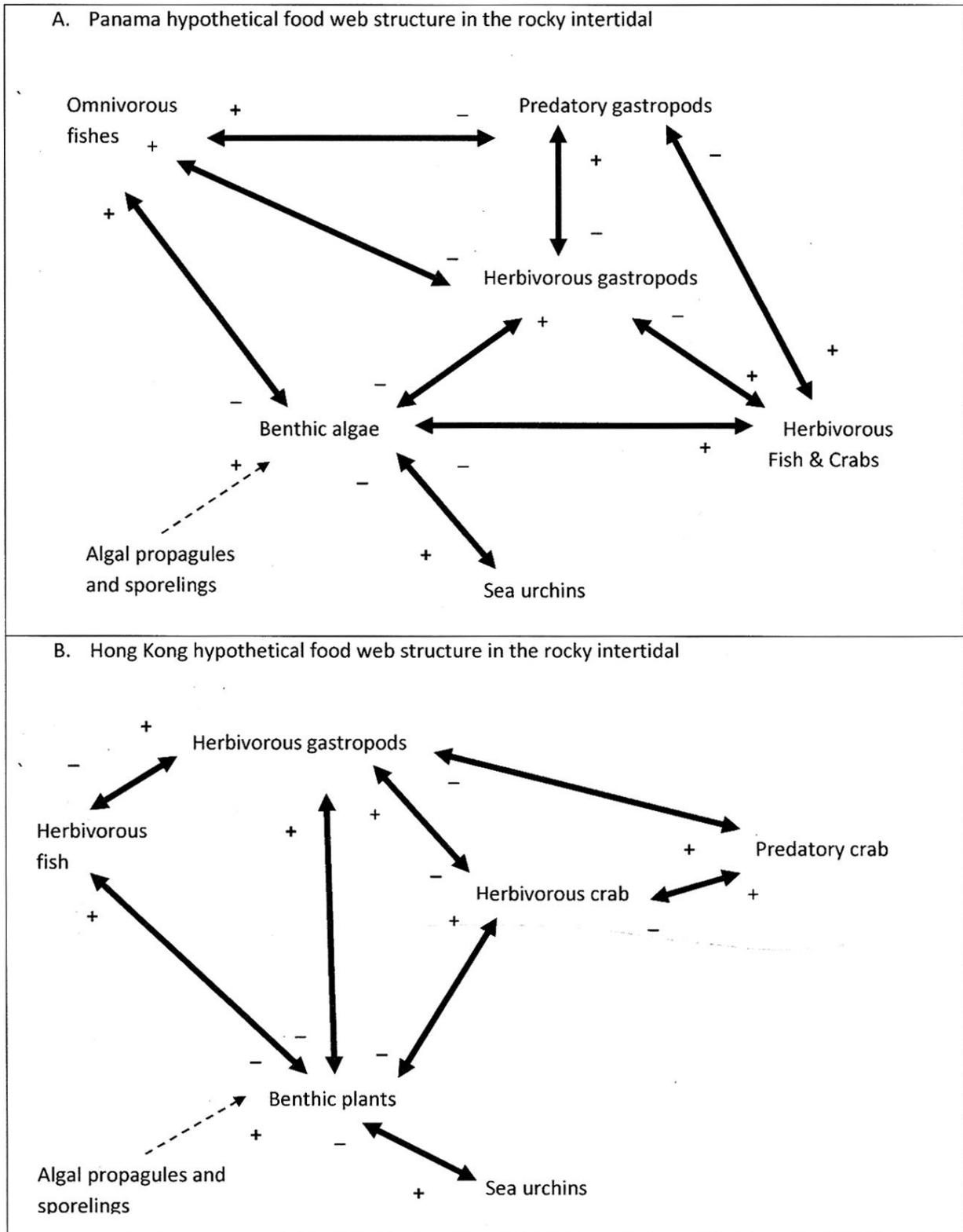


Figure 2: Comparison of interaction web of rocky shore communities in (A) Panama and (B) Hong Kong. The thick and broken lines suggests the qualitative strengths of the interaction and + & - means positive and negative effects, respectively. Arrow heads point to groups affected and a blunt end means insignificant effect.

Competition

Most of the observed living spaces in tropical rocky shores thrive mostly on barren patches, boulders and rocky reefs that creates effective refuge areas due to the holes, cracks and crevices that hosts several consumers and even patchily growing algae. This contrasts greatly to temperate areas where algae compete for spaces to colonize aggressively when present (Dayton 1971). Space competition does not seem to occur in non-seasonal tropical rocky shores (Dayton 1971, 1975; Menge and Lubchenco 1981; Santileces 1990). Because, both food and non-food resources are abundant and there is no competition that occurs among inhabitants of the shore at all tidal levels (Navarrete and Menge 1997). Fish predation has been known to control and affect to lower the recruitment of sessile organisms (Menge 1991; Navarrete and Menge 1997). The upper intertidal zone of rocky shores in Panama has been observed to be dominated by barren space, while the mid- and low-shores are dominated by crustose algae. There were no observations that suggest a competition between crustose algal species is present. Post experimental analysis by Menge (1991) suggests that when the recruitment of invertebrates and foliose algae increases, the coverage of the crustose algae declines. Since the crustose algae generally covers 90% of the space in Panama, he concludes that low recruitment seem to be the norm in the area. In the case of Hong Kong, observations of competition were not recorded except the overgrowth of ephemeral greens of the space during winter which also dies off during the summer. Garrity (1984) concluded that generally tropical climate prevents the establishment of foliose macro-algae in the upper shores because of intense heat and desiccation. Earlier, Wilson (1951) correctly suggested that sharp temperature changes can only be tolerated by few species so that no aquatic organisms will survive these changes. The result would be only few organisms colonizes the upper shores and the number and diversity of organisms only increases as you move from the upper to the lower intertidal zone.

CONCLUSION

Tropical rocky shores are affected by many factors from sediment scouring, strong wave action, pulse disturbances namely typhoons, storms and nutrient loading, herbivory, heat and desiccation, habitat structure, and larval and propagule supply. In comparison to temperate shores, the mid- and high-shore of tropical rocky shores experiences a greater degree of heat and desiccation year round due to its topography; when seasonal changes interacts with location, possible succession of algal functional groups occurs in the shore with erect algae dominating this change and displacing the competitively inferior crustose algae. This effect of physical factors in tropical rocky shores can influence the structure of algal communities as well as consumers in the shore. Distribution patterns of algae in temperate rocky shores follow distinct banding patterns of fauna and flora but this is less distinct in many tropical rocky shores around the world. Herbivory in most tropical rocky shores can be due to fish, crabs, molluscs and iguanas; molluscan herbivores in

Hong Kong dominates the rocky shore and plays the major role in structuring the algal community during the winter. While fish and crabs may be present, these herbivores do not have as strong effect as the ubiquitous and more abundant molluscan herbivores. Algal escapes from molluscan grazing and cyanobacteria form the bulk of foods used by crabs during winter while encrusting algae are also utilized; fish on the other hand may browse on turf algae. Molluscan grazers preclude the establishment of algae by bulldozing algal sporelings. Grazer exclusion in Hong Kong and Panama suggests that foliose and filamentous algae can colonize the low shore as well as the mid-shore areas but the higher shore levels are physically constrained by physical factors such as heat and desiccation. In addition, fish and crabs can have a significant effect on the abundance and distribution patterns of tropical intertidal algae but whose effects may vary on groups of algae or depends on the abundance of fish and crabs on the shore as well as the presence of other grazers such as limpets. In Panama, fish acts as top predator in the system dominating and affecting the grazing behavior of most herbivorous gastropods. While in the Galapagos, climate perturbations such as the El Niño have a detrimental and large scale effects on the intertidal community. The keystone species concept at present definition does not seem to apply in tropical rocky shores probably as a result of the presence of more diverse and redundant consumers in the area. Site specific characteristics in Panama would include a tropical non-seasonal rocky shore being affected mainly by its year round exposure to the Sun. Rocky reefs are abundant in the area and barren grounds also abound. The most abundant predators are the fishes which affect the behaviors of the molluscan grazers and possibly cause the observed "barrenness" of the area. There are also no clear zonation patterns whether in the low- or mid-shore zone. Hong Kong on the other hand is more of a seasonal type, with the summer season causing a widespread grazer and algal die offs during which the encrusting algae dominate the shores. During winter, some foliose algae settle and colonize not only the low shore but even the mid-shore. The effects of fish are quite negligible but may still play a role in structuring the assemblage cover. Subtidal predators which clearly impacts in Panama are therefore absent in most of the Hong Kong shores. We suggest that more varieties of experimental manipulations are needed to determine significant biological and physical processes affecting the structure of algal and faunal assemblages across broad areas in the tropics.

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