BIG SHOES TO FILL: THE POTENTIAL OF SEAWALLS TO FUNCTION AS ROCKY SHORE SURROGATES

SAMANTHA LAI

BSc. (Hons.), NUS

A thesis submitted for the degree of Master of Science

Department of Biological Sciences

National University of Singapore

2013

Declaration

I hereby declare that this thesis is my original work and it has been written by me in its entirety. I have duly acknowledged all the sources of information which have been used in the thesis. This thesis has also not been submitted for any degree in any university previously

Samantha Lai

August 2013

Acknowledgements

I would like to extend my heartfelt gratitude to my supervisor, Dr. Peter Todd, whom without which, I would never have taken up this MSc, much less see it to completion. He has been unfailingly supportive, encouraging and been an endless source of advice. Being in his lab has been one of the best experiences of my life, and has changed me for the better (I hope).

I have to thank my fellow EMEL labbies: fellow seawall auntie, Lynette, for suffering with me, through fieldwork, endless specimen sorting, and painful statistic courses; and the Twinnies, Siti and Mei Lin, for being there for me every time I needed a sympathetic ear, good advice, or a cold beer. You guys are more than friends, *you're family*.

A huge thank you to all my friends and fieldwork volunteers, who have helped in one way or another throughout my project: Samuel, Ross, Ian, Aizat, Brian, Henrietta, Jamie, Desmond, Aaron, Ambert, Karmun, ZiXing, Karen, Yasmin, Yuen May, Wan Ting and Kareen.

I am also grateful to the Singapore Delft-Water Alliance, who had provided me with a salary, a grant and allowed me to pursue my Master's while working as a Research Assistant.

Thank you to: Shao Wei, Sentosa Development Corporation, and Shangri-La Rasa Sentosa, for allowing me to conduct my research on Tanjong Rimau; MINDEF and SAF Mapping Unit, who have kindly permitted me to use their topographical maps to map the coastal changes in my first chapter; and the boat crew of Heng Lee Charter, for being extremely helpful even at 5am in the morning.

Finally, although I know no amount of thanks will ever suffice, I want to thank my parents, who have been so endlessly (and unquestioningly) supportive, even when it meant taking over the freezer to store twelve months' worth of specimens. Last but not least, thank you Keith, for being my rock.

Table of contents

Summary

Land reclamation and coastal development have converted or degraded large areas of natural intertidal habitats in Singapore, resulting in the loss of mangrove forests, coral reefs and sand/mudflats. The disappearance of these habitats was documented between the 1950s and the 1990s, but there has been no assessment of the changes that have occurred during the past two decades. **Chapter 1** quantifies the significant coastal transformations over this period and evaluates the future of marine habitat conservation and sustainability in Singapore. Analyses of topographical maps indicate that total cover of intertidal coral reef flats and sand/mudflats has decreased largely due to extensive land reclamations, while mangrove forests have increased slightly due to restoration efforts, greater protection, and relative isolation from development. However, 15 and 50-year projections based on Singapore's 2008 Master Plan and 2011 Concept Plan show that all habitats are predicted to shrink further in coming years. In their place, the total length of seawalls is set to increase, from 319.23 km of presently to more than 600 km by 2060.

Most studies have focused on the destructive nature of marine artificial structures; however researchers are beginning to move beyond their negative impacts and focusing on assessing and modifying artificial habitats as surrogates for natural ones. Given the ubiquity of seawalls and their potential for supporting coastal communities, it is important that conservationists embrace ecological engineering as an additional tool to conserve near shore biodiversity. **Chapter 2** focuses on comparing the communities on seawalls with those of natural rocky shores to evaluate the artificial habitat's potential as a surrogate of the natural one. A year-long survey of both habitats revealed that seawalls had a different community structure to rocky shores, with lower algal and faunal diversity in general, but a higher presence of detritivorous isopods. These results suggest that seawalls Singapore lack the primary productivity to support high trophic levels, leading to a fewer number of species and abundance overall. There was, however, a substantial overlap in the species found in both habitats, indicating that while seawalls are still limited by the lower primary productivity, they have the potential to host a similar range of species to rocky shores.

Understanding the trophic interactions of common intertidal species can help further elucidate the ecological causes for the community differences observed between seawalls and rocky shores. In **Chapter 3**, $\delta^{15}N$ and $\delta^{13}C$ isotopes were used to examine the diets of several common species found in both habitats. The isotopic values were highly variable due to the diverse diets of many of the species, although there was little evidence to show that the diets were substantially different between habitats. Turf algae were the most dominant food source among the herbivores, while these herbivores were the dominant food species for the secondary consumers. The detritivorous isopods (abundant on seawalls) were, however, of a much lower trophic level, and most likely fed on decaying algae. This supports the conclusions from Chapter 2, i.e. that seawalls lack the productivity to sustain the higher trophic levels and complexity needed for high biodiversity. These findings allude to the possibility of improving seawall capacity to support greater diversity by increasing algal diversity and abundance.

List of Tables

List of Figures

General introduction to the thesis

The conservation of biodiversity is becoming increasingly difficult in urban environments. Traditionally, environmental managers have aimed to protect native species by safeguarding their habitats from degradation, allowing them to thrive within protected areas (Rosenzweig, 2003). However, in cities and countries where populations can reach very high densities, the demand for land can supersede the need to conserve natural spaces (Miller, 2005). Singapore is a prime example of this struggle between conservation and development. This city-state's economic output, social structure and physical landscape has transformed radically over the past century. From a British colonial trading outpost, Singapore now has one of the highest gross domestic product (GDP) per capita and standards of living in the world (World Bank, 2012). The resident population has also grown dramatically, from just over 2 million people in 1970 to 3.8 million in 2012, in a country with a total area of just 714 km^2 (Singapore Department of Statistics, 2013). This combination of rising affluence and expanding population has created great pressure on the very limited land area, and the Singapore Government has addressed this problem partly by reclaiming large stretches of land along the coast. Reclamation has caused many of Singapore's natural coastal habitats, and consequently associated biodiversity, to be irreversibly lost (Hilton and Manning, 1995).While there have been attempts to conserve marine biodiversity through protection of key habitats (e.g. Sungei Buloh Wetland Reserve), this strategy is seen as impractical among policy-makers due to the value of the land, and incompatible with the Government's priority of economic development. It is becoming increasingly apparent that to maximise the efficacy of conservation in Singapore, other options aside from *habitat protection* need to be employed.

Restoration and *reconciliation* are two such options. Restoration aims to return a degraded environment back to its original state, thus restoring its function and value (Edwards and Gomez, 2010). While this has been attempted for mangroves in Singapore (Liow, 2000), it is similar to the habitat conservation approach in that it requires a commitment to repair and maintain an area in its natural state, necessarily excluding it from human utility (other than activities in line with the area's conservation). Additionally, restoration of a habitat is rarely fully successful and is almost always costly, especially in the case (of Singapore) where the habitats have been completely destroyed or are extremely degraded. More recently, the concept of reconciliation has been introduced as an alternative to restoration and habitat protection (Rosenzweig, 2003). Reconciliation seeks to modify anthropogenic structures and habitats to improve their capacity to support wild species, while still allowing them to serve their intended functions. It has the additional benefit of encouraging interactions between humans and the natural environment in an increasingly disconnected society, which can serve to improve public support for conservation as well as enhance personal well-being (Miller, 2005). There have been attempts at reconciliation in a variety of habitats. In China, cliff faces of abandoned quarries were drilled with holes to encourage the growth of native climbing plants (Wang et al., 2009), while in the United Kingdom, roof garden substrates have been altered to mimic nesting sites of the black redstart, *Phoenicurus ochruros* (Grant, 2006). Current efforts are underway to improve the ability of these gardens to recruit invertebrates of conservation concern (Grant, 2006). In Singapore, park connectors were created to improve biological connectivity between green areas (e.g. nature reserves, parks etc.) while serving as a recreational space for the general public (Sodhi et al., 1999).

Given that Singapore is an island-state with many artificial coastal structures (e.g. man-made beaches, jetties, seawalls, breakwaters), there are plenty of opportunities for reconciliation. The potential of these types of urban habitats have not gone unnoticed elsewhere. Seawalls in particular, have been extensively studied in temperate regions as surrogates for other hard substrate habitats such as rocky shores, and there have been various attempts to improve the species carrying capacity of these structures. Chapman and Underwood (2011) categorised the efforts into 'soft' and 'hard' approaches. The soft approach requires the removal or rearrangement of the wall, replacing it with natural habitats (e.g. marshes, sand dunes) or creating a hybrid environment, which combines natural vegetation with the walls. The hard approach, on the other hand, deals with physical manipulation of the wall, either by changing the slope angle or increasing its surface complexity, to improve its ability to recruit intertidal assemblages. These two strategies have different outcomes as the resulting habitats are often suited for a different assemblage of species. The soft approach favours soft-sediment infauna, while the hard approach is generally more relevant to hard-substrate benthic taxa.

In this thesis, I examine the potential for seawall reconciliation in Singapore, in particular, the capacity of these walls to act as surrogates for rocky shore species. Rocky shores used to be common along the southern coastline of Singapore stretching inshore from the intertidal coral reef flats, but have been reduced to a single 300 m stretch on the mainland (Todd and Chou, 2005). They are, however, still present on several of the Southern Islands, although most have been fragmented by seawalls and jetties. If rocky shore communities can recruit onto the seawalls, they may yet be conserved in the face of future coastal development. Chapter 1 provides an overview of coastal change in Singapore in the last two decades and a projection of future changes for the next 15 to 50 years, and documents the increasing pervasiveness of seawalls as a novel coastal habitat. Chapter 2 examines the communities currently existing on seawalls around the Southern Islands in Singapore, and compares them to those in adjacent natural rocky shores to assess their suitability as a rocky shore surrogates. To further elucidate and understand the findings of Chapter 2, trophic interactions of common species are investigated in Chapter 3 using stable isotopes.

Chapter 1: Coastal change in Singapore: Habitats lost and gained

1.1 Introduction

Coastal populations worldwide have been growing rapidly. In 2003, approximately three billion people lived within 200 km of the sea, and this number is set to double within the next 15 years (Creel, 2003). As these cities are predicted to expand, land reclamation is one of the few options available for satisfying demands for space. The rate of accompanying coastal armouring may also be accelerated by sea level rise and more frequent storms as a consequence of global climate change (Moschella et al., 2005). The resulting loss of natural shores and gain in artificial ones has profound implications on how marine species can be conserved in this urban setting. The extreme urban development in the island nation of Singapore serves as an highly illustrative case study of the ecological future that many coastal cities may eventually face, especially in still less developed but currently rapidly developing countries.

Singapore’s coastal landscape has been altered extensively since British colonial establishment in 1819. As it has grown into a Southeast Asian economic powerhouse, its coastline has been slowly shifting seawards via land reclamation to accommodate ports, industries, infrastructure, parks, and homes. Many opine that Singapore’s development has been at the expense of its natural habitats (Brook et al., 2003; Chou, 2006; Castelletta et al., 2008) and that the government’s priorities have been geared towards economic progress largely ignoring the need to maintain biodiversity and forgoing opportunities to integrate growth with ecological sustainability (Hilton and Manning, 1995). Widely-employed management tools, such as environmental impact assessments (EIAs) are inadequately developed and there is no legislation making them mandatory (Chun, 2007). Even when they are conducted, they are often restricted to the immediate stakeholders, and exclude public involvement (Chou, 2008). Singapore has only two marine protected areas, both of which are located on coastal areas of the mainland, with very little protection accorded to the variety of marine habitats situated around its offshore islands. What little legislation to safeguard marine biodiversity and habitats exists is limited and outdated, and lacks the applicability and scope to deal with contemporary environmental issues (Lye, 1991, Chun, 2007).

Hilton and Manning (1995) documented the historical coastal changes of Singapore up to 1993 and showed that coastal habitats had been systematically converted or destroyed, and their evaluation of the government's approach to sustainable development was candidly critical. From 1922 to 1993, areas of mangroves (75 km^2 reduced to 4.83 km^2), coral reefs (32.2 km^2 reduced to 17 km^2) and intertidal sand/mudflats (32.75 km^2 reduced to 8.04 km^2) shrank dramatically. During this time, the percentage of natural coastline dropped from 95.9% to 40%. However, the extensive coastal straightening that resulted from the multitude of land reclamation projects actually led to an overall decrease in coastline from 528.84 km in 1953 to 480.19 km in 1993. Hilton and Manning (1995) projected that, by 2030, land reclamation would eventually increase the coastline to 531.81 km. They ultimately concluded that the Singapore government's approach to managing resources was not in line with their stated commitments to protect biodiversity and achieve sustainable development.

It has been eighteen years since Hilton and Manning's (1995) paper was published and Singapore's physical, as well as social landscape has changed significantly during this time. The resident population has swelled by over 40%, to reach 3.8 million in 2012. Demand for land remains high, and reclaiming land from coastal areas remains one of Singapore's key strategies to alleviating this need. Land area has also increased by 14% to 714.3 km^2 (Singapore Department of Statistics, 2013). The length of Singapore's artificial coastlines has concomitantly increased, while natural shoreline has decreased. Reclamation is so extensive along the southern coast of Singapore, that the only remaining natural stretch is a 300 m wide rocky shore in Labrador Park (Todd and Chou, 2005). As the coastline becomes progressively altered, there is a need for paradigm shift in the way artificial habitats are perceived and designed. These habitats include armoured revetments built to protect the coast; and usually come in the form of seawalls, representing a variety of slopes, materials and designs, which have the potential to host substantial levels of biodiversity (Glasby and Connell, 1999). It is imperative that the current extent of natural and artificial shores, and how these habitats are likely to be impacted in the future, is known. Hence, this paper aims to quantify the transformations to Singapore's coastline over the past two decades and predict future changes based on the Singapore Government's 2008 Master Plan and 2011 Concept Plan.

1.2 Materials and methods

Estimates of mangrove, coral reef and intertidal sand/mud flats were obtained from the 2002 and 2011 1:50,000 topographic maps published by the Singapore Armed Forces Mapping Unit. The boundaries of each fragment of habitat were traced in ArcGis 10.0 (ESRI®, 2012) which was also used to calculate the area of each habitat. Hilton and Manning (1995) performed this using the squares method, although differences in estimation due to technique are not likely to be very large.

Areas of remaining mangroves marked in the topographic maps included remnant patches that once lined the estuaries of Sungei (=River) Poyan and S. Besar along the northern coastline, both of which have now been converted to freshwater reservoirs. These remnants are no longer connected to the marine environment, and were therefore not calculated within the total area of mangroves. On the other hand, some fragments not recorded in the topographic maps were included based on a contemporary publication by Yee et al. (2010) which documented the extent of mangroves in 2010. Accessible areas were ground-truthed by the first author to confirm their presence in 2013. Compared to Hilton and Manning (1995), these estimates of mangrove area are probably more accurate as (1) the ArcGIS mapping technique employed in this study is less likely to overestimate the area in complex configurations than the squares method; (2) the areas marked out in this study were based on ground-truthed data collected by the authors and Yee et al. (2010).

My estimates of the intertidal coral reef and sand/mudflat areas were based solely on the topographic maps. The categorisation of the reef flat areas and sand/mud flats can be challenging as the delineation between intertidal sands and reefs is not always clear, and there tends to be an overlap of the two habitats, particularly in the

Southern Islands. Parts of the intertidal areas around Pulau (=Island) Pawai, P. Senang and P. Semakau, previously labelled as ‘intertidal sands’ are marked as coral reefs in contemporary maps. The coral reef areas marked out on the topographic maps used here represent intertidal reef flats only. The sub-tidal reef slopes are excluded, but as these are steep and shallow, they represent a small area relative to the intertidal flat. Some underestimations are possible, but these would be consistent with Hilton and Manning’s (1995) past calculations, hence allowing for direct comparisons.

The present length of seawalls was determined based on satellite images from Google Earth™ mapping service (Google, 2009), data collected from ground-truthing, and observations from various researchers who have conducted studies around Singapore’s coasts. Seawalls were traced onto the 2011 topographic map using ArcGis 10.0 (ESRI®, 2012) and grouped into three categories: sloping and un-grouted, sloping and grouted, and vertical. Sloping walls generally have a slope between 14 to 35° (Lee et al., 2009b) and consist of granite rip rap that is often grouted with mortar to fill in the crevices between rocks. Vertical walls are typically made of cement and are usually found in port areas. Categorisation was based on the satellite images (the resolution was generally high enough to discern between sloping and vertical walls), personal observations, or inferred from the use of the area (e.g. walls in docks were assumed to be vertical).The total area covered by sloping seawalls was obtained by multiplying the total length by 10.54 m, i.e. the average width of seawalls calculated from seawall measurements provided by Lee et al. (2009). It was not possible to calculate the average width of vertical seawalls as these data are not published and the ports and docks where they are found have restricted access. The total length of the coastline around Singapore (combining both mainland

and offshore islands) was obtained by adding the non-armoured and natural lengths of the coastline, which were also digitised using ArcGis 10.0 (ESRI®, 2012).

The predicted conversion of coastal habitats over the next decade, including changes in mangrove, coral reef and sand/mudflat areas, as well as seawall length, were determined using the 2008 Singapore Urban Redevelopment Authority’s (URA) Master Plan and 2011 Concept Plan. The Master Plan is a statutory land use plan that directs development over the next 10 to 15 years while the longer-termed Concept Plan guides development over the next 40 to 50 years (URA, 2008). Natural habitats in areas slated for future development or reclamation were considered to be destroyed, and the new resultant coastlines were assumed to be protected with seawalls. Habitats not directly affected by the developments were presumed to remain the same size over the period.

1.3 Results

The area of intertidal reef flat and sand/mudflat have declined further since the last estimates of the natural coastal habitats in Singapore in 1993 (Hilton and Manning, 1995). Over the last two decades, continued development and land reclamation along the southern coastline and offshore islands of Singapore has led to the loss of many of these vital habitats. However, mangrove areas have increased due to the lack of development along the northern coast, coupled with active restoration efforts.

1.3.1 Mangrove forests

Estimates from the 2002 topographical map show that total mangrove area in Singapore had increased to 6.26 km^2 relative to the 4.87 km^2 recorded in 1993 (Hilton and Manning, 1995). Comparing the distributions of mangroves in Hilton and Manning's (1995) 1993 map (Fig.1.3.1), it is clear that the bulk of the increase has occurred at S. Buloh and P. Ubin. Mangroves in areas that remained undisturbed also expanded, such as on the military training islands of P. Pawai (0.26 km^2 in 1993 to 0.48 km^2 in 2002), P. Tekong (0.73 km^2 to 1.62 km^2) and P. Senang (0.15 km^2 to 0.17 km^2).

Based on the 2011 map the total area of mangroves increased further, albeit marginally, to 6.44 km^2. However, according to the 2008 Master Plan, more than 33% of this existing mangrove forest is at risk of being lost. The mangroves in S. Simpang and S. Khatib Bongsu (0.23 km^2), P. Seletar (0.12 km^2), P. Tekong (0.76 km^2) and S. Mandai (0.20 km^2) are all slated to be reclaimed, while future development on P. Ubin threatens another 0.82 km^2. If these losses are realised, Singapore will only retain 5.64% (4.23 km^2) of its original 75 km^2 mangrove area by the end of the 2030.

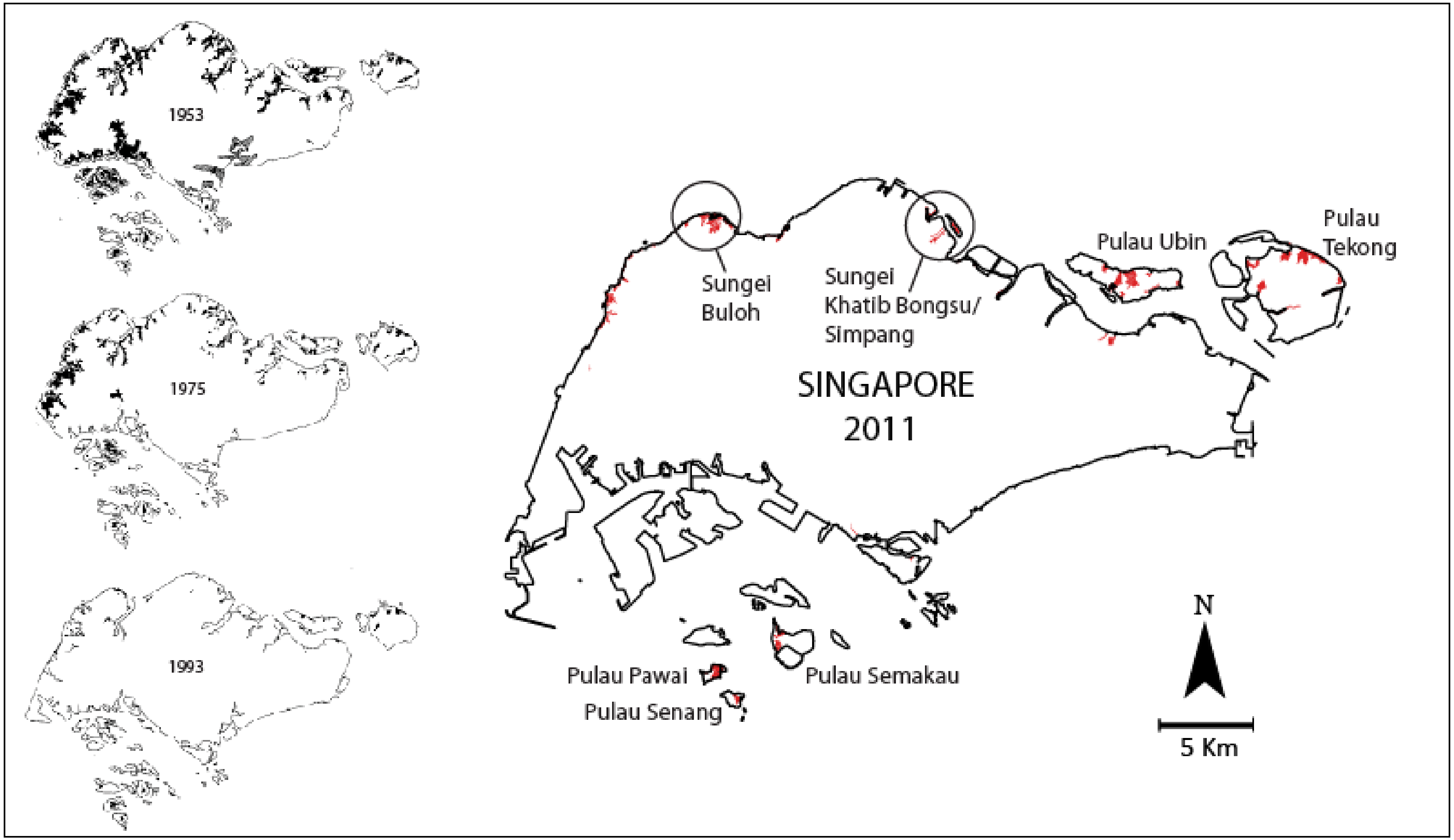

Fig. 1.3.1: Distribution of mangroves in 2011 (in red, from present study), 1993, 1975 and 1953 (from Hilton and Manning, 1995).

1.3.2 Intertidal reef flats

The period between 1993 and 2002 was marked by several large reclamation projects, by the end of which the area of intertidal coral reef habitat was just 10.13 km^2. The most prominent changes include: 1) the reclamation of the Ayer group of (ten) islands and their fringing reefs for the petrochemical industry; 2) the merging of island Buran Darat with Sentosa Island to create land for a marina and exclusive residences (Ramcharan, 2002); and 3) the construction of the bund around Semakau landfill (Chou et al., 2004), which covered the fringing reef on P. Sakeng, the eastern shore of P. Semakau and the patch reefs in between. The remaining reef along the coast of P. Semakau was protected during the reclamation process (Chou and Tun, 2007) and an extensive 1.23 km^2 of reef flat was still present in 2002.

A total of 9.51 km^2 of intertidal coral reef was present in 2011 as indicated on the map (Fig. 2). This decline (much smaller compared to the 1993 to 2002 period) was due to reclamation works to connect and extend P. Seringat and Lazarus Island, which resulted in the loss of the fringing reefs and two small patch reefs northwest of P. Seringat. In addition, the P. Bukom petrochemical complex was expanded to encompass the islands of P. Bukom Kechil, P. Ular and P. Busing.

Three patch reefs (Terumbu [=Patch reef] Pemalang Besar, T. Pemalang Kechil and T. Sechirit) currently present in the unused cell of P. Semakau, totalling 0.39 km^2, will eventually be covered as the landfill is filled up. Several other reefs are expected to be lost in the years to come. The small island of P. Tekukor and a patch reef east of it are slated for reclamation in the 2008 Master Plan. In the 2011 Concept Plan, two large areas around P. Bukom and P. Semakau (Fig. 1.3.2) are marked out for ‘possible reclamation’, which could result in the destruction of many of the large patch reefs such as T. Pempang Tengat (0.31 km^2) and T. Pempang Darat (0.28 km^2).

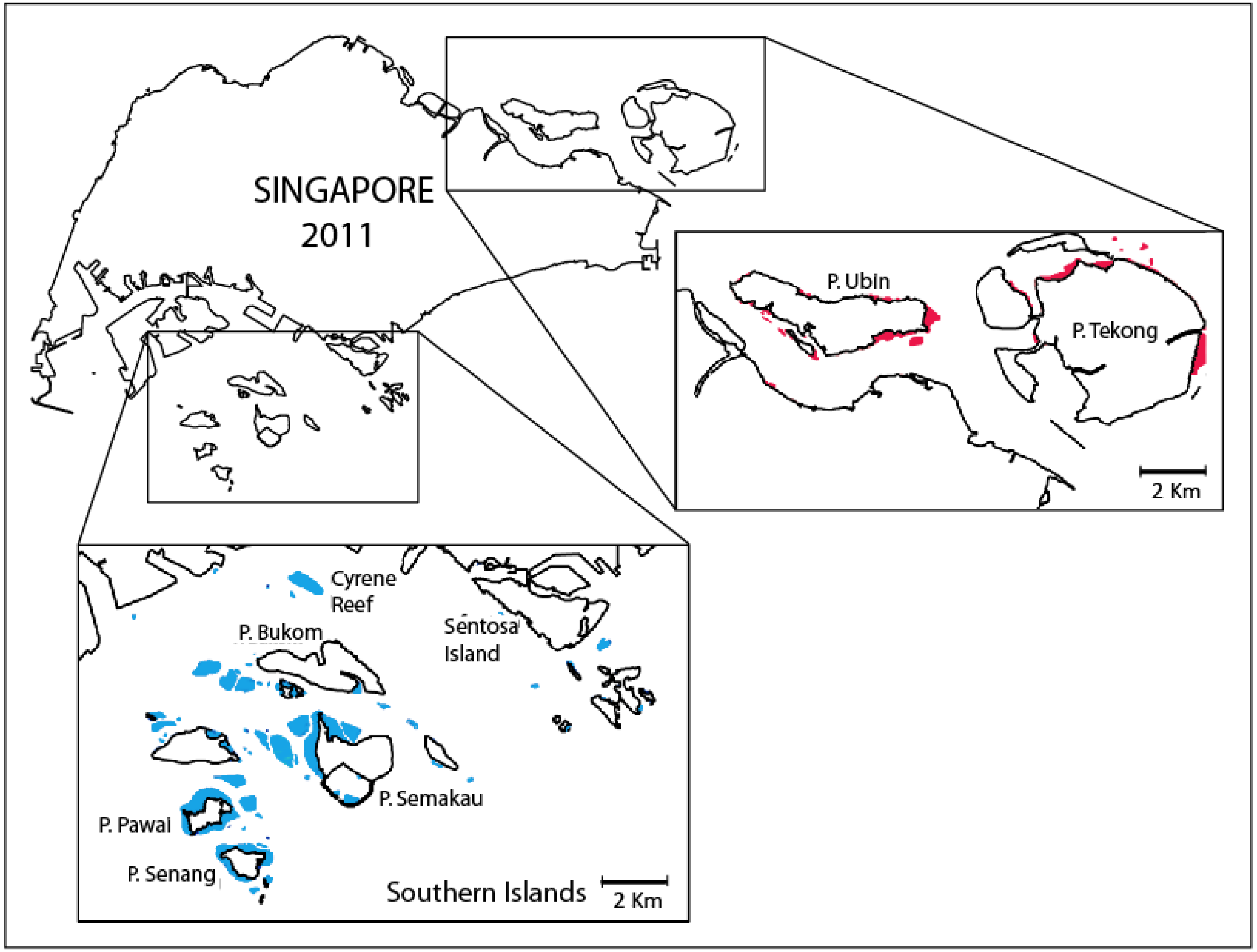

Fig. 1.3.2: Distribution of coral reefs in the Southern Islands (in blue) and sand/mudflats around P. Ubin and P. Tekong (in red) in 2011.

1.3.3 Sand and mudflats

In the decade between 1993 and 2002, there was little major development in the north, and the sand/mudflats there were relatively unaffected. By 2002, the total area of sand/ mudflats in Singapore had dropped only slightly to 7.63 km^2, due to small losses along the northern coast of P. Tekong (0.33 km^2) and the eastern coast of P. Ubin (0.21 km^2). However, by 2011, reclamation at P. Tekong encompassed the neighbouring islands of P. Tekong Kechil, P. Sajahat, P. Sajahat Kechil and their extensive sand and mudflats, after which a country-wide total of only 5.00 km^2 of sand/mudflats was left (Fig. 1.3.2).

Future estimates based on the Master Plan and Concept Plan show that the area of sand/mudflats may decline to 2.65 km^2 within the next 10 to 15 years. The bulk of the loss will come from the completion of the P. Tekong reclamation (which is currently underway) (1.28 km^2) and from the eastern coast of P. Ubin, where 1 km^2 of sand flats is liable to reclamation in the 2008 Masterplan.

1.3.4 Present coastline and seawall distribution

The length of the Singapore coast has increased significantly over the past two decades as a result of reclamation, following the trend predicted by Hilton and Manning (1995). Based on the 2011 map, the total length of coastline is 504.53 km (compared to 480.19 km in 1993), and this figure will continue to climb with the completion of the reclamation works in P. Tekong and Tuas industrial estate. Currently, the total length of seawalls is 319.23 km, constituting 63.3% of the coastline. Of these, 5.5% are sloping and grouted, 41.0% are sloping and un-grouted, 26.9% are vertical (26.6% could not be verified from satellite images and/or were not accessible for ground-truthing). The estimated total area of the sloping seawalls is

1.56 km^2 and 0.29 km^2. Unsurprisingly, the locations with the most seawalls are those that have undergone the most reclamation work, e.g. Tuas Industrial Estate (59.47 km), Jurong Island (46.51 km) and Changi (19.38 km) (Fig.1.3.3).

By 2030, it is expected that Singapore's coastline will exceed 600 km (Fig. 4), far surpassing Hilton and Manning's (1995) estimate of 531.81 km. The ratio of artificial to natural coastline will increase, with seawalls and created beaches constituting 82.9% (2011) to 85.8% (2030) of total coastline length. If all the land reclamation efforts proposed in the 2011 Concept Plan are carried out (including the "possible future reclamation" areas near P. Semakau and P. Bukom), an additional 125 km of seawalls can be expected to be constructed within the next fifty years (Fig.1.3.4).

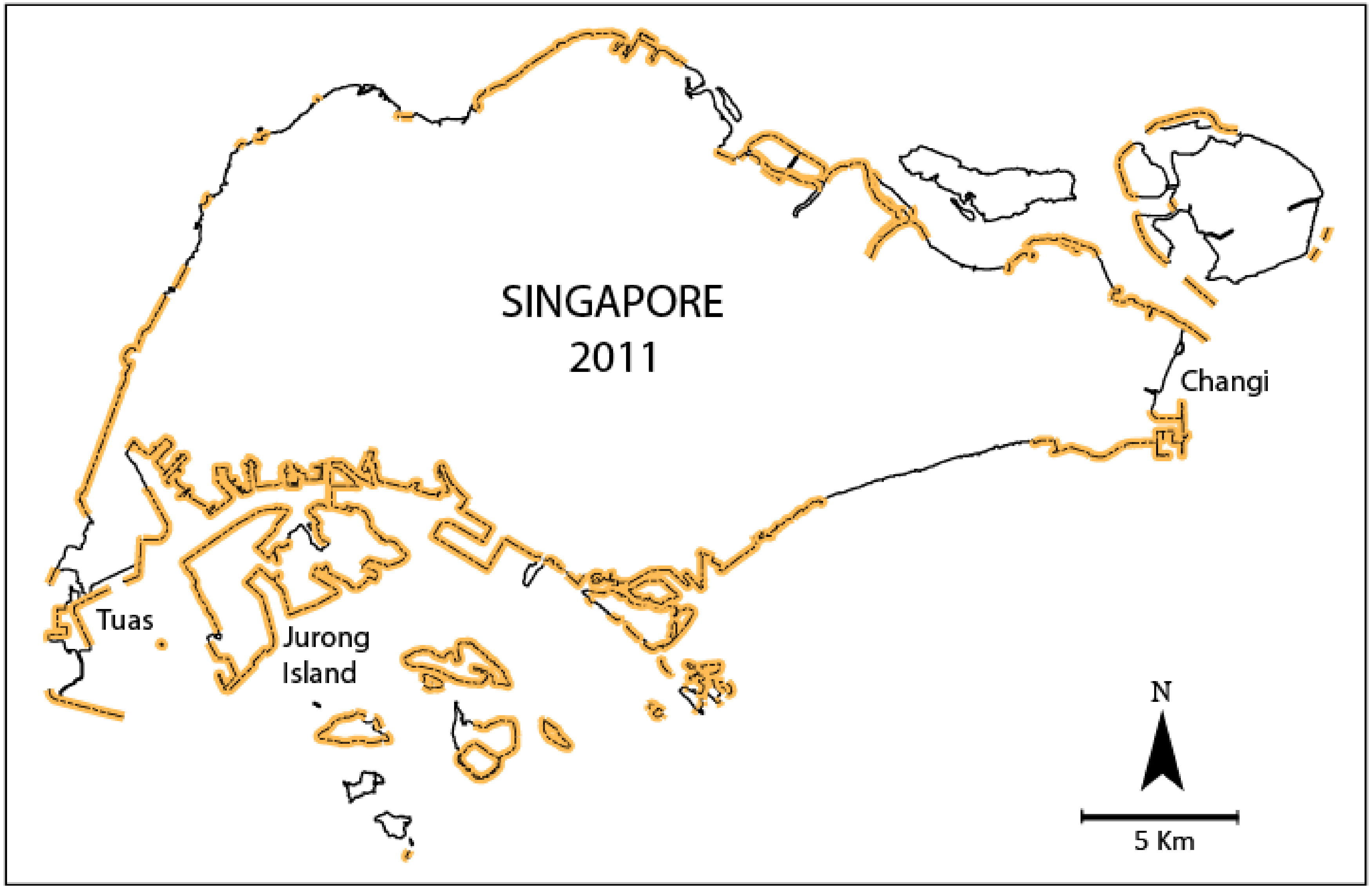

Fig. 1.3.3: Distribution of seawalls (in orange) in 2011.

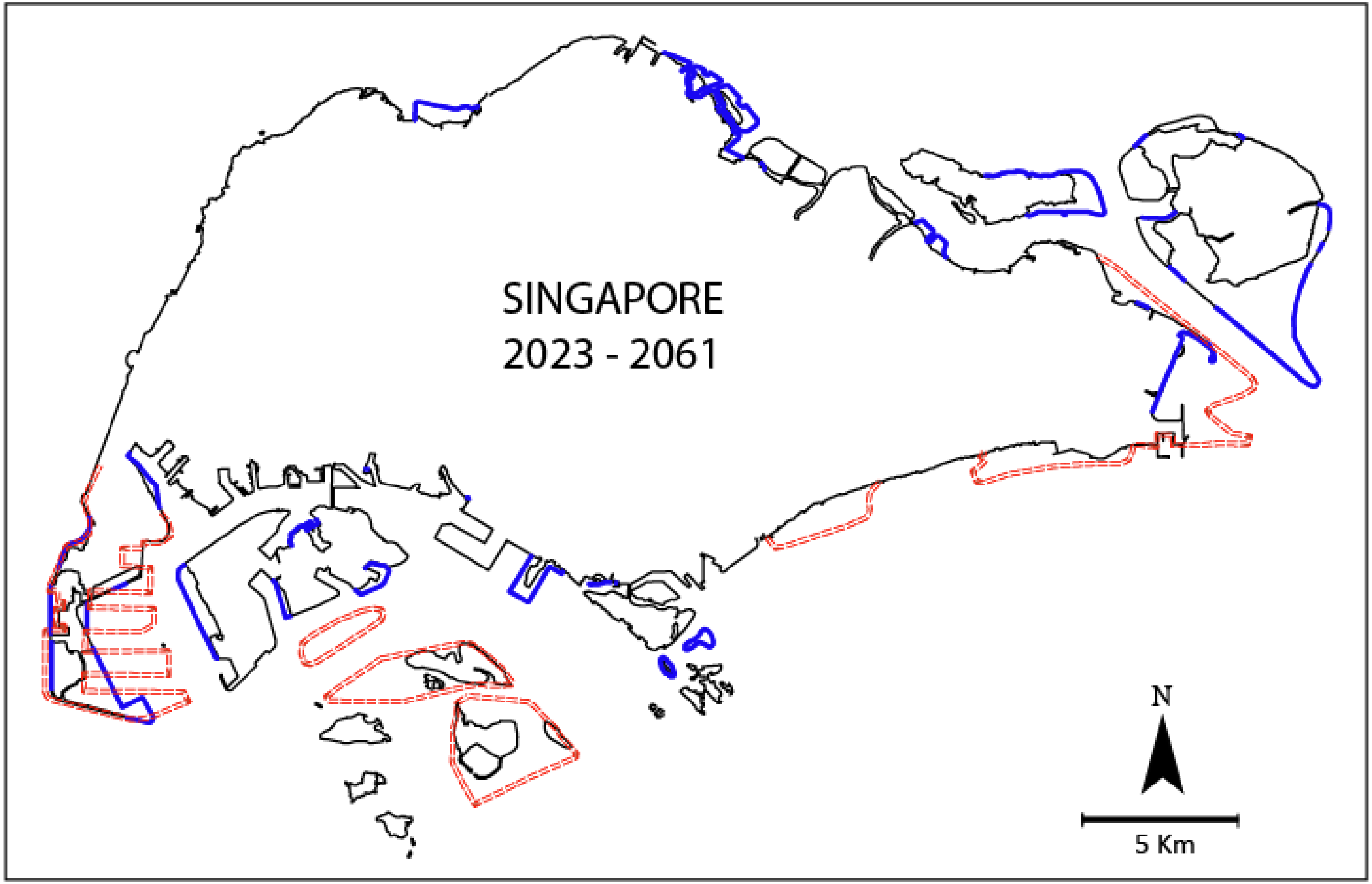

Fig. 1.3.4: Coastline changes proposed in the 2008 Master Plan (blue) and 2011 Concept Plan (red dotted line).

1.4 Discussion

Improved environmental protection and various reforestation programmes have contributed in part to the increase in mangrove forest area between 1993 and 2011. In 2002, 130 ha of mangrove and surrounding land in S. Buloh were gazetted as a Nature Reserve, upgrading it from its previous status of Nature Park (Yee et al., 2010). Reforestation efforts have also sped up regeneration in areas such as P. Ubin and Pasir Ris (Kaur, 2003; Yee et al., 2010). However, these forests are still at risk, as most of the existing remnants are either fragmented or polluted (Ng and Low, 1994; Bayen et al. 2005; Cuong et al., 2005). The S. Buloh mangrove, one of the largest remaining patches, is experiencing severe erosion, possibly due to the damming of S. Kranji (Bird et al., 2004). Turner et al. (1994) estimate that coastal habitats in Singapore, including mangroves, have lost almost 40% of plant species, particularly the rich diversity of epiphytic orchids typically found on old mangrove trees (Corlett, 1992).The fragmentation of many of the mangroves (e.g. Mandai mangrove from S. Buloh mangrove and Peninsula Malaysian mangroves) may interfere with propagule import and export, and lead to genetic isolation (Friess et al., 2012). This could be compounded by the lack of suitable pollinators due to disturbance from the nearby industrial area (Friess et al., 2012). The fauna that inhabit these remnant patches are also at threat. The restored mangroves in Pasir Ris were found to have as many as 71 different species of fish (Jaafar et al., 2004), while extensive collections in various northern mangrove yielded five species of alpheid shrimps, including two new species to science (Anker, 2003). In 2002, a new species of mangrove crab, *Haberma nanum* was discovered in Mandai mangrove. This species, which forms a new genus, is currently only found on the northern coast of Singapore (Ng and Schubart, 2002).

Further degradation could potentially lead to the loss of many local species, some of which are unique to Singapore.

The massive reduction in intertidal reef area due to reclamation projects has resulted in loss of coral diversity and abundance over the past two decades. For example two species of corals, *Stylophora pistillata* and *Seriatopora hystrix*, have not been sighted in recent years (Chou, 2006) and coral cover has declined at numerous sites, with as much as 72.6% lost at a reef off P. Hantu between 1986 and 2003 (Chou, 2006). In addition to the destruction of many large fringing reefs, several studies have indicated that the existing reefs and their associated fauna are in decline due to sedimentation and turbidity caused by on-going land reclamation and dredging operations (Chou et al., 2004; Dikou and van Woesik, 2006; Hoeksema and Koh, 2009). However, some recent mega-projects could have unexpected positive effects on local natural habitats and species. Studies on giant clam (Neo et al., 2013) and coral larval (Tay et al., 2012) dispersal established that larvae flow west-wards out of the Singapore Straits. However, the extension of Tuas (to the extreme southwest of mainland Singapore, see Fig. 3) could prevent the export of these larvae, and improve settlement rates around the Southern Islands.

Intertidal sand and mudflats are most common along the northern coast of mainland Singapore and the islands of P. Ubin and P. Tekong. Similar to the fate of mangroves and coral reefs, most of the original stretches have already been lost to land reclamation for industrial, residential and recreational purposes (Hilton and Manning, 1995). Information regarding the ecological impact of development on sand and mudflats is limited, although contemporary surveys have indicated that the communities in the remaining patches are persisting. For example, initial reports from the Comprehensive Marine Biodiversity Survey—a consolidated effort by a government agency, academia and volunteer groups to document Singapore’s marine biodiversity—revealed that diversity in the country’s mudflats is relatively high with 77 fish species, 62 snail species and 37 crab species recorded (National Parks Board NParks, 2012). Monitoring by local groups has also determined that seagrass meadows on sandflats have not declined within the past seven years (Yaakub et al., 2013).

The decline of natural marine habitats has persisted since Hilton and Manning’s (1995) assessment and this trend can be expected to continue with pending reclamation projects. The 2008 Master Plan, which identifies future developments over the next ten to fifteen years, is not dissimilar to the longer-termed 1991 Concept Plan reviewed by Hilton and Manning (1995), suggesting that few changes have been made to Singapore’s development strategies, with the Government prioritising economic progress above long-term environmentally sustainable development (Hilton and Manning, 1995). In 2013, Parliament endorsed the Population White Paper; a roadmap for Singapore’s future population policies to deal with the country’s ageing population and prevent economic stagnation. The White Paper proposes encouraging immigration to boost the workforce, and estimates that total population could reach 6.9 million by 2030—an increase of almost 30% from the current 5.31 million (Ministry of National Development [MND], 2013). The reclamation efforts marked out in the 50-year Concept and 30-year Master Plans are linked to the impending population boom. If the reclamation efforts proposed in the recent 2011 Concept Plan are fully realised (possibly by 2050), many more natural coastal areas and their associated biodiversity will be lost.

However, there are signs that the Singapore Government’s attitudes towards marine conservation have become more positive over the last two decades. During the formulation of the last two Concept Plans, focus groups consisting of members of the public and invited individuals, were consulted for the first time to involve citizens in the decision making process. Consequently, the Focus Groups Reports included several recommendations to conserve freshwater and marine habitats around Singapore (Urban Redevelopment Authority [URA], 2000; URA 2011). Public funding has also been allocated for research (Low, 2012) into applying ecological engineering in Singapore (Hong, 2012), as well as for detailed studies of a range of marine organisms such as hard corals (Huang et al., 2009) and sea anemones (Fautin et al., 2009). Efforts to repopulate iconic species, including giant clams, are currently underway (e.g. Neo and Todd, 2012). These efforts signal a growing top-down involvement in marine conservation, and could lead to improved protection of species and habitats in the future.

Additionally, many of the man-made coastal structures that have been gained over the decades of development can potentially serve as habitats for coastal species. Of these structures, the large majority of are seawalls, yet few studies have attempted to document the type assemblages that live on them. The limited research conducted has shown that that a variety of intertidal and sub-tidal communities occupy sloping seawalls around Singapore. An island-wide survey of twelve walls revealed 30 marine autotrophic taxa and 66 invertebrate taxa (Lee et al., 2009b), as well as several new records of algae (Lee et al., 2009a). In addition, coral assemblages were discovered on seawalls at a yacht club in Changi, with over 1,700 colonies from 37 genera recorded (Tan et al., 2012), while seawalls in the Southern Islands have been found to host coral communities with densities averaging 17 colonies per m^2 (Ng et al., 2012). These findings suggest that these ‘replacement habitats’ might harbour a rich biodiversity (albeit lower to those of natural shores) and could potentially serve as a refuge for species as their natural habitats are destroyed.

The communities that naturally recruit to seawalls are not enough to replace the biodiversity that have been lost. A more pro-active approach to improve the carrying capacity of these marine artificial structures for different species is required. The ‘reconciliation’ concept has been proposed as a means to conserve biodiversity in urban environments (Rosenzweig, 2003). It has wide applicability to different man-made habitats, both terrestrial and marine, but has been especially used to mitigate the impact of seawalls and other coastal defences (Rosenzweig, 2003; Lundholm and Richardson, 2010). There has been extensive research to incorporate knowledge about ecological processes with engineering principles to design and build seawalls capable of supporting a wide range of organisms while retaining their original function (Bergen, 2001). Most of the designs involve reducing the slope of the wall or increasing substrate complexity as a means of improving biodiversity (Chapman and Underwood, 2011). This is presently being tested by researchers in Singapore who, in an effort to enhance biodiversity, have experimented with cement tiles moulded with various patterns to increase the complexity of the seawall surfaces (Hong, 2012). Future advances in this field could help maintain coastal biodiversity in Singapore and other coastal cities in the face of dwindling natural habitats.

The fate for ecological conservation in Singapore is not yet sealed, and many factors many still come into play. The White Paper identifies the need for maintaining a Singaporean identity despite increased immigration, an essential component of which would be preserving the nation’s natural heritage (MND, 2013). Increasing public participation indicates a rise in environmental awareness, and could be a major force in shaping the social, as well as physical, landscape in the future. The larger arsenal of conservation tools, such as habitat reconciliation, restoration and creation, represent different approaches to protecting native biodiversity and all can be applied locally. However, with the Government's priorities largely unchanged since the 90's despite a greater awareness of the nature conservation, it is likely that conservation will only take place when it does not hamper with economic and social development. It is therefore crucial to demonstrate that these two concepts are not mutually exclusive, and that it is possible to achieve both with concerted effort. As Singapore becomes increasingly and inevitably urbanised, planners and managers should consider all options for conserving Singapore's coastal environment.

Chapter 2: Are seawalls good surrogates for rocky shores communities?

2.1 Introduction

The overwhelming extent of seawalls along Singapore's coastline described in Chapter 1 is fast becoming a worldwide phenomenon. With the rapid expansion and development of coastal cities, there has been a surge in the number and array of artificial structures that now dominate many urban shores (Moschella et al., 2005). Many of them, for example groynes, seawalls and breakwaters, serve protective functions, while others such as jetties and pontoons, have industrial or recreational purposes. These marine structures have been well studied and are known to host a large variety of organisms. Their assemblages can vary widely, with some substrates being dominated by fouling species (Qvarfordt et al., 2006; Bacchiocchi and Airoldi, 2003), and others supporting communities not unlike those found on natural shores (Bulleri et al., 2005). Alien and invasive species are also known to capitalise on the novel environment that artificial structures provide to outcompete native species that would otherwise be well-adapted to local habitats and conditions (Tyrell and Byers, 2007; Glasby et al., 2006).

To date, most studies have focused on the destructive nature of artificial coastal structures. The very existence of the structure indicates that the original habitat is likely to have been destroyed, leading to an inevitable obliteration of the associated community (Moschella et al., 2005). Even after construction, they can alter local hydrology, affecting larval (and hence gene) dispersion, sediment deposition and other ecosystem functions essential to maintaining the health of neighbouring natural shores, leading to a drastic change in community and a loss of species and genetic diversity (Fauvelot et al., 2009). A change in environmental conditions on the artificial structures can also favour the establishment of exotic species, facilitating their spread and competition with native species. This has been observed in the north Adriatic Sea, where biological invasion of green alga *Coidum fragile* spp. *tomentosoides* has been attributed to the construction of breakwaters (Bulleri and Airoldi, 2005).

In recent years, research foci are beginning to move beyond the negative impacts of artificial marine structures, instead focusing on assessing artificial habitats as surrogates for natural ones (Connell, 2000; Davis et al. 2002; Chapman and Bulleri 2003; Bulleri and Chapman 2004). Some wild species are able to naturally exploit and colonise urbanised areas, but these generally form a small proportion of the overall biodiversity (McKinney, 2008). Studying the species that have already recruited to artificial habitats allows for a better understanding of the organismal traits and environmental conditions that promote their survival. These traits can help researchers assess how well these artificial habitats serve as natural analogues, and improve the attempts to reconcile them with the natural habitats they have replaced (Lundholm and Richardson, 2010). Reconciliation represents the middle ground, i.e. (re)designing anthropogenic habitats so that they can harbour a wide variety of species, while retaining their original function (Rosenzweig, 2003). There is evidence that artificial substrates can recruit communities similar to those in natural habitats, for example, Connell and Glasby (1999) found that epibiotic assemblages on natural sandstone reefs were not significantly different to those on sandstone retaining walls, while Bulleri et al. (2005) reported that seawalls and rocky shores in Sydney Harbour, Australia, supported a similar suite of species. The majority of studies, however, find that artificial structures are poor surrogates of natural habitats, often having less species diversity (Moschella et al., 2005), lower abundances (Connell, 2001), or different assemblages entirely (Bulleri and Chapman, 2010; Megina et al, 2012).

The similarity of the distribution and abundance of species on natural and anthropogenic substrates is dependent on the basis of the comparison (e.g. choice of natural habitat and artificial structure to compare), as well as physical and biological factors over a range of spatial and temporal scales (Airoldi et al., 2005). Physical factors such as the effects of hydrodynamics, microhabitat heterogeneity or building material can determine the nature of the community that develops (Connell and Glasby, 1999; Airoldi et al., 2005), and biological factors, such as the interactions among species, larval supply, and food or nutrient availability can also be influential. These factors are rarely exclusive and can often interact both synergistically and antagonistically. This contextual dependence of community establishment makes it difficult to make generalised claims about the suitability of all artificial substrates as surrogates for natural habitats. It is therefore vital that the comparisons made between the natural and artificial habitat are specific, ecologically relevant, and reflect the local situation. To determine whether seawalls in Singapore host similar assemblages to natural habitats, the comparison first needs to be set in context. Most seawalls in Singapore are made of sloping granite riprap that extends through the intertidal zone (see Chapter 1). The natural habitat that most closely resembles this environment is likely to be the rocky shore, which is also a hard-substrate intertidal habitat.

Rocky shores in Singapore, which are commonly found on the southern coastline and islands, have declined precipitously since the 1960s, with large tracts lost to land reclamation efforts in the industrial boom. The last remaining fragment on the mainland, Labrador beach, stretches merely 300 metres long (Huang, 2006b) and is part of a protected nature reserve. Research into of the communities on rocky shores and seawalls in Singapore is limited. The earliest published study was of the zonation of flora and fauna on the rocky shores of P. Satumu (12 km south of

Singapore) (Denison and Enoch, 1954), while later community surveys were conducted at Tanjong Teritip (Lee, 1966) and Labrador beach (Todd and Chou, 2005; Huang et al., 2006a; Huang et al., 2006b). Seawalls were only more recently surveyed, albeit more comprehensively. Intertidal assemblages on seawalls all over the mainland and southern islands were documented and compared (Lee et al., 2009b; Lee and Sin, 2009), and several new records of marine algae discovered (Lee et al., 2009a). However, no study to date has directly compared the assemblages on natural rocky shores with those on man-made seawalls in Singapore. Even though comparative studies between these two habitats have been conducted in temperate regions like Sydney (Chapman and Bulleri, 2003; Bulleri et al., 2005), California (Pister, 2009), and Italy (Bulleri and Chapman, 2004), research in the tropics has been absent. These temperate studies have generally found frequent community differences in the high- and mid-shore, with fewer differences at the low-shore (Chapman and Bulleri, 2003). Differences were commonly attributed to wave energy or the presence of micro-habitats such as pits, crevices and pools. Pister (2009) found that the three variables identified that best explained species distribution were related to the wave forces experienced by the habitat: wave height, surf zone width and steepness of the shore. Seawalls tend to have higher average incident wave energy, leading to a lower diversity in mobile species. The lack of complexity and heterogeneity of micro-habitats on seawalls also resulted in less small-scale variability in seawalls than rocky shores (Chapman and Bulleri, 2003; Bulleri and Chapman, 2004).

Most of the past research did not compare rocky shores and seawalls from the same area of coast, and each habitat was exposed to different environmental conditions. In my study, I surveyed the communities of natural rocky shores and of adjacent granite rip-rap seawalls, minimising the variation of large-scale physical factors (e.g. wave energy) and biological factors (e.g. larval supply). To evaluate the capacity of seawalls to serve as surrogate habitats of rocky shores, the community composition, species richness and diversity of the two habitats were compared. In addition, the species driving the differences between the artificial and natural shores were identified. Communities were also analysed across sites and over time, while physical parameters such as rugosity, temperature, and slope angle were measured to see if they differed between habitats as well. These comparisons helped to elucidate key distributional and ecological differences between the natural and artificial habitats that are essential to advancing future seawall reconciliation efforts.

2.2 Materials and methods

2.2.1 Study sites

Surveys were conducted at four sites on three islands south of mainland Singapore – P. Tekukor (1°13’50”N 103°50’15”E), Sentosa Island (1°14’55”N 103°49’53”E), St. John’s Island 1 (1°13′11″N 103°50′52″E) and St. John’s Island 2 (1°12′58″N 103°50′55″E) (Fig. 2.1.1). Each site was selected such that rocky shore and seawall habitats were within close proximity of each other (<200 m apart), so that abiotic differences due to location were minimised. At each site, permanent belt transects parallel to shore were marked out at both habitats so that the same area could be sampled every month. The start points were marked simultaneously at all the different sites to ensure that they were at the same tidal heights across all the sites. These permanent start points were used to mark out the belt transects which demarcated the areas surveyed each month. The lengths of the belt transects were either 50 or 80 m, and the width was from mean water level (defined as 1.8 m above chart datum) to chart datum. The average shore angle was obtained from eight points along the transect at both the low- and mid-shore to derive the actual width of the transect available for sampling based on the aforementioned tidal heights (see Fig. 2.1.2 in Appendix) Transect width, length and shore angle of both seawalls and rocky shores are presented in Table 2.2.1.

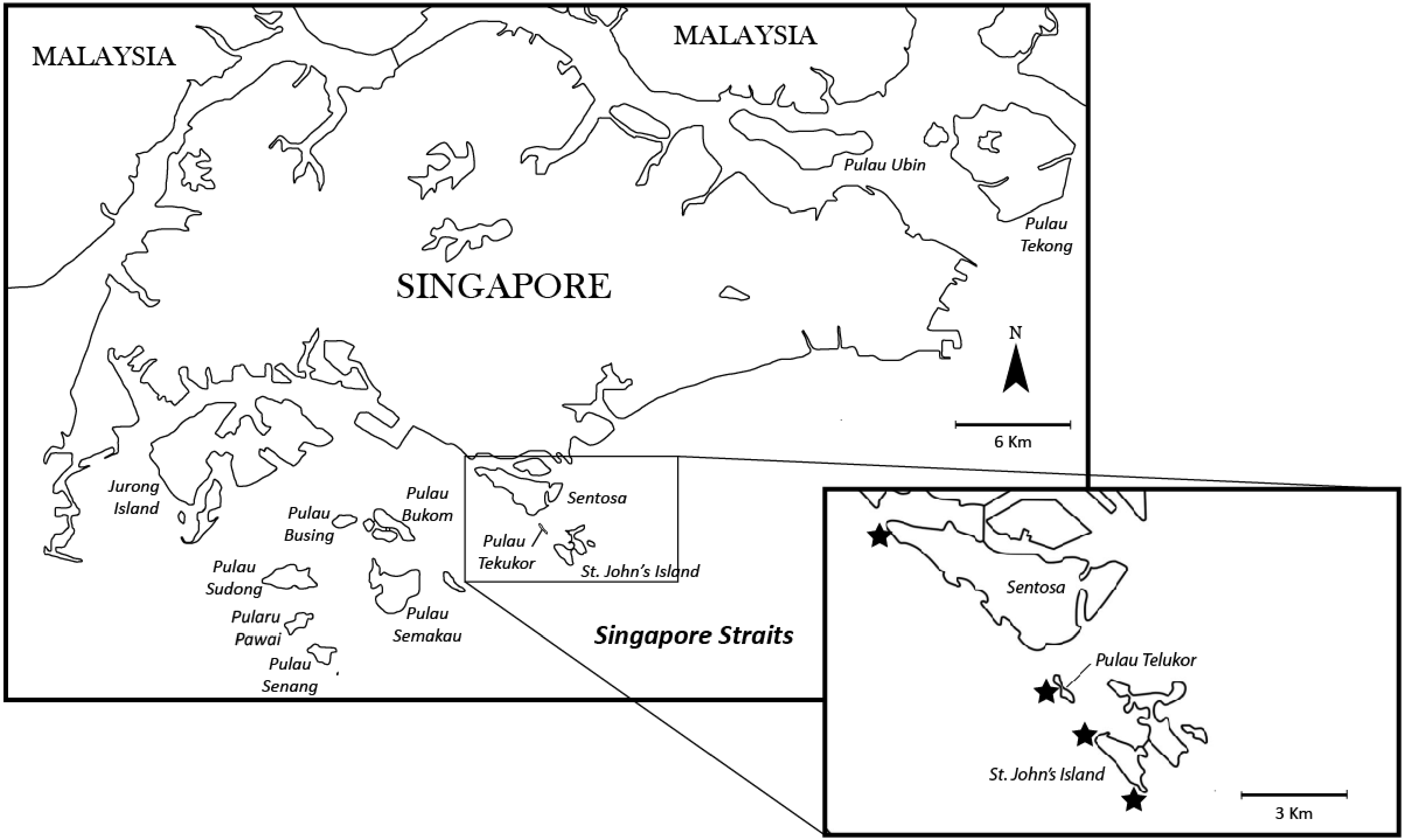

Fig. 2.2.1: Map of Singapore with study sites marked with ★

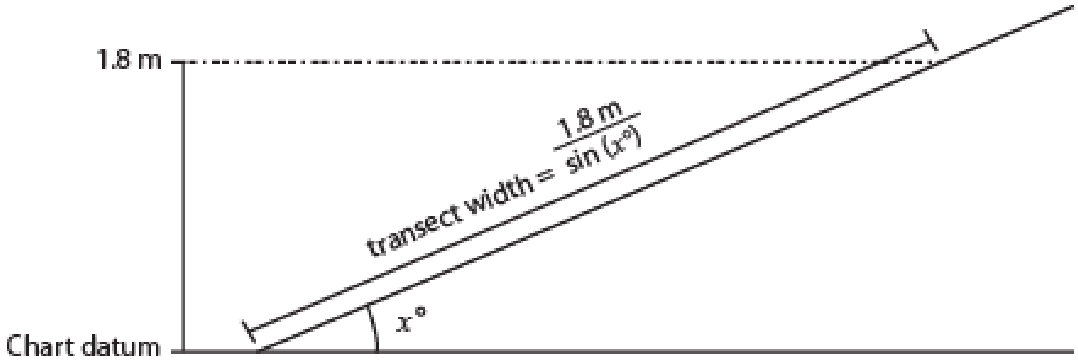

Fig. 2.2.2: Calculation of transect width based on average shore angle (*x*°).

Table 2.2.1: Transect width, length and shore angle of both seawalls and rocky shores at each site.

	Rocky shore			**Seawall**		
Site	Transect length (m)	Transect width (m)	Average slope±SD (°)	Transect length (m)	Transect width (m)	Average slope±SD (°)
St. Johns Island 1	50	9.6	10.7±3.9	50	4.5	23.7±6.0
St. Johns Island 2	50	9.6	10.8±5.1	50	3.9	27.8±8.6
Pulau Tekukor	80	9.7	10.7±2.9	80	6.2	17.3±4.2
Sentosa	80	12.6	8.2±1.3	80	4.2	25.5±3.2

2.2.2 Survey technique

The surveys were conducted monthly during low spring tides over a period of one year (from November 2011 to October 2012). Each month, six 50 × 50 cm^2 quadrats were placed randomly within the belt transects, using coordinates generated from a random number generator. Photographs of each quadrat were taken with a Canon PowerShot G10 and were later analysed for percentage cover of 1) common algae functional groups (e.g. turf algae, *Sargasuum* sp., *Padina* sp., *Amphiroa* sp., *Lobophora* sp. and other macroalgae), 2) sand, and 3) rock. Percentage cover of these variables was estimated using thirty randomly assigned points in Coral Point Count with Excel extensions (Kohler and Gill, 2006). The quadrats were then vacuumed with a modified Makita petrol-powered vacuum/blower (BHXV2500) for one minute (crevices found within the quadrat area were sampled, as were the undersides of any movable rocks), following which, any other organisms (e.g. gastropods, algae etc.) were collected by hand for two minutes or till exhaustion (whichever occurred first). All specimens were separated from the sand after collection, and were frozen in a -20 °C freezer until they were sorted, identified and quantified. Most organisms were sorted to genus or species levels, while unidentified specimens were sorted to morphospecies. It is assumed that the collection from one month does to affect the collections of other months due to the small size of the sampled area relative to the shore, and the random placement of the quadrats each month.

2.2.3 Measurement of physical parameters

Temperature, light and rugosity were measured at both habitats at all four sites to investigate the potential effects of the physical environment on the communities. Temperature and light were measured using data loggers (HOBO Pendant® UA-002-64), four of which were attached to the substrate at both habitats at all sites for one month. All loggers were fixed directly to the substrate to record surface temperatures. Daily maximum, minimum and average temperatures were compared across sites and between habitats.

Rugosity, commonly referred to as topographic complexity, can strongly influence the structure of benthic communities (Wilding et al, 2007). Measurements of rugosity were based on an estimation of scale-dependent perceived distance (Frost et al., 2005). Perceived distance techniques can be tailored to varying scales (in this case, tens of metres), and allow for comparison among different habitat types. It is expressed as the ratio between perceived distance (affected by the topography of the substrate) and linear distance (a pre-determined straight-line distance). The linear distances were four randomly chosen 10 m stretches (start point coordinates determined by a random number generator) along both rocky shore and seawall, and the perceived distances were measured using a distance wheel (10.16 cm diameter).

2.2.4 Statistical analyses

The faunal counts and alga percentage cover data were averaged across the six rocky shore and seawall quadrats of each site, resulting in centroids that represented the assemblage for each habitat per site every month. The experimental design therefore consisted of three factors: site (four levels, fixed), habitat (two levels, fixed) and month (twelve levels, random) (n=6). Non-parametric analyses were used for this multivariate dataset due to the large number of zeros and skewed distribution of many species. The data were first standardised across the variables to account for the different measurement scales (i.e. counts for fauna and percentage cover for algae) (Clarke and Gorley, 2006), and dispersion weighted to down-weight organisms that had clumpy distributions (which might mask the distribution patterns of other species) (Anderson et al., 2006). A resemblance matrix of similarities between each pair of centroids was calculated using the Bray-Curtis index of similarity, and a non-parametric multivariate analysis of variance (NPMANOVA) was used to test for differences between habitats and among sites. P-values were based on 999 permutations. Student-Newman-Keuls tests were used for pairwise comparisons among sites when interactions between the factors were significant.

A principal coordinate analysis (PCO) was used to visualise the differences between the communities found in each month, site and habitat. Species that had a Pearson's correlation with the PCO axes of >0.5, and therefore more had a more dominant influence on the differences, were identified. Similarity percentage (SIMPER) was also used to identify the percentage contribution that each species made to the measures of dissimilarity within and among habitats (Clarke, 1993) to elucidate the species driving the community differences. A constrained ordination using canonical analysis of principal components (CAP) was also performed to help visualise the separation among the four sites.

Species richness and Shannon-Weiner diversity of fauna and species richness of algae were calculated for each site and habitat. Species richness was compared with a two-way ANOVA using GMAV5. To elucidate changes in the number of species with increasing shore height, average algal and faunal species richness in both seawalls and rocky shores were plotted over ranges of heights and the relationship between the means were determined with a Spearman's rank correlation coefficient. To establish if the physical variables had an effect on structuring the communities, temperature, rugosity and slope were compared between sites and habitats using a two-way ANOVA, and were also overlaid on a PCO plot of the community data (averaged across months).

2.3 Results

A total of 267 species/morphospecies were identified, with algae (137), crustaceans (38) and molluscs (93) being the dominant groups. A total of 223 morphospecies were found on rocky shores, and 175 were found on seawalls. There were no distinct patterns in faunal species richness or algal species richness across the year in either habitat (Fig. 2.3.1). Sentosa had the greatest species richness of algae and fauna, with an average of 4.58 faunal and 8.04 algal morphospecies collected in each quadrat. P.Tekukor had the lowest species richness, with an average of 3.23 faunal and 4.97 algal morphospecies collected in each quadrat.

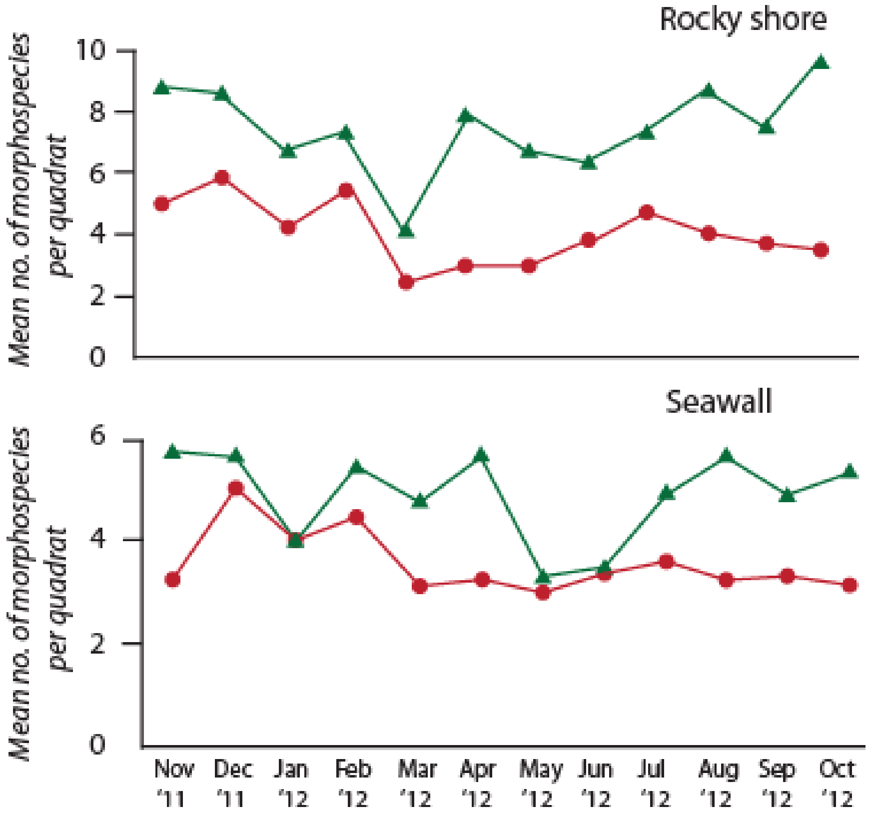

Fig. 2.3.1: Average algal species richness (green) and faunal species richness (red) over the year on rocky shores and seawalls.

The PERMANOVA showed that communities were different among sites (p(perm)<0.001), between habitats (p(perm)<0.005) and across months (p(perm)<0.001)with a significant interaction between all factors (p(perm)<0.001), aside from Habitat × Month. Pair-wise comparisons between rocky shores and seawalls across all months and sites were performed to identify the source of the interactions (Table 2.3.1).

Table 2.3.1: Pair-wise comparisons between rocky shore and seawall communities for each site over all months. * - significance<0.05, ** - significance<0.01, *** - significance≤0.001

Month	P. Tekukor	St. John's 1	St. John's 2	Sentosa
1	0.034*	0.265	0.003**	0.002**
2	0.057	0.049*	0.01*	0.041*
3	0.001***	0.021*	0.111	0.04*
4	0.008**	0.334	0.004**	0.006**
5	0.221	0.016*	0.005**	0.004**
6	0.077	0.018*	0.445	0.209
7	0.177	0.409	0.042*	0.01*
8	0.258	0.564	0.154	0.004**
9	0.043*	0.39	0.015*	0.036*
10	0.001***	0.086	0.108	0.031*
11	0.001***	0.893	0.005**	0.004**
12	0.006**	0.548	0.004**	0.26
Habitat × Site	**0.001****	**0.023***	**0.002****	**0.002***

Pair-wise comparisons also showed that communities between habitats were significantly different for all sites (Table 2.3.1), with the similarity index between habitats the lowest at St. John's 2 (12.16), followed by P. Tekukor (14.63), Sentosa (15.48), and St. John's 1 (17.24).

When the quadrats of each month were averaged, and plotted on a PCO plot, the differences in communities is between the habitats was clear (Fig. 2.3.2), even though the first two PCO axes only explained 11.1% and 7.4% of the variability in the dissimilarity matrix. Three variables had a Pearson's correlation of > 0.5 with the PCO axes: namely 1) turf algae, 2) the carnivorous drill *Cronia magariticola,* and 3) the detritovore *Ligia exotica.* From the SIMPER analysis, turf algae and *C.*

magariticola collectively contributed almost 8.6% of the habitat differences, while *L. exotica* contributed 6.3%. Other species that contributed to the dissimilarities included gastropod grazer *Monodonta labio* (3.65%) and amphipods (3.4%). The PCO plots also showed that there was some overlap between the communities of both habitats. Of the 267 morphospecies examined, 44 were found exclusively on seawalls, while 92 exclusively on rocky shores. However, these were generally rare species. Only eight morphospecies from the rocky shores—one algae (Phaeophyceae), one hermit crab, four molluscs (*Echinolittorina malaccana*, *Modiolus* sp., *Nodilittorina trochoides, Planaxis sulcatus*) and one anemone morphospecies (*Anthopleura* sp.)—had more than 10 individuals collected throughout the year-long survey. On seawalls, there was only one such species, barnacle *Euraphia* sp., which was found higher up the shoreline, and was only sampled once at St. John’s 2 (but in large quantities due to its clumpy distribution).

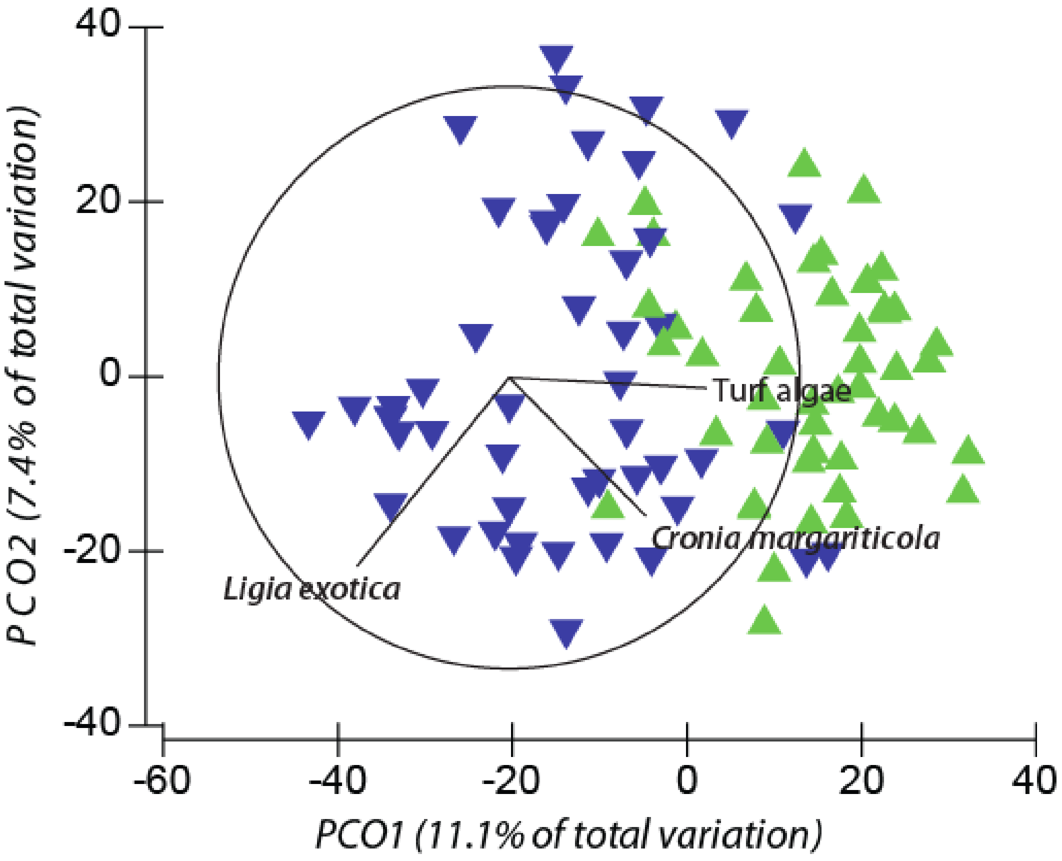

Fig. 2.3.2: PCO plot of the community in each habitat, of each site every month, overlaid with correlated variables of r >0.5 – turf algae, *Cronia margariticola* and *Ligia exotica*. Blue – seawall; green – rocky shore

Differences between sites were less apparent. Despite PERMONOVA showing a significant difference between communities among sites, these were not reflected by a clear separation in the PCO plot. However, the constrained ordination of the CAP plot (due to limited computing power, quadrats within each month were averaged to reduce the number of samples) revealed that Sentosa, St. John’s 2 and P. Tekukor has relatively distinct communities, while the communities on St. John’s 1 was more similar P. Tekukor than the other two sites (Fig. 2.3.3).

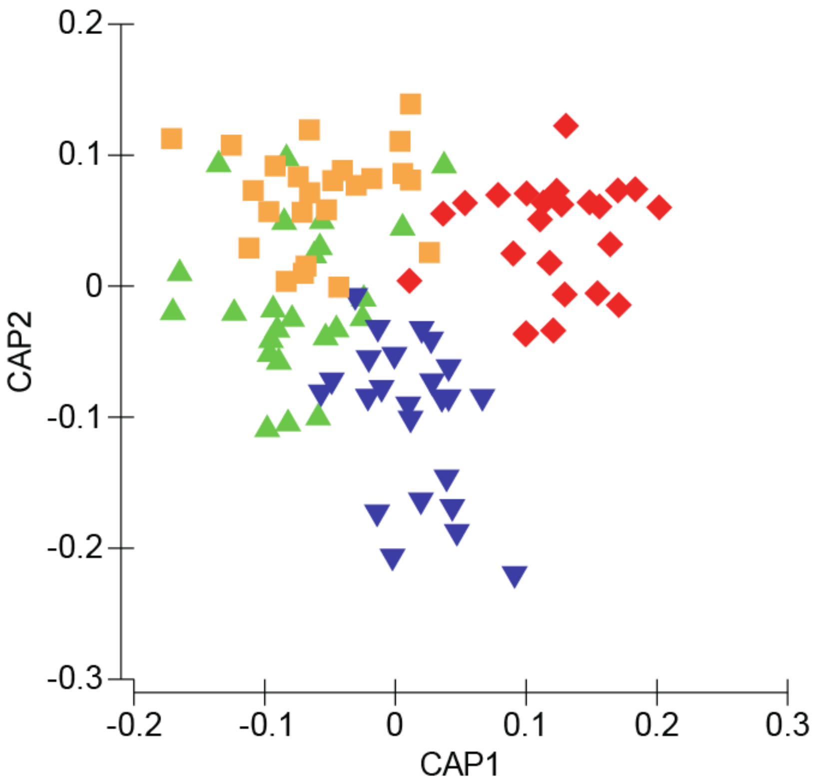

Fig. 2.3.3: CAP plot of the community in each habitat, of each site every month. Orange squares – St. John's 1; blue triangles – St. John's 2; green triangles – P. Tekukor; red squares – Sentosa.

Faunal species richness was significantly lower across all seawalls ($p<0.001$), with rocky shores having an average of 4.13 (SE±0.12) species per quadrat, as opposed to 3.57 (SE±0.11) on seawalls. Faunal Shannon-Weiner diversity was also consistently lower in seawalls, aside from St. John's 1, where seawall diversity was actually higher, despite having a fewer number of species. Algal species richness was also significantly different between habitats ($p<0.001$), with an average of 7.46 (SE±0.21) species per quadrat on rocky shores and 4.91 (SE±0.19) species on seawalls. When the number of species was averaged over a range of shore heights (at 0.2 m intervals), rocky shores showed a negative correlation for both algal ($r= -0.95$, $p<0.01$) and faunal species richness ($r= -0.77$, $p<0.05$)(Fig. 2.3.4). A similar trend was observed on seawalls, with a negative correlation for algal ($r= -0.89$, $p<0.01$) and faunal species richness (r= -0.77, p<0.05). Both algal and species richness decreased sharply between 0.6 to 0.8 m (Fig. 2.3.4).

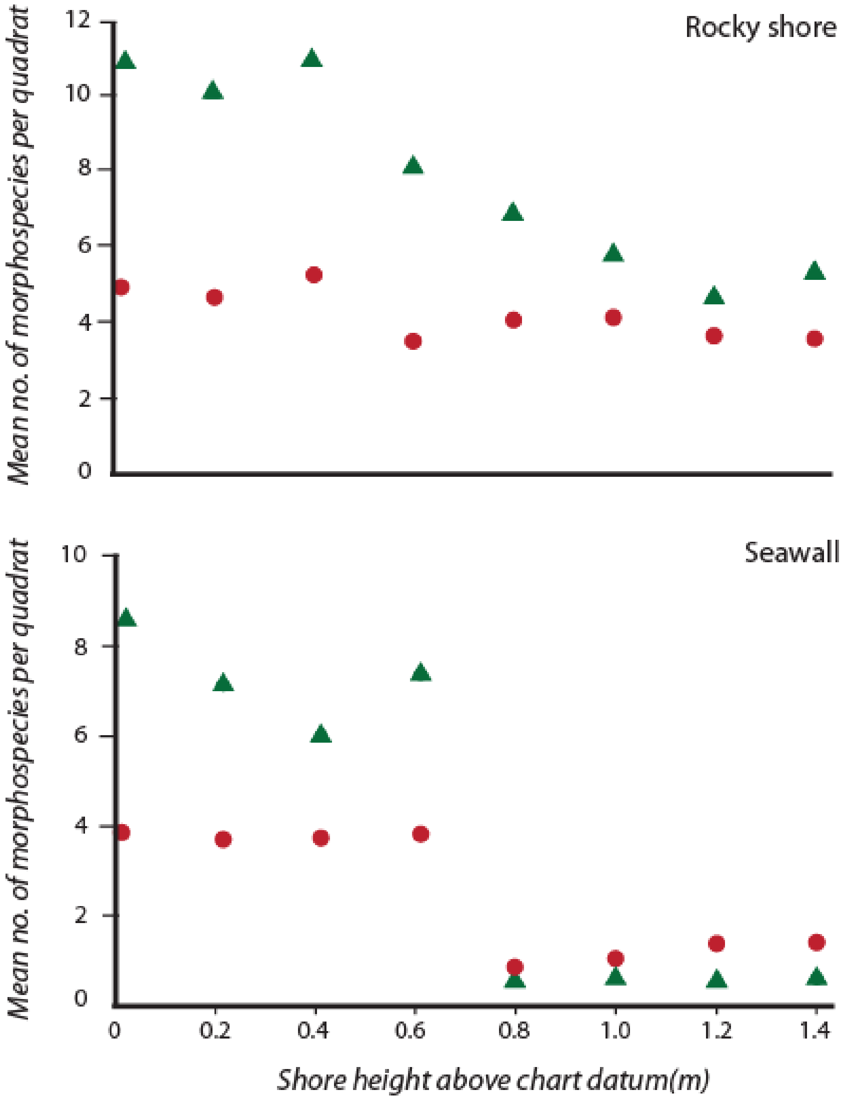

Fig. 2.3.4: Correlation between average algal species richness (green) and faunal species richness (red) with shore height chart datum in both rocky shores and seawalls.

Maximum and average daily temperatures were not significantly different between the two habitats, but both rugosity (p<0.01) and slope angle (p<0.001) were significantly higher on seawalls. The average rugosity ratio was highest on the seawalls of St. John's 2 (1.45) compared to P. Tekukor (1.14), St. John's 1 (1.09) and

Sentosa (1.09). When rugosity and angle were correlated to the PCO axes of the community data (averaged over habitats and sites), the r-values were >0.5, suggesting that these variables are important drivers of seawall community structure (Fig. 2.3.5).

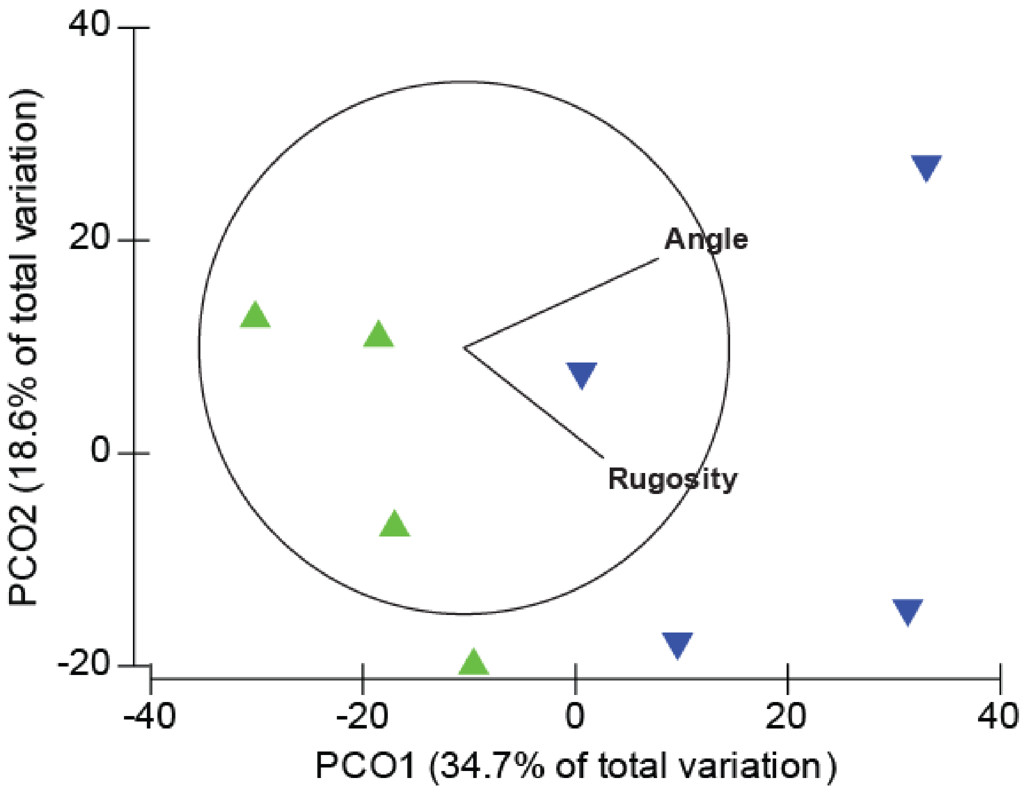

Fig. 2.3.5: PCO plot of the community in each habitat of each site, with overlaid of correlated variables of r > 0.5 – slope angle and rugosity. Blue – seawall; green – rocky shore.

2.4 Discussion

This aim of this study was to evaluate whether seawalls in Singapore currently serve as good surrogate habitats for rocky shore communities. The results indicate that this is not the case. The species driving the differences between habitats, as well as the tight coupling of algal and faunal species richness observed, suggest that seawalls might be too productivity-limited to support complex trophic interactions and consequently, a high diversity. While this does not unilaterally prove that low faunal richness is *caused* by low primary productivity, further investigations into the food web and trophic interactions should shed some light on this matter (see Chapter 3). Despite this, there was considerable overlap in the species present in both types of habitats, indicating that seawalls are potentially capable of sustaining the similar assemblage to rocky shores. Communities among the four sites (P. Tekukor, Sentosa, St. John’s 1 and St. John’s 2) and over the twelve months also differed significantly, although no distinct spatial or temporal patterns were apparent.

Communities surveyed were significantly different among sites, between habitats, and across months. There were also significant interactions among the three factors (habitat, site and month) and pair-wise comparisons were required to elucidate the underlying patterns. When these comparisons were examined, there was no temporal pattern in seawall-rocky shore differences across the sites, suggesting a lack of the distinct seasonal shifts in intertidal communities often observed on temperate and sub-tropical shores (Underwood, 1981; Williams, 1993). This was further supported by the lack of apparent temporal patterns in algal or faunal species richness in either habitat, which is not uncommon in equatorial areas where there is little seasonality. Visualising the communities among the sites on the constrained CAP plot revealed St. John’s 1 and P. Tekukor had more similar assemblages, while those on

Sentosa and St. John’s 2 were more distinct. Despite these differences, the PCO plot showed a large amount of overlap between communities of different sites, indicating that they shared many of the same species. Given that all four sites were found within the Singapore Strait, with the largest distance between sites being slightly over 7 km, the patterns observed are not unexpected.

There was also overlap between the species found in the natural rocky shores and artificial seawalls, despite the communities being significantly different. This has been previously observed (Chapman and Bulleri, 2003; Pister, 2009), and is likely an artefact of similar hard substrate intertidal environments. Several species were identified as contributing the most towards the dissimilarities between communities — with the rocky shores being characterised by having more of turf algae and a secondary consumer (*C. magariticola)*, and the seawalls typified by the presence of the detritivore *L. exotica*. Additionally, algal and faunal species richness was significantly lower on seawalls than on rocky shores. Together these results suggest the seawalls currently do not serve as surrogates for rocky shores.

The community structure observed is inherently linked to the environmental conditions it is subjected to. As mentioned before, previous studies comparing assemblages on artificial substrates and natural shores have attributed many of the differences to slope angle and surface complexity. My analyses of the physical variables suggest that rugosity and shore angle are correlated to, and therefore possibly influence, the communities in both habitats. Contrary to past findings, seawalls in this study had higher average rugosity than rocky shores. A high rugosity is generally associated with higher biodiversity as it indicates the presence of crevices and microhabitats, which allows for species with different niches to co-exist within the same area (Martins et al., 2010). In Singapore, the granite riprap seawalls have large crevices between the boulders (often more than 20-30 cm in length) that lead to higher rugosity scores despite the rock substrate itself being relatively smooth. However, the scale of the crevices might have been too large to have an effect on the communities living there, and they reduced the water retaining ability as they drained through to the bottom of the wall. Instead, smaller microhabitats which would have been ecologically relevant on rocky shores could not be picked up by the 10.16 cm diameter distance wheel. The slope angle was also significantly higher on seawalls, which is a common trait of most shoreline defence. A steeper slope means that there is less area available to sustain a community, and forces organisms that live at different tidal heights to be in closer proximity to each other (Chapman and Underwood, 2011). The combination of steepness, smooth rock surfaces, and large crevices that drain water, means that seawalls in Singapore do not retain much moisture during low tides. This desiccation stress during low tides could be one of the main factors explaining the lower algal richness and abundance (Vadas et al., 1992), especially above 0.6 m, where the steeper portions of the seawalls are located. Desiccation is compounded by the high mid-day temperatures, which reach an average daily maximum of 32.3°. This problem is less apparent at the bottom of the walls, where the slope is more gradual (Lee et al., 2009b), and is emersed for shorter periods of time, reducing the period of desiccation stress (Freidenburg et al., 2007), and resulting in a higher abundance of algae.

These physical factors have a profound effect on the underlying ecological processes within the community that culminate in the species composition and distribution observed. In the past, marine benthic ecologists have focused on the interactions between physical stresses and conditions on the biological assemblage as the main determinants of community structure (Menge, 1992). This is particularly true with regards to artificial habitats, where the bulk of the research has centred around surface complexity, wave energy or slope angle (Moschella et al., 2005; Chapman and Underwood, 2011). While these factors undoubtedly heavily influence the communities on artificial habitats, it is important to understand how they affect different species and their interactions, and how that can result in the observed community differences. The presence or lack of certain dominant species can alter ecosystem functions such as nutrient cycling, grazing rates and predation rates, and the multitude of interactions within a complex system makes it difficult to tease out the underlying differences between rocky shores and seawalls (Downing and Leibold, 2002).

Most of the processes that regulate communities have been split into either top-down and bottom-up. Simply put, top-down control emphasises community regulation by trophic interactions of consumers, either primary (herbivores, detritivores, suspension feeders) or secondary (predators), while bottom-up control places importance on the nutrients and primary productivity as a main driver of community structure (Menge, 1992). Substantial research on the effects of these two processes has been conducted on natural rocky intertidal habitats worldwide, and traditionally, it is thought that top-down forces dominate these communities (Menge, 2000). In his landmark paper linking food webs to diversity, Paine (1966) demonstrated that top predator *Pisaster ochraceus* (a carnivorous sea-star) was crucial in maintaining high biodiversity on temperate rocky shores as they removed spatially-competitive barnacles, allowing other species to colonise the otherwise covered areas. Excluding these predators caused the systems to ‘converge to simplicity’, with open areas quickly colonised by barnacle *Balanus cariosus*, which were later overgrown by the mussel *Mytilus californianus* or the barnacle *Mitella polymerus*..

A more recent meta-analysis of food web studies found that indirect consumer effects are the main drivers of ecosystem structure and function on coastal benthic systems including rocky shores (Heck and Valentine, 2007). Biomass of algae is also generally more affected by grazing pressure than by nutrient availability, while overharvesting of consumers can lead to trophic cascade effects that lead to lower species diversity. Benthic consumers, both grazers and predators, frequently have substantial effects on their food sources, and hence on the community composition in general (Heck and Valentine, 2007). I found that a carnivorous drill, *C. magariticola*, was one of the functional groups correlated to rocky shore communities and was one of the top contributors to the differences between the artificial and natural habitat. It is, hence, possible that the presence of this predator helps maintain higher species richness on the natural rocky shore. While it is not known what prey preferences this species of drill has, many Indo-Pacific muricid drills feed on barnacles, other gastropods and bivalves (Tan, 2003), which form the bulk of the faunal species richness on Singapore rocky shores (and of which there is significantly less on seawalls).

Some have argued that, in extreme cases, bottom up factors (i.e. nutrients, primary producers) are the basis of all interactions within the community, as without them, the community cannot exist (Hunter and Price, 1992). The amount of primary production determines the energy input into the system, and could regulate the number of trophic levels, which is a major component of community structure (Menge, 1992). There is evidence of bottom-up forces shaping communities in rocky shores, although this occurs less often than top-down processes. Such a switch can happen during ecologically-significant events, such as El Niño. During one such event on Santa Cruz Island in the Galápagos, nutrient upwelling from the ocean became limited, wave action intensified and seal level rose, leading to a change in algal assemblage that resulted in an overall transformation of the entire rocky shore community (Vinueza et al., 2006). There is also evidence that bottom-up processes can dominate on shores with severe environmental conditions. Studies of mussel populations on South African rocky shores found that strong wave action, and consequently availability of food, was the most important factor driving the growth and mortality rates of this filter-feeding bivalve (McQuaid and Lindsay, 2000).

The top-down versus bottom-up dichotomy is oversimplified, and in reality, they are never exclusive of each other and both play an important role in most systems. The interactions between the two forces, as well as the mechanisms that cause them, can significantly influence the structure of a community (Menge, 2000). It is possible that in areas where nutrients and primary productivity are lacking, bottom-up factors could be more dominant. The harsher environmental conditions (e.g. steeper slope, less water retention) on artificial seawalls might be causing bottom-up factors to limit the trophic complexity and species diversity observed in the present study. The tight coupling of faunal and algal species richness shows that primary producers have a large effect on the presence of consumers; while the dominance of turf algae on rocky shores and detritivores on seawalls points to different nutrient sources sustaining the two habitats. Detritivorous *Ligia* populations are known to fluctuate depending on food availability in the form of imported algae (Koop and Field, 1980), and the abundance of *L. exotica* on seawalls suggests a dependence on allochthonous detrital sources on seawalls (as opposed to attached algae growing *in situ*). While algae is present on seawalls, the lower diversity and abundance (even on the lower portions of the wall) could mean that the seawalls are unable to support a trophic system as complex as the one found on the natural shores, leading to lower biodiversity. Consequently, organisms dependent upon imported nutrient sources (e.g. detritivores) become more dominant and drive the habitat differences when both communities are compared. Conversely, where productivity is sufficient to support a complex trophic structure, top-down consumer effects exert a stronger influence on the community structure, diversity and abundance (Worm, 2002). On rocky shores, where algae diversity and abundance is high, consumers (e.g. carnivorous drills, gastropod grazers) might be essential to maintaining overall biodiversity. This is especially true on the low shore, where both faunal and algae richness are highest.

Admittedly, the findings from this study alone is insufficient to conclude whether there are dominant top-down or bottom-up controls that lead to differences in the communities of the two habitats. Further research has to be invested to test this premise. Possible experiments include artificially increase primary productivity on seawalls (e.g. via nutrient enrichment) and excluding predators on rocky shores to determine if the diversity of the area would be affected. It is also important to find out how changing the physical conditions on the seawalls can lead to changes in these biotic interactions, so that efforts can be directed towards designing and manipulating artificial structures to improve their capacity to support higher diversity.

Chapter 3: Trophic ecology of the intertidal: A dual stable isotope ($\delta^{13}C$, $\delta^{15}N$) analyses of dominant seawall and rocky shore species

3.1 Introduction

Food web and trophic interaction studies have been conducted in temperate coastal environments for decades, with benthic communities on rocky shores particularly well examined (Paine, 1966; Dayton, 1971; Menge, 2000, Schiel, 2004; Sala, 2004). It is generally agreed that food webs on rocky shores can be extremely complex, with some communities sustaining more than 1350 species in five trophic levels (Sala, 2004). Trophic complexity has a strong influence on community structure and biodiversity (Paine, 1966; Polis and Strong, 1996) and human disturbances such as fishing (Sala, 2004), harvesting (Heck and Valentine, 2007) and eutrophication (Worm and Lotze, 2006) can often affect trophic interactions, leading to a dramatic shift in the algal and faunal assemblages. It is therefore likely that the novel physical environments in artificial habitats such as seawalls could result in altered trophic structures and significantly different communities from those found on natural shores.

In Chapter 2, the species driving the community differences between rocky shores and seawalls hint at a top-down influence on rocky shores and bottom-up limitations on seawalls. However, little is known about the trophic interactions on tropical rocky shores or seawalls, or the diets of many common intertidal shore species in Singapore, which form the basis of the food webs. Without this information, it is difficult to make inferences about the underlying trophic influences in both habitats based purely on the community structure observed. The diet compositions of common species found on the rocky shores and seawalls surveyed in Chapter 2 were examined, including those of the taxa driving community differences, i.e. *L. exotica*, *C. magariticola*, and turf algae.

One of the most common ways to examine the trophic interactions of communities is to analyse the stable isotope ratio of the constituent organisms (Yoshioka et al., 1994; Dauby et al., 1998; Grall et al., 2006). A powerful tool that has applications in many fields, stable isotope analysis, has the potential to resolve many ecological questions if harnessed appropriately (Peterson and Fry, 1987). Based on the natural heavy-to-light ratios of carbon, hydrogen, sulphur, oxygen and nitrogen isotopes in natural matter (e.g. plant or animal tissue, soil, etc.), information on sources (e.g. pollutants), physiological or environmental processes (e.g. soil carbon turnover rates) and proportional inputs (e.g. dietary contribution) can be inferred (Sulzma, 2007). The ratio of heavy to light isotopes in organic matter (e.g. ^{13}C to ^{12}C, or ^{15}N to ^{14}N) is influenced by *fractionation*, or the isotopic differences between the source and product compounds of a chemical transformation (Sulzma 2007). In plant or animal tissues, the chemical transformation often includes metabolic processes (e.g. excretion, food assimilation) that may favour the retention of one isotope and the exclusion of another. Accordingly, the isotope ratios of diet or source input also play an important role in determining the isotope ratios found in the subject (Michener & Kaufman 2007). When the isotope ratio of a certain compound in a subject is higher (i.e. has more heavy isotopes) relative to its diet/source, it is considered *enriched*, and *depleted* if it has a lower isotope ratio. Isotopic composition is calculated relative to an international standard ratio and is expressed in part per thousand (‰) deviation from the standard (Sulzma 2007).

Carbon and nitrogen isotopes are commonly used as tracers in ecological studies as carbon ratios often reflects diet, while nitrogen ratios are indicative of trophic level (Michener 2007). In general, there is a 0.5‰ to 1‰ enrichment of ^{13}C in an animal relative to its diet (trophic enrichment factor) because of preferential loss of

^{12}C during respiration and uptake of ^{13}C during assimilation. Due to the conservative enrichment relative to diet, if there are large differences isotopic compositions between different food sources (e.g. C3 vs. C4 plants, terrestrial vs. marine systems, near-shore vs. offshore), diet composition may be traced solely based on isotopic composition of the animal's tissue (Lepoint et al., 2004). Hence, carbon is commonly used to distinguish among different sources of organic matter and enable food web tracing (Ben-David, 1997; Peterson, 1999). Together with nitrogen isotopes, mixing models can be used to determine the proportion contribution of different organic sources to the diet. Generally (in the absence of specific information about the fractionation of C and N isotopes from diet to consumers), consumers are considered to be within -1‰ to 2‰ δ^{13}C relative to diet and +1 to 5 ‰ δ^{15}N relative to diet (Bunn & Boon 1993). Trophic enrichment factor of ^{15}N is much larger in general, with an enrichment value of +3.4‰ on average in consumers relative to their diet (Minagawa and Wada, 1984). This enrichment value is thought to be generally independent of habitat and widely applied to many ecological studies (Grall et al., 2006, Yoshioka et al., 2004). Recent research, however, has shown that this is not always accurate and ^{15}N trophic enrichment has been found to be as low as 1.5‰ in coastal habitats.

When multiple isotope signatures are combined, they can reveal more information about the food sources. They have been used to explore trophic links between adjacent habitats (Kwak and Zedler, 1997; Schaal et al., 2008), distinguish main producers supporting communities (Bode et al., 2006), identify temporal and environmental gradient variations in trophic structures (Sala, 2004; Schaal, 2009), and examine the effects of human disturbance on natural communities (Schaal, 2009). They are especially useful for elucidating food webs in coastal environments such as rocky shores, as consumers have access to a pelagic, benthic or terrestrial (via runoff from further inland) food sources, and diets can often be a mix of several sources. In past isotope-based studies, detrital matter from macroalgae (e.g. kelp) have been often identified as important sources of food for benthic communities on temperate rocky shores (Riera and Hubas, 2003; Bode et al., 2006). Only a small percentage of macroalgal production was consumed directly (10%), as most of it was in the form of detritus (Duggins et al., 1989). However, some studies have suggested that other sources of organic matter, such as epilithic algae (i.e turf algae) and epiphytic biofilm may play an significant role in sustaining rocky shore and seawalls communities (Jenkins and Hartnoll, 2001; Schaal et al., 2009; Ivesa et al., 2010).

Stable isotope analysis can also be used to detect the occurrence of omnivory, which can be quite common in intertidal ecosystems. Omnivory leads to a varied diet composition and increases the complexity of food webs (Polis, 1996; Post, 2002). The idea of discrete trophic levels does not account for the prevalence of omnivory in many communities, including those on rocky shores. This is usually characterised by low average enrichments for both carbon and nitrogen (Bode et al., 2006). Omnivory subsidises the energetic needs of consumers, allowing them to utilise “non-normal prey” to increase in size or survive during periods of low prey availability (Polis, 1996). It can be life-history dependent and change either discontinuously or slowly, and can take the form of detritovory or saprophagy. This has the effect of spreading the effects of consumption across the food web, allowing for a more diverse community. It also changes prey-predator dynamics, and consequently, top-down or bottom-up processes (Polis, 1996), further influencing the structure of the community.

The community distributions observed on seawalls and rocky shores in Singapore (Chapter 2) indicate a possible bottom-up limitation on artificial shores that leads to a lower diversity. However, it is unclear what the diets of most of the common species actually consist of, restricting the conclusions that can be made based solely on the assemblage differences. Hence, this study aims to examine the trophic structure and diet composition of the common species on seawalls and rocky shores in Singapore..

3.2 Materials and methods

3.2.1 Sampling method

Algae, encrusting/sessile species and mobile species were collected as described in Chapter 2. The organisms were sorted, identified, then frozen until they could be prepared for isotopic composition analysis. Not all organisms collected over the year-long sampling period were analysed; only species/taxon that were common (encountered every month) were selected. Algae species within the turf algal matrix could not be separated for individual analysis due to the small size of the individual filaments, and were thus pooled together and treated as a single functional group. A total of six primary sources and 21 consumers common on seawalls and rocky shores at the four sites (Section 2) were chosen for processing. Suspended particulate matter (SPM) samples (which would include plankton and detrital matter) were obtained by filtering two five-litre surface water samples through a GF/F 0.7 µm glass-fibre filter. Due to limitations on time and resources, the SPM was not separated into its constituent groups (e.g. zooplankton, phytoplankton, detrital matter) and analysed separately.

3.2.2 Stable isotope analysis

Gastropods and bivalves were dissected to remove their shell or carapace before treatment, while whole organisms were used for all the other taxa, including crustaceans, as they were small (<3 cm in length). The samples were soaked in 10% HCl to remove carbonates that might affect the carbon isotope reading, then rinsed with deionised water and dried at 60°C for 48 h. Depending on the organism size, occasionally several individuals of the same species (and from the same site) were pooled and analysed as a single sample to reduce intraspecific variation. SPM samples were suctioned filtered, rinsed with 10% HCl (to remove any calcium carbonate) followed by deionised water, then dried at 60°C for 24 h (Kwak and Zedler, 1997). All the dried samples were then ground to a fine powder and sealed in tin capsules before being sent for analysis. Analysis was conducted using whole organisms or muscle tissue as opposed to gut analysis due to technical limitations for the small specimens.

Dual δ13C and δ15N isotope analysis were performed using a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) at the UC Davis Stable Isotope Facility. Isotopic composition (δ) obtained from ratios (R) of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ obtained are relative to the international standards (Vienna Pee Dee Belemnite for carbon; atmospheric nitrogen for nitrogen) using the follow equation:

$$\delta(‰) = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1000$$

Kurskal-Wallis tests were used to determine if isotopic values of $\delta^{13}C$ and $\delta^{15}N$ differed between the organisms in rocky shores and seawalls. Due to logistical constraints, only the most common species in both habitats, *Pictocolumbella ocellata*, was used to test for differences in isotopic signatures among sites (n=165). Diets of the different organisms were also estimated using the IsoSource mixing model (Phillips and Gregg, 2003). Since none of the organisms could be safely assumed to consume a single food source, a combination of diets/food sources was assumed for all. The mixing model was used to give a range of proportional diet contributions from several identified main sources. This particular mixing model is an expansion of the linear mixing model, which calculate the proportions of source isotopic signatures

(f_A, f_B, and f_C) based on the isotopic signature of the target organism (δ_M), the isotopic signatures of the diet (δ_A, δ_B and δ_C) as follows:

$$\delta_M = f_A\delta_A + f_B\delta_B + f_C\delta_C$$

$$1 = f_A + f_B + f_C$$

The IsoSource model analysed diet contributions to a maximum of six sources due to computing constraints. These six sources identified were the most differentiated for both $\delta^{13}C$ and $\delta^{15}N$ values to maximise the resolving power. The model examined all possible the diet combinations of using source increments of 1%, and accepted combinations within a mass balance tolerance of 0.1‰ (Phillips and Gregg, 2003). The isotopic signatures of each consumer were corrected to account for the enrichment during digestion and assimilation. These were taken to be 0.8‰ for $\delta^{13}C$ and 1.5‰ for $\delta^{15}N$, based on past food web studies (France and Peters, 1997; Vanderklift and Ponsard, 2003; Bode et al., 2006).

3.3 Results

Isotopic values for the common sources and consumers on rocky shores and seawalls are presented in Table 3.3.1. Variability within each taxon was large, with the carnivorous drill *C. magaritacola* having the largest standard deviations among all organisms tested. Similar to previous studies (Kwak and Zedler, 1997, Grall et al., 2007), the SPM was the lowest isotopic value for both isotopes, with a δ^{13}C value of -27.66‰ and δ^{15}N of -2.94‰. The algae sources had more similar isotopic values, with *Bryoposis* sp. and *Sargassum polycystum* more ^{13}C-depleted (-19.17‰ and -17.69‰), turf algae less so (-15.25‰), and *Padina* sp. and *Lobophora variegate* the least (-11.05‰ and -12.39‰). With the exception of *Tetraclita* sp.*, Balanus* sp.*, Siphonaria javanica, Patelloida saccharinoides* and L. *exotica*, most of the isotopic signatures of the primary consumers (when adjusted for fractionation) fell within the boundaries of these six sources, indicating that the sources were likely contributors to their diets.

The overlapping ranges δ^{15}N and δ^{13}C (Fig. 3.3.1) led to poor separation between the trophic levels of the primary producers and the primary consumers (known herbivores such as *Nerita* sp.*, Trochus maculatus, Turbo bruneus,* and limpets *Siphonaria sp.* and *Patelloida* saccharinoides) (Fig. 3.3.2A). *Barbatia amygdalumtostum,* a filter feeding bivalve as well as crabs like *Myomenippe hardwickii* and *Nanosesarma* sp.*,* were also found within this range as well. On the other hand, the trophic separation of the secondary consumers (carnivorous drills) was more distinct (Fig. 3.3.2B), with a δ^{15}N range 8.73‰ to 9.40‰. Filter feeding barnacles *Tetraclita* sp. and *Balanus* sp., and detritivorous isopod *Ligia exotica* were also on the extreme ends, with the highest (10.16‰ to 10.64‰; Fig. 3.3.2C) and lowest (4.81‰) δ^{15}N values respectively. Average enrichment values between trophic levels were +1.41‰ δ^{15}N and +0.73‰ δ^{13}C.

Table 3.3.1: δ^{13}C (‰) and δ^{15}N (‰) (average ± SE) of common sources (suspended particulate matter and algae) and consumers (crustaceans and molluscs) on rocky shores and seawalls.

	Type	**n**	**δ^{13}C (‰)**	**δ^{15}N (‰)**
Suspended particulate matter	-	4	-27.66 ± 1.28	-2.94 ± 0.88
Bryopsis sp.	Algae	2	-19.17 ± 0.46	6.18 ± 0.40
Lobophora variegata	Algae	5	-12.39 ± 1.30	5.14 ± 0.34
Padina sp.	Algae	1	-11.05	5.73
Sargassum polycystum	Algae	12	-17.69 ± 0.50	6.53 ± 0.45
Turf (Combined)	Algae	6	-15.25 ± 0.32	7.12 ± 0.27
Barbatia amygdalumtostum	Mollusc	6	-16.84 ± 0.42	7.56 ± 018
Cellana radiata	Mollusc	4	-15.08 ± 0.50	6.60 ±0.36
Cronia magaritacola	Mollusc	10	-15.40 ± 0.90	8.73 ± 0.68
Monodonta labio	Mollusc	8	-14.30 ± 0.94	6.32 ± 0.21
Morula fusca	Mollusc	6	-13.71 ± 0.65	8.74 ± 0.24
Morula musiva	Mollusc	6	-15.98 ± 0.45	9.40 ±0.39
Nerita chamaeleon	Mollusc	5	-12.57 ± 0.83	6.59 ±0.34
Nerita undata	Mollusc	7	-13.43 ± 0.78	7.26 ±0.35
Pardalina testudinaria	Mollusc	4	-16.52 ± 0.88	8.53 ±0.34
Patelloida saccharinoides	Mollusc	3	-11.11 ± 0.80	6.44 ±0.50
Pictocolumbella ocellata	Mollusc	165	-14.91 ± 0.14	7.73 ±0.06
Siphonaria guamensis	Mollusc	5	-14.79 ± 1.15	6.68 ± 0.64
Siphonaria javanica	Mollusc	5	-11.55 ± 0.62	5.88 ± 0.59
Trochus maculatus	Mollusc	9	-15.12 ± 0.59	7.52 ± 0.32
Turbo bruneus	Mollusc	7	-15.10 ± 0.29	6.44 ± 0..22
Balanus sp.	Crustacean	3	-17.50 ± 0.12	10.16 ± 0.02

Myomenippe hardwickii	Crustacean	2	-17.16 ± 0.22	7.01 ± 0.57
Ligia exotica	Crustacean	7	-15.10 ± 0.26	4.81 ± 1.03
Nanosesarma sp.	Crustacean	5	-16.07 ± 0.26	6.40 ± 0.24
Hermit crab	Crustacean	1	-14.01	6.20
Tetraclita sp.	Crustacean	3	-17.46 ± 0.28	10.64 ± 0.20

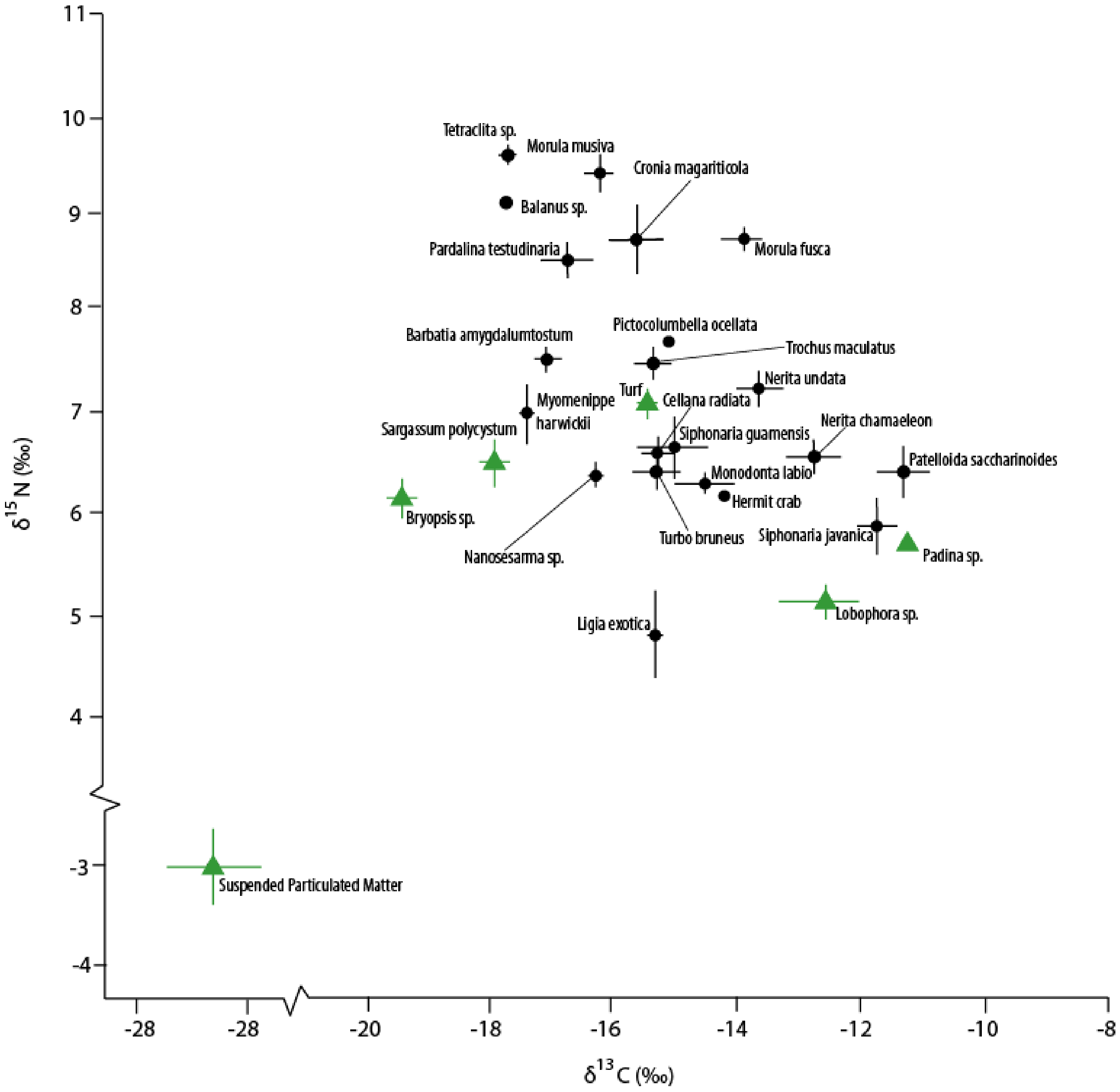

Fig 3.3.1: Scatterplot of average δ^{13}C (‰) vs δ^{15}N (‰) values of food sources (error bars indicate SE). Green triangles - sources, black circles - consumers.

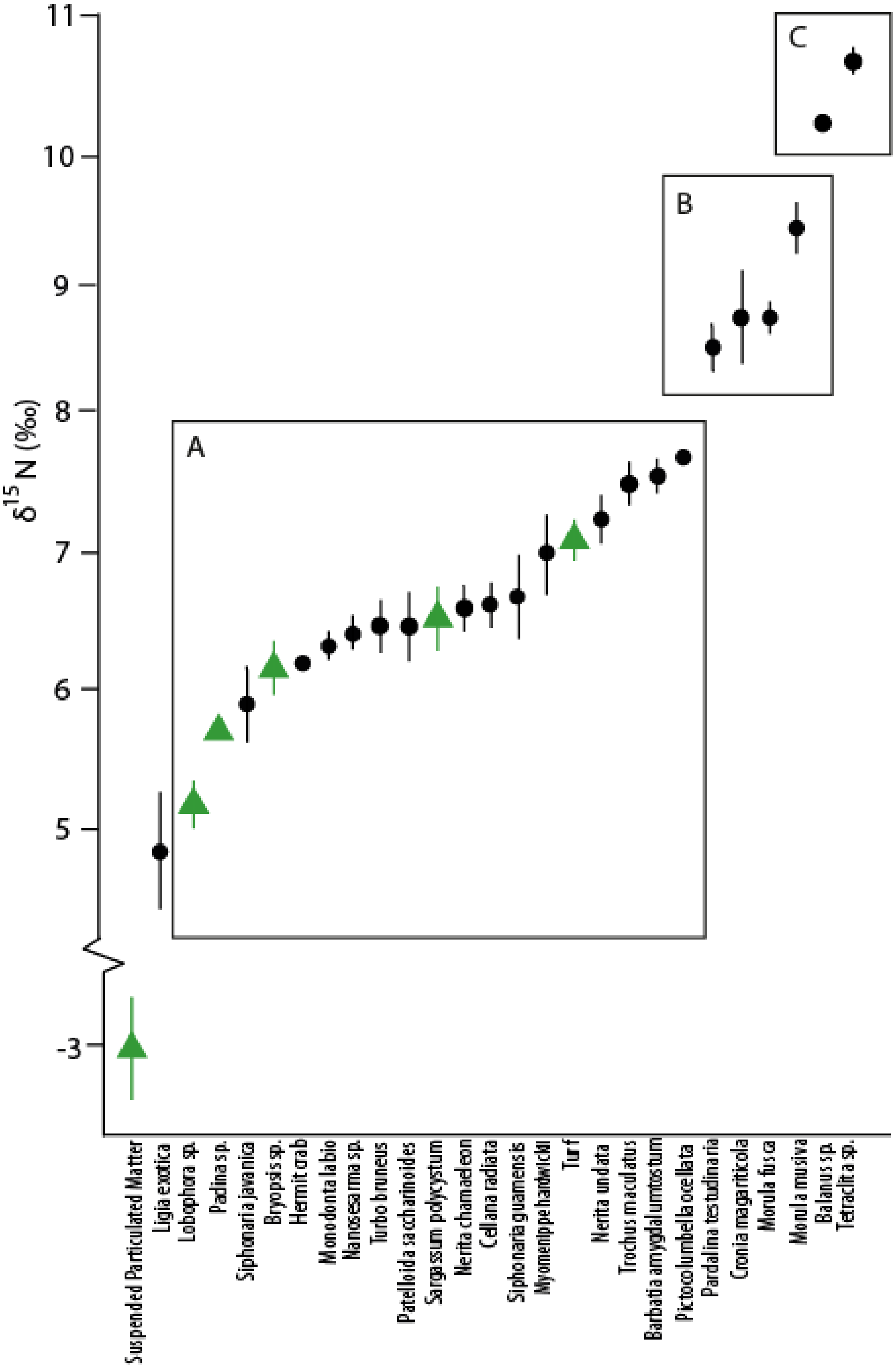

Fig. 3.3.2: Average δ^{15}N (‰) for each taxon (error bars indicate SE). Green triangles - sources, black circles - consumers. Boxes delineate algae and primary consumers (A), carnivores (B), and barnacles (C).

The isotopic values of both ^{15}N and ^{13}C of *P. ocellata* did not differ significantly among sites. In addition, the isotopic values of both ^{15}N and ^{13}C of all species did not differ between habitats, with the exception of dove snail *P. ocellata* ($p<0.01$ for both isotopes). As such, diet analyses were performed separately for each habitat for that species (Table 3.3.2). The IsoSource analyses for the primary consumers based on the six sources (five algae and SPM) showed that some species had a wide range of proportional source contribution, which is not unknown to intertidal communities (Hill and McQuaid, 2008). Of the eight species that had small ranges (and therefore more distinct feeding patterns), turf algae was a significant contributor to the diets of all but one – *B. amygdalumtostum* (Table 3.3.2). This functional group, consisting of many small epilithic algal species, was nonetheless present in the all species' diet scenarios with at least a minimal contribution, with the exception of *L. exotica.* . Contributions from *Padina sp.* and *Lobophora variegata* had comparable ranges for most of the consumers due to their similar isotopic values, and were generally less dominant contributors to diet than turf algae. Both are potentially substantial contributors for many species, reaching a maximum diet proportion of more than 0.3 in nine out of the thirteen taxa tested. *Bryopsis sp*. and *Sargassum sp*. contributed very little to their overall diets, with the exception of filter-feeder *B. amygdalumtostum*, for which *Sargassum sp*. made up more the half its diet. Diet contributions for limpets *S. javanica* and *P. saccharinoides* were not able to be resolved as their isotopic values fell outside those of the six sources.

Table 3.3.2: Range of proportion contributions of six sources towards the diets of primary consumers from the IsoSource mixing model.

Species	*Bryopsis sp.*	*Sargassum sp.*	Turf algae	*Padina sp.*	*Lobophora variegata*	SPM
Cellana radiata	-	-	0.48 - 0.53	0.00 - 0.24	0.00 - 0.35	0.13 - 0.15
Barbatia amygdalumtostum	-	0.54 - 0.72	0.16 - 0.38	0.00 - 0.04	0.00 - 0.04	0.06 - 0.08
Hermit crab	-	-	0.20 - 0.24	0.00 - 0.50	0.08 - 0.65	0.12 - 0.16
Ligia exotica	-	-	0.00 - 0.02	0.00 - 0.69	0.00 - 0.77	0.22 - 0.29
Monodonta labio	-	-	0.28 - 0.33	0.00 - 0.52	0.00 - 0.56	0.11 - 0.16
***Myomenippe hardwickii* (juvenile)**	-	-	0.48 - 0.53	0.00 - 0.34	0.00 - 0.38	0.13 - 0.16
Nerita chamaeleon	-	-	0.10 - 0.13	0.00 - 0.75	0.02 - 0.86	0.04 - 0.10
Nerita undata	-	-	0.42 - 0.45	0.00 - 0.44	0.00 - 0.52	0.04 - 0.07
Nanosesarma minutum	-	-	0.57 - 0.68	0.00 - 0.17	0.00 - 0.25	0.18 - 0.20
***Pictocolumbella ocellata* (Rocky shore)**	-	0.00 - 0.01	0.83 - 0.88	0.00 - 0.07	0.00 - 0.07	0.07 - 0.08

***Pictocolumbella ocellata* (Seawall)**	-	0.00 - 0.01	0.70 - 0.75	0.00 - 0.22	0.00 - 0.23	0.05 - 0.07
Siphonaria guamensis	-	-	0.46 - 0.51	0.00 - 0.35	0.00 - 0.42	0.11 - 0.15
Trochus maculatus	-	-	0.75 - 0.80	0.00 - 0.14	0.00 - 0.15	0.08 - 0.10
Turbo bruneus			0.44 - 0.49	0.00 - 0.35	0.00 - 0.38	0.15 - 0.17

The diets of the three carnivorous drills were based on six sources consisting of grazing gastropods *T. bruneus, P. ocellata*, *Nerita undata* and *T. maculatus*, barnacle *Balanus* sp., and bivalve *B. amygdalumtostum* (Table 3.3.3). *Balanus* sp. was the least common contributor to diet overall, while *B. amygdalumtostum* was the highest contributor (0.21 to 0.90) for two of the three predators. *N. undata* contributed little to the diets of the drills, with the exception of *M. fusca*, which had 60 to 70% of its diet was attributed to the nerite.

Table 3.3.3: Range of proportion contributions of six sources towards the diets of secondary consumers from the IsoSource mixing model.

Species	*Turbo bruneus*	*Balanus sp.*	*Pictocolum-bella ocellata*	*Trochus maculatus*	*Nerita undata*	*Barbatia sp.*
Cronia magariticola	0.18 - 0.02	-	0.00 - 0.05	0.00 - 0.16	0.04 - 0.12	0.68 - 0.73
Morula fusca	0.01 - 0.03	-	0.00 - 0.03	0.00 - 0.15	0.60 - 0.70	0.21 - 0.31
Morula musiva	0.01 - 0.04	0.10 - 0.18	0.00 - 0.03	0.00 - 0.01	0.00 - 0.01	0.70 - 0.90

The isotopic values of barnacles, *Tetraclita* sp. and *Balanus* sp. fell outside those of the other organisms and sources, indicating that sources of these organisms’ diets were not analysed.

3.4 Discussion

The findings of this study have elucidated the major trophic interactions and dietary patterns of common species on rocky shore and seawall intertidal habitats. The isotopic analyses for δ^{15}N and δ^{13}C signatures for the six sources and 21 consumers showed that variation within each species was large relative to those observed in past intertidal habitat research (Dauby et al., 1998; Schaal et al., 2009). The trophic separation between sources and their primary consumers were not distinct, and were found within a continuous δ^{15}N range, suggesting the existence of some omnivory at this trophic level. However, separation between the primary consumers and the next trophic level, the predatory snails, was clearer with the latter being more δ^{15}N enriched. The IsoSource mixing model showed that diets of the primary consumers were mainly from four of the six sources, of which turf algae was the dominant contributor in most species. The analyses also showed that *B. amygdalumtostum* and *N. undata* were the main prey source for the secondary consumers.

The large variability observed in the isotopic signatures of many of the samples could have been due to a variety of reasons. The number of potential food sources for many of the consumers was large (in reality, more than six), given the high diversity of species found within the intertidal zones of Singapore. The diet analyses show that the consumers do not strictly consume a single source, which can lead to variations in isotopic signatures among individuals of the same species, depending on the food source immediately available to them. Sampling error (due to a relatively small number of individuals sampled) could possibly have contributed to this variability as well. However, judging from the substantial variation observed within the species with the greatest sample size (n=165), *P. ocellata*, this is unlikely.

The large variability and overlapping isotopic values made it impossible to distinguish between the trophic levels of the sources and primary consumers. This phenomenon has been reported previously by Riera et al. (2009) who, in their study of a rocky shore community within a zone of brown algae *Ascophyllum nodosum*, found a heterogeneous spread of δ^{15}N values among the herbivores. This was attributed to the high δ^{15}N values of the food sources, and diversity of feeding behaviour among the consumers, including detritovory, as opposed to just strict herbivory (Riera et al., 2009). In the present study, suspended particulate matter was found in the diets of all of the primary consumers despite many of them being grazers as opposed to filter feeders. This could have been due to incidental ingestion during grazing, as sediment often gets trapped between the filaments that make up turf algae in rocky intertidal environments (Airoldi, 1998). Detritus accounts for 10% to 78% of the organic matter in turf algae (Wilson et al., 2003), and the incidental ingestion of it could constitute a small degree of detritivory. This omnivory of food sources from different trophic levels could lead to the low isotopic enrichment observed in this study (Eggers and Jones, 2000; Rolff, 2000). The trophic separation between the primary and secondary consumers was more distinct, suggesting that omnivory was less prevalent or absent at the higher trophic level. In general, more fractionation occurs when consumers have a more specialised diet (Fredriksen, 2003).

Two particular taxa were found outside range of δ^{15}N values of most of the consumers, namely the isopod *L. exotica*, and the barnacles, *Tetraclita* sp. and *Balanus* sp.. Isopods from the genus *Ligia* are known to be a scavengers or detritivores that feed on algal debris (Koop and Field, 1980; Pennings et al., 2000;

Laurand and Riera, 2006) and the results of the present study supports this. The bulk of the diet of *L. exotica* coming from algae *Padina sp.*, *L. variegata* and SPM, but was generally more ^{15}N depleted than the other primary consumers. This could indicate that *L. exotica* preferential fed on more decayed algal matter (as opposed to fresh matter), as consuming detritus generally leads to lower enrichment (Vanderklift and Ponsard, 2003). The barnacles had the greatest difference in $\delta^{15}N$ values above those of the secondary consumers (3.36‰ on average). Given that their filter feeding habit limits their diet to organic matter found within the water column, it demonstrates that barnacles selectively feed on more enriched organisms as opposed to detrital matter or algae within the SPM. Past studies report that barnacles can exhibit higher average isotopic values as they consume animal matter, in the form of zooplankton (e.g. copeopods, nauplii), polycheate needles and porifera needles, and can be considered secondary consumers (Schaal, 2009; Steinarsdóttir et al., 2009). In addition, their position on the shore can influence their feeding habits. Filter feeders located on the low shore, such as *B. amygdalumtostum* are more likely to obtain their food from broken down algal matter around them than compared to those higher up the shore (e.g. barnacles), which can selectively feed on other food sources in the water column (Steinarsdóttir et al., 2009). It is therefore not surprising that the major diet contributor for *B. amygdalumtostum* was *S. polycystum,* the most dominant algae in terms of percentage cover at the low shore.

The high $\delta^{15}N$ values of the barnacles highlight the fact that there are other sources that could be important in the rocky shore and seawall environment that were not sampled. Future research should be directed at including more sources to achieve better resolution of the diets and trophic connections within the communities. For example, characterising the components of the suspended particulate matter, such as zooplankton, phytoplankton, and detrital matter, could help resolve the diets of the filter feeders. Additional information about different sources might also serve to identify the diets of species which change ontogenically. Stone crabs *M. hardwickii* are generally thought to be a carnivore that prey on mollusc species (Neo and Todd, 2011). However, the isotopic values of the juveniles were closer to those of the primary consumers than the secondary ones, suggesting that the species has a more algal-dominant diet at the juvenile stage.

Information about the trophic interactions and diets of the dominant consumers from this study provides new insights into communities on rocky shores and seawalls. It is evident that the primary producers do support a wide range of consumers, from grazing gastropods to crustaceans and filter-feeding bivalves. In particular, turf algae contributes the most to the diets of these consumers in general, while larger macroalgae such as *Sargassum* sp. and *Bryoposis* sp. do not, despite being available in large quantities. Even in *P. ocellata*, which had significantly different isotopic values for individuals of rocky shores and seawalls, the diets were still dominated by turf algae, with a slight difference in consumption of *Padina* sp. and *L. variegata.* This underscores the importance of turf algae in the bottom-up regulation of these intertidal communities. The lack of turf algae could lead to a reduced capacity to sustain grazer populations and subsequently, predator populations. Scavengers or detrivores such *L. exotica* that are less dependent on turf algae, and can survive off imported decayed algae would be more common as well. This corresponds to the distributional patterns observed on seawalls in Chapter 2 and lends support to the premise that in environments where primary production is limiting, bottom-up processes are the main drivers of community structure.

This study has shown that there is high δ^{15}N and δ^{13}C variability for many of the consumers on rocky shores and seawalls in Singapore, highlighting that the diets of each taxon can be broad and that omnivory is probably prevalent within the primary consumer level. The importance of turf algae, *Padina sp.* and *L. variegata* as food sources support the possibility of bottom-up processes limiting diversity and trophic complexity on seawalls as postulated in Chapter 2. Further research needs to be directed to find out if primary productivity is a limiting factor to the diversity on seawalls, and if manipulating the physical structure of the seawall can correct such a constraint.

Overall conclusions of the thesis

My research shows that seawalls currently fail to act as surrogate habitats of rocky shores, and suggests that the lack of primary productivity could be one of the root causes for the lower diversity observed in the artificial habitat. With a substantial portion of the natural coastline already replaced by reclaimed land, seawalls have become the dominant structure on most of Singapore's shores. According to the Government's Master Plans and Concept Plans, these reclamation efforts show no sign of abating. As the resident population is set to rise considerably over the next two decades, the creation of new land, and the development of unused land, will inevitably continue. By 2030, the total length of seawalls around Singapore is projected to exceed 600 km, and it is important that this novel coastal habitat can be used to aid in the conservation of the marine biodiversity that will be lost with the destruction of natural habitats.

As evinced by the results in the surveys and stable isotope analyses, seawalls sustain distinctly different communities to those on rocky shores, although they do share many of the same species. Seawalls have a lower diversity of fauna and lower algal species richness and abundance, and are characterised by the detritivore *L. exotica*, which mainly feed on imported decaying algae. Rocky shores, on the other hand, are characterised by the carnivorous gastropod *C. magariticola* and turf algae, which is a major food source for many herbivorous snails. These observations suggest that seawalls lack the algal abundance and diversity (particularly turf algae) to support higher trophic levels and complexity that are necessary for a diverse community. This problem is absent on the rocky shore due to the higher abundance of algae, leading to a relative dominance of higher trophic level species such as *C. margariticola.*

Further investigation into the possible effects of productivity limitations on seawalls is crucial as it could open a new avenue of manipulating these artificial structures to improve its diversity. Combining of theoretical ecological information with engineering principals is the basis of reconciliation ecology. In the past, a multitude of techniques to improve various physical factors of seawalls—topographic complexity, slope angle, elevation etc.—have been attempted, but none have been targeted directly at recruiting a high abundance and diversity of algae. Given that many past studies have focused on removing or preventing algal growth (which is often perceived as a fouling organism) (Shafir et al., 2009; Ng et al., 2013), it is imperative that future research is directed towards algal recruitment and growth, and how it can be enhanced in a controllable manner. Potential ideas include enriching the substrate with nutrients, improving water retention further up the slope of the seawalls, or even direct seeding of various algal species that are known to be important food groups for herbivores. Reconciliation efforts on Singapore's seawalls can potentially produce novel techniques that might be suitable on other productivity-limited coasts.

These reconciliation and enhancement efforts, however, should be carried out with caution. Increasing the productivity of the habitat may increase its ability to support a greater diversity of species, but may make the system more susceptible to invasive species. Artificial structures, being novel environments, are more open to invasion, and can act as stepping stones for marine alien species into neighbouring natural environments. In North America, an estimated 90% of all alien species found on hard substrate are recorded in artificial environments like docks and marinas (Mineur et al., 2012). Given that international shipping is one of the chief means of introduction (Molnar et al., 2008), Singapore, one of the world's largest ports, is extremely vulnerable to marine invasive species. While this study was not focused on identification of the species found in both natural and artificial habitats, future studies might want to investigate the extent of marine aliens found on our shores, and determine if seawalls in Singapore are indeed similarly prone to invasion.

My study highlights the ubiquity of the seawall habitat in Singapore, and the lack of diversity it supports compared to its natural analogue – the rocky shore. However, it does also hint at a bottom-up limitation on seawalls that could be corrected to improve the carrying capacity of these artificial structures. It is imperative that more is done to enhance our seawalls, as has been attempted on many temperate shores. Few cities have more than 20% of land reclaimed or 80% of artificial coastline as Singapore does. However, with increasing population growth globally leading to greater urbanisation, coupled with the threat of sea level rise, Singapore’s may not be unique for very long. The extreme urban development in this island nation serves as a highly illustrative case study of the ecological future that many coastal cities may eventually face, especially in rapidly developing countries. Lesson learnt from ongoing reconciliation initiatives in Singapore should benefit urban marine sustainability management in coastal cities worldwide.

References

Airoldi L, Virgilio M. (1998) Responses of turf-forming algae to spatial variations in the deposition of sediments. Marine Ecology Progress Series 165: 271-282

Airoldi L, Abbiati M, Beck MW, Hawkins SJ, Jonsson PR, Martin D, Moschella PS, Sundelof A, Thompson RC, Aberg P. (2005) An ecological perspective on the deployment and design of low-crested and other hard coastal defence structures. Coastal Engineering 52(10-11): 1073-1087

Anderson MJ, Ellingsen KE, McArdle BH. (2006) Multivariate dispersion as a measure of beta diversity. Ecology letters 9(6): 683-93

Anker A. (2003) Alpheid shrimps from the mangroves and mudflats of Singapore. Part 1. Genera *Salmoneus*, *Athanas* and *Potamalpheops*, with the description of two new species (Crustacea: Decapoda: Caridea). Raffles Bulletin of Zoology 51(2):283-314

Bacchiocchi F, Airoldi L. (2003) Distribution and dynamics of epibiota on hard structures for coastal protection. Estuarine, Coastal and Shelf Science 56(5-6): 1157-1166

Bayen S, Wurl O, Karuppiah S, Sivasothi N, Lee HK, Obbard JP. (2005) Persistent organic pollutants in mangrove food webs in Singapore. Chemosphere 61(3): 303-13

Ben-David M, Schell DM. (2011) Mixing models in analyses of diet using multiple stable isotopes : A response. Ecology 127(2): 180-184

Bergen SD, Bolton SM, Fridley JL. (2001) Design principles for ecological engineering. Ecological Engineering 18: 201-210

Bird M, Chua S, Fifield LK, Teh TS, Lai J. (2004) Evolution of the Sungei Buloh–Kranji mangrove coast, Singapore. Applied Geography 24(3): 181-198

Bode A, Alvarez-Ossorio MT, Varela M. (2006) Phytoplankton and macrophyte contributions to littoral food webs in the Galician upwelling estimated from stable isotopes. Marine Ecology Progress Series 318: 89-102

Bulleri F, Chapman MG. (2004) Intertidal assemblages on artificial and natural habitats in marinas on the north-west coast of Italy. Marine Biology 145(2): 381-391

Bulleri F, Airoldi L. (2005) Artificial marine structures facilitate the spread of a non-indigenous green alga, *Codium fragile* ssp. tomentosoides, in the north Adriatic Sea. Journal of Applied Ecology 42(6): 1063-1072

Bulleri F, Chapman MG, Underwood AJ. (2005) Intertidal assemblages on seawalls and vertical rocky shores in Sydney Harbour, Australia. Austral Ecology 30(6): 655-667

Bulleri F, Chapman MG. (2010) The introduction of coastal infrastructure as a driver of change in marine environments. Journal of Applied Ecology 47(1): 26-35

Bunn SE, Boon PI. (1993) What sources of organic carbon drive food webs in billabongs? A study based on stable isotope analysis. Oecologia 96(1): 85–94

Castelletta M, Sodhi NS, Subaraj R. (2008) Heavy Extinctions of Forest Avifauna in Singapore: Lessons for Biodiversity Conservation in Southeast Asia. Conservation Biology 14(6): 1870-1880

Chapman MG, Bulleri F. (2003) Intertidal seawalls—new features of landscape in intertidal environments. Landscape and Urban Planning 62(3): 159-172

Chapman MG, Underwood AJ. (2011) Evaluation of ecological engineering of ‘armoured’ shorelines to improve their value as habitat. Journal of Experimental Marine Biology and Ecology 400(1-2): 302-313

Chou LM. (2006) Marine habitats in one of the world’s busiest harbours. In: Wolanski E (ed.) The Environment in Asia Pacific Harbours. Springer Press, The Netherlands, pp 377-391

Chou LM. (2008) Nature and Sustainability of the Marine Environment. In: Wong T-C, Yuen BKP, Goldblum C. (eds.) Spatial Planning for a Sustainable Singapore. Ministry of the Environment, Singapore, pp 169-182

Chou, LM, Yu JY, Loh TL. (2004) Impacts of sedimentation on soft-bottom benthic communities in the southern islands of Singapore. Hydrobiologia 515: 91-106

Chou, LM, Tun KPP. (2007) Conserving reefs beside a marine landfill in Singapore. Coral Reefs 26(3): 719-719

Chun J. (2007) Wildlife Law in Singapore: Protecting Wildlife in the 'Garden City'. In: Panjwani R. (ed.) Wildlife Law: A Global Perspective, American Bar Association, USA, pp 201-260

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Austral Ecology 18(1): 117-143

Clarke KR, Gorley RN. (2006) Primer v6: user manual/tutorial. PRIMER-E, Plymouth

Connell SD. (2000) Floating pontoons create novel habitats for subtidal epibiota. Journal of Experimental Marine Biology and Ecology 247(2): 183-194

Connell SD. (2001) Urban structures as marine habitats: an experimental comparison of the composition and abundance of subtidal epibiota among pilings, pontoons and rocky reefs. Marine Environmental Research 52: 115-125

Connell SD, Glasby TM. (1999). Do urban structures influence local abundance and diversity of subtidal epibiota? A case study from Sydney Harbour, Australia. Marine Environmental Research 47(4): 373-387

Corlett RT. (1992) The ecological transformation of Singapore, 1819-1990. Journal of Biogeography 19(4): 411

Creel L. (2003) Ripple effects: Population and coastal regions. Population Reference Bureau: Washington, USA.

Crossland AC. (2002) Seasonal abundance of waterbirds at Tanah Merah beach, a newly formed inter-tidal habitat on the edge of reclaimed land in Singapore. The Stilt 42: 4-9

Cuong DT, Bayen S, Wurl O, Subramanian K, Wong KKS, Sivasothi N, Obbard JP (2005). Heavy metal contamination in mangrove habitats of Singapore. Marine Pollution Bulletin 50(12): 1732-1738

Dauby P, Khomsi A, Bouquegneau JM. (1998) Trophic relationships within intertidal communities of the Brittany coasts: a stable carbon isotope analysis. Journal of Coastal Research 14(4): 1202–1212

Davis JLD, Levin L, Walther SM. (2002) Artificial armored shorelines: sites for open-coast species in a southern California bay. Marine Biology 140(6): 1249-1262

Denison PR, Enoch I. (1954) Zonation of the marine fauna and flora on a rocky shore near Singapore. The Bulletin of the Raffles Museum 25: 47-65

Dikou A, van Woeksik R. (2006) Survival under chronic stress fro sediment load: Spatial patterns of hard coral communities in the southern islands of Singapore. Marine Pollution Bulletin 52: 7-21

Duggins DO, Simenstad CA, Estes JA. (1989) Magnification of secondary production by kelp detritus in coastal marine ecosystems. Science 245:170–173

Edwards AJ, Gomez E. (2010) Objectives and scope of this manual. In: Edwards AJ. (ed.) Reef Rehabilitation Manual. Coral Reef Targeted Research & Capacity Building for Management Program, St. Lucia, Australia, pp 113-123

Eggers T, Jones TH. (2000) You are what you eat…or are you? Trends in Ecology and Evolution 15: 265–266

Fautin DG, Tan SH, Tan R (2009) Sea anemones (Cnidaria: Actiniaria) of Singapore: abundant and well-known shallow- water species. Raffles Bulletin of Zoology Supplement 22: 121-143

Fauvelot C, Bertozzi F, Costantini F, Airoldi L, Abbiati M (2009) Lower genetic diversity in the limpet *Patella caerulea* on urban coastal structures compared to natural rocky habitats. Marine Biology 156(11): 1-32

France RL, Peters, RH. (2011) Ecosystem differences in the trophic enrichment of 13C in aquatic food webs. Canadian Journal of Fisheries and Aquatic Sciences 54(6): 1255-1258

Fredriksen S. (2003) Food web studies in a Norwegian kelp forest based on stable isotope (δ13C and δ15N analysis. Marine Ecology Progress Series 260: 71-81

Freidenburg TL, Menge BA, Halpin PM. Webster M, Sutton-Grier A. (2007) Cross-scale variation in top-down and bottom-up control of algal abundance. Journal of Experimental Marine Biology and Ecology 347(1-2): 8-29

Friess DA, Phelps J, Leong RC, Lee WK, Wee AKS, Sivasothi N, Oh RRY, Webb EL. (2012) Mandai mangrove, Singapore: Lessons for the conservation of Southeast Asia’s mangroves. The Raffles Bulletin of Zoology 25:55-65

Frost NJ, Burrows MT. (2005) Measuring surface complexity in ecological studies. Limnology and Oceanography Methods 3 (Apr): 203-210

Geh M, Sharp I. (2008) Singapore’s natural environment, past, present and future: A construct of national identity and land use imperatives. In: Wong T-C, Yuen BKP, Goldblum C. (eds.) Spatial Planning for a Sustainable Singapore. Ministry of the Environment, Singapore, pp 183-204

Glasby TM, Connell SD. (1999) Urban structures as marine habitats. Ambio 28(7): 595-598

Glasby TM, Connell SD, Holloway SD, Hewitt MG, Hewitt CL. (2006) Nonindigenous biota on artificial structures: could habitat creation facilitate biological invasions? Marine Biology 151(3): 887-895

Grall J, Leloch F, Guyonnet B, Riera P. (2006) Community structure and food web based on stable isotopes (δ15N and δ13C) analysis of a North Eastern Atlantic maerl bed. Journal of Experimental Marine Biology and Ecology 338(1): 1-15

Grant G. (2006) Extensive green roofs in London. Urban Habitats 4:51–65

Heck KL, Valentine JF. (2007) The primacy of top-down effects in shallow benthic ecosystems. Estuaries and Coasts 30(3): 371-381

Hill J.M., McQuaid C.D. (2008) δ^{13} C and δ^{15}N biogeographic trends in rocky intertidal communities along the coast of South Africa: Evidence of strong environmental signatures. Estuarine, Coastal and Shelf Science 80(2) 261-268

Hilton MJ, Manning SS. (1995) Conversion of coastal habitats in Singapore: indications of unsustainable development. Environmental Conservation 22(4): 307-322

Hoeksema BW, Koh EGL. (2009) Depauperation of the mushroom coral fauna (Fungiidae) of Singapore (1860s–2006) in changing reef conditions. Raffles Bulletin of Zoology Supplement 22: 91-101

Hong J. (2012) Turning sea walls into ‘housing’ units for marine life. The Straits Times.

Huang D, Chou LM, Todd PA, Ang KH, Boon PY, Cheng L. (2006a). Algal and invertebrate diversity of the intertidal zone at Labrador Nature Reserve, Singapore. Malayan Nature Journal 59(1): 93

Huang D, Todd PA, Chou LM, Ang KH, Boon PY, Cheng L. (2006b) Effects of shore height and visitor pressure on the diversity and distribution of four intertidal taxa at Labrador Beach, Singapore. Raffles Bulletin of Zoology 54(2): 477–484

Huang D, Tun KPP, Chou LM, Todd PA. (2009) An inventory of zooxanthellate scleractinian corals in Singapore, new species records. Raffles Bulletin of Zoology Supplement 22: 69-80.

Hunter MD, Price PW. (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73(3): 724-732

Ivesa L Chapman MG, Underwood AJ, Murphy RJ. (2010) Differential patterns of distribution of limpets on intertidal seawalls: experimental investigation of the roles of recruitment, survival and competition. Marine Ecology Progress Series 407: 55-69

Jaafar Z, Hajisamae S, Chou LM, Yatiman Y. (2004) Community structure of coastal fishes in relation to heavily impacted human modified habitats. Hydrobiologia, 511:113-123

Jenkins SR, Hartnoll RG. (2001) Food supply, grazing activity and growth rate in the limpet *Patella vulgata* L.: a comparison between exposed and sheltered shores. Journal of Experimental Marine Biology and Ecology 258(1): 123-139

Kaur, S. (2003) The Garden City is getting greener. The Straits Times Interactive.

Kendrick GA. (1991) Recruitment of coralline crusts and filamentous turf algae in the Galapagos archipelago: effect of simulated scour, erosion and accretion. Journal of Experimental Marine Biology and Ecology 147(1): 47-63

Kohler KE, Gill SM. (2006) Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. Computers and Geosciences 32(9): 1259-1269

Koop K, Field JG. (1980). The influence of food availability on population dynamics of a supralittoral isopod, *Ligia dilatata brandt*. Journal of Experimental Marine Biology and Ecology 48(1): 61-72

Kwak TJ, Zedler JB. (1997) Food web analysis of southern California coastal wetlands using multiple stable isotopes. Oecologia 110(2): 262–277

Laurand S, Riera P. (2006) Trophic ecology of the supralittoral rocky shore (Roscoff, France): A dual stable isotope (δ13C, δ15N) and experimental approach. Journal of Sea Research 56(1): 27-36

Lee AC, Sin TM. (2009) Intertidal assemblages on coastal defence structures in Singapore II. Contrasts between islands and the mainland. Raffles Bulletin of Zoology (22): 255–268

Lee AC, Liao LM, Tan KS. (2009a) New records of marine algae on artificial structures and intertidal flats in coastal waters of Singapore. Raffles Bulletin of Zoology Supplement 22: 5-40

Lee AC, Tan KS, Sin TM. (2009b) Intertidal assemblages on coastal defence structures in Singapore I: A faunal study. Raffles Bulletin of Zoology 22: 237-254

Lee Q, Yaakub SM, Ng NK, Erftemeijer PLA, Todd PA. (2012) The crab fauna of three seagrass meadows in Singapore: A pilot study. Nature in Singapore 5: 363-368

Lee SK. (1966) The natural history of the shore flora and fauna off Tanjong Teritip, Singapore. Malayan Nature Journal 19: 259–274

Lepoint G, Dauby P, Gobert S. (2004) Applications of C and N stable isotopes to ecological and environmental studies in seagrass ecosystems. Marine Pollution Bulletin 49(11-12): 887-91

Liow LH. (2000) Mangrove conservation in Singapore: A physical or a psychological impossibility? Biodiversity and Conservation 9: 309-332

Low J. (2012) Conservation of our natural heritage: The Singapore experience. Proceedings of the 12th International Coral Reef Symposium, Cairns, Australia, pp 10-13

Lundholm JT, Richardson PJ. (2010) Mini-review: Habitat analogues for reconciliation ecology in urban and industrial environments. Journal of Applied Ecology 47(5): 966-975

Lye LH. (1991) Wildlife protection laws in Singapore. Singapore Journal of Legal Studies (1991): 287-319

Martins GM, Thompson RC, Neto AI, Hawkins SJ, Jenkins SR. (2010) Enhancing stocks of the exploited limpet *Patella candei* d’Orbigny via modifications in coastal engineering. Biological Conservation 143(1): 203-211

McKinney, ML. (2008) Effects of urbanization on species richness: A review of plant and animals. Urban Ecosystems 11: 161-176

McQuaid CD, Lindsay TL. (2000) Effect of wave exposure on growth and mortality rates of the mussel Perna perna: bottom-up regulation of intertidal populations. Marine Ecology Progress Series 206: 147-154

Megina C, González-Duarte MM, López-González PJ, Piraino S. (2012) Harbours as marine habitats: hydroid assemblages on sea-walls compared with natural habitats. Marine Biology 160(2): 371-381

Menge BA. (1992) Community regulation: under what conditions are bottom-up factors important on rocky shores? Ecology 73(3): 755-765

Menge BA. (2000) Top-down and bottom-up community regulation in marine rocky intertidal habitats. Journal of Experimental Marine Biology and Ecology 250: 257-289

Michener RH, Kaufman L. (2007) Stable isotope ratios as tracers in marine food webs: An update. In: Michener RH, Lajtha K. (eds.) Stable Isotopes in Ecology and Environmental Science, Blackwell Publishing, Oxford, England, pp 238-282

Miller JR. (2005) Biodiversity conservation and the extinction of experience. Trends in Ecology & Evolution 20(8): 430-4

Minagawa M, Wada E. (1984) Stepwise enrichment of 15N along food chains: Further evidence and the relation between δ15N and animal age. Geochimica et Cosmochimica Acta 48(5): 1135-1140

Minuer F., Cook E.J., Minchin D., Bohn K., Macleod A., Maggs C.A. (2012) Changing coasts: marine aliens and artificial structures. Oceanography and Marine Biology 50: 189-234

Ministry of National Development (MND). (2013) A sustainable population for a dynamic Singapore: Population White Paper. Ministry of National Development, Singapore.

Molnar J.L., Gamboa R.L., Revenga C., Spalding M.D. (2008) Assessing the global threatof invasive species to marine biodiversity. Frontiers in Ecology and the Environment 6: 485-492

Moschella P, Abbiati M, Aberg P, Airoldi L, Anderson J, Bacchiocchi F, Bulleri F, Dinesen G, Frost M, Gacia E. (2005) Low-crested coastal defence structures as artificial habitats for marine life: Using ecological criteria in design. Coastal Engineering 52(10-11): 1053-1071

National Parks Board (NParks). (2012) Comprehensive Marine Biodiversity Survey: Resources. Retrieved Mar 27 2013 from the National Parks Board Comprehensive Marine Biodiversity Survey website: http://www.nparks.gov.sg/cmbs/index.php?option=com_content&view=article&id=9&Itemid=5

Neo ML, Todd PA. (2011) Predator-induced changes in fluted giant clam (Tridacna squamosa) shell morphology. Journal of Experimental Marine Biology and Ecology 397(1): 21-26

Neo ML, Todd PA. (2012) Population density and genetic structure of the giant clams Tridacna crocea and T. squamosa on Singapore's reefs. Aquatic Biology 14:265-275

Neo ML, Erftemeijer PLA, van Beek JKL,van Maren DS, Teo SL-M,Todd PA. (2013) Recruitment constraints in Singapore's fluted giant clam (Tridacna squamosa) populations – A dispersal model approach. PLoS ONE 8(3): e58819

Ng CSL, Chen D, Chou LM. (2012) Hard coral assemblages on seawalls in Singapore. In: Contributions to Marine Science. Tropical Marine Science Institute, Singapore, pp 75-79

Ng CSL, Toh TC, Toh KB, Guest JR, Chou LM. (2013) Dietary habits of grazers influence their suitability as biological controls of fouling macroalgae in ex situ mariculture. Aquaculture Research 2013: 1-9

Ng, PPKL, Low JKY. (1994) Status of Mangroves in Singapore: Conservation beyond the year 2000. In: Wilkinson C, Sudara S, Chou LM. (eds.) Third ASEAN-Australia Symposium on Living Coastal Resources, Chulalongkorn University, Bangkok, pp. 229-232

Ng PPKL, Schubart CD. (2002) Haberma nanum, a new genus and new species of mangrove crab (Custace: Decapoda: Brachyura: Sesarmidae) from Singapore. The Raffles Bulletin of Zoology 50(2):437-442

Paine RT. (1966) Food web complexity and species diversity. The American Naturalist 100(910): 65–75

Pennings SC, Carefoot TH, Zimmer M, Danko JP, Ziegler A. (2000) Feeding preferences of supralittoral isopods and amphipods. Canadian Journal of Zoology 78: 1918-1929

Peterson BJ, Fry B. (1987) Stable Isotopes in Ecosystem Studies. Annual Review of Ecology and Systematics 18(1): 293-320

Peterson BJ. (1999) Stable isotopes as tracers of organic matter input and transfer in benthic food webs: a review. Acta Oecologica 20(4): 479–487

Phillips DL, Gregg JW. (2003) Source partitioning using stable isotopes: coping with too many sources. Oecologia 136(2): 261-9

Pister B. (2009) Urban marine ecology in southern California: the ability of riprap structures to serve as rocky intertidal habitat. Marine Biology 156(5): 861-873

Polis GA, DR Strong. (1996) Food web complexity and community dynamics. The American Naturalist 5: 813-846

Post DM. (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83(3): 703-718

Qvarfordt S, Kautsky H, Malm T. (2006) Development of fouling communities on vertical structures in the Baltic Sea. Estuarine, Coastal and Shelf Science 67(4): 618-628

Ramcharan, R. (2002) Forging a Singaporean Statehood, 1965-1995: The Contribution of Japan. Kluwer Law International, The Netherlands.

Riera P, Hubas C. (2003) Trophic ecology of nematodes from various microhabitats of the Roscoff Aber Bay (France): importance of stranded macroalgae evidenced through δ13C and δ15N. Marine Ecology Progress Series 260(1989): 151-159

Riera P, Escaravage C, Leroux C. (2009) Trophic ecology of the rocky shore community associated with the *Ascophyllum nodosum* zone (Roscoff, France): A δ13C vs δ15N investigation. Estuarine, Coastal and Shelf Science 81(1): 143-148

Rolff C. (2000) Seasonal variation in δ13C and δ15N of size-fractionated plankton at a coastal station in the northern Baltic proper. Marine Ecology Progress Series 203: 47-65

Rosenzweig ML. (2003) Reconciliation ecology and the future of species diversity. Oryx 37(02): 194-205

Sala E. (2004) The Past and Present Topology and Structure of Mediterranean Subtidal Rocky-shore Food Webs. Ecosystems 7(4): 333-340

Schaal G, Riera P, Leroux C. (2008) Trophic coupling between two adjacent benthic food webs within a man-made intertidal area: A stable isotopes evidence. Estuarine, Coastal and Shelf Science 77(3): 523-534

Schaal G, Riera P, Leroux C, Grall J. (2009) A seasonal stable isotope survey of the food web associated to a peri-urban rocky shore. Marine Biology 157(2): 283-294

Schiel DR. (2004) The structure and replenishment of rocky shore intertidal communities and biogeographic comparisons. Journal of Experimental Marine Biology and Ecology 300(1-2): 309-342

Shafir S, Abady S, Rinkevich B. (2009) Improved sustainable maintenance for mid-water coral nursery by the application of an anti-fouling agent. Journal of Experimental Marine Biology and Ecology 368(2): 124-128

Singapore Department of Statistics (2013) Latest data: Population & Land Area Retrieved Mar 27 2013 from the Singapore Department of Statistics Website: http://www.singstat.gov.sg/statistics/latest_data.html#12

Sodhi NS, Briffett C, Kong L, Yuen, B. (1999) Bird use of linear areas of a tropical city: implications for park connector design and management. Landscape and Urban Planning 45(2-3): 123-130

Steinarsdóttir MB, Ingólfsson A, Ólafsson E. (2009) Trophic relationships on a fucoid shore in south-western Iceland as revealed by stable isotope analyses, laboratory experiments, field observations and gut analyses. Journal of Sea Research 61(4): 206-215

Sulzma EW. (2007) Stable isotope chemistry and measurement : a primer. In: Michener RH, Lajtha K. (eds.) Stable Isotopes in Ecology and Environmental Science, Blackwell Publishing: Oxford, England, pp 1-21

Tan K-S. (2003) Feeding ecology of common intertidal Muricidae (Mollusca: Neogastropoda) from the Burrup Peninsula, Western Australia. In: Wells FE, Walker DI, Jones DS. (eds.) The Marine Flora and Fauna of Dampier, Western Australia. Western Australian Museum, Perth, pp 173-192

Tan YZ, Ng CSL, Chou LM. (2012) Natural colonisation of a marina seawall by scleractinian corals along Singapore’s east coast. Nature in Singapore 5: 177-183

Tay YC, Todd PA, Rosshaug PS, Chou LM. (2012) Simulating the transport of broadcast coral larvae among the Southern Islands of Singapore. Aquatic Biology 15(3): 283-297

Todd PA, Chou LM. (2005) A tale of survival: Labrador Park, Singapore. Coral Reefs 54(2): 477-484

Turner IM, Tan HTW, Wee YC, Ibrahim AB, Chew PT, Corlett RT (1994) A study of plant species extinction in Singapore : Lessons for the conservation of tropical biodiversity. Conservation Biology 8(3): 705-712

Tyrrell MC, Byers JE. (2007) Do artificial substrates favour nonindigenous fouling species over native species? Journal of Experimental Marine Biology and Ecology 342(1): 54-60

Underwood, AJ. (1981) Structure of a rocky intertidal community in New South Wales: Patterns of vertical distribution and seasonal changes. Journal of Experimental Marine Biology and Ecology 51: 57-85

Urban Redevelopment Authority (URA) (2000) Concept Plan review 2000: Focus group consultation on land allocation. Urban Redevelopment Authority, Singapore

Urban Redevelopment Authority (URA) (2010) About land use planning. Retrieved Mar 27 2013 from Urban Redevelopment Authority of Singapore website: https://www.ura.gov.sg/land_use_planning/

Urban Redevelopment Authority (URA) (2011) Concept Plan review 2011: Final report of focus group on sustainability and identity. Urban Redevelopment Authority, Singapore

Vadas Sr. RL, Johnson S, Norton TA. (1992) Recruitment and mortality of early post-settlement stages of benthic algae. British Phycological Journal 27(3): 37-41

Vanderklift MA, Ponsard S. (2003) Sources of variation in consumer-diet delta 15N enrichment: a meta-analysis. Oecologia 136(2): 169-82

Wang Z-Q, Wu L-H, Liu T-T. (2009) Revegetation of steep rocky slopes: Planting climbing vegetation species in artificially drilled holes. Ecological Engineering 35(7): 1079-1084

Wee YC, Hale R. (2008) The Nature Society (Singapore) and the struggle to conserve Singapore's nature areas. Nature in Singapore 1: 41-49

Whorff JS, Whorff LL, Sweet MH. (1995) Spatial Variation in an algal turf community with respect to substratum slope and wave height. Journal of the Marine Biological Association of the United Kingdom 75: 429-444

Wilding TA, Rose CA, Downie MJ. (2007) A novel approach to measuring subtidal habitat complexity. Journal of Experimental Marine Biology and Ecology 353(2): 279-286

Williams, GA. (1993) Seasonal variation in algal species richness and abundance in the presence of molluscan herbivores on a tropical rocky shore. Journal of Experimental Marine Biology and Ecology 167: 261-275

Wilson SK, Bellwood DR, Choat JH, Furnas MJ. (2003) Detritus in the epilithic algal matrix and its use by coral reef fishes. Oceanography and Marine Biology: An Annual Review 41: 279-309

World Bank (2012) GDP per capita (current US$) Retrieved July 19 2013 from the World Bank Website: http://data.worldbank.org/indicator/NY.GDP.PCAP.CD

Worm B, Lotze HK, Hillebrand H and Sommer U. (2002) Consumer versus resource control of species diversity and ecosystem functioning. Nature 417(6891): 848-51

Worm B, Lotze HK. (2006) Effects of eutrophication, grazing, and algal blooms on rocky shores. Limnology Oceanography 51(1-2): 569-579

Yaakub SY, Lim RLF, Lim WL, Todd PA. (2013) The diversity and distribution of seagrass in Singapore. Nature in Singapore 6: 105-111

Yee ATK, Ang WF, Teo SY. (2010) The present extent of mangrove forests in Singapore. Nature in Singapor, 3: 139-145

Yoshioka T, Wada E, Hayashi H. (1994) A stable isotope study on seasonal food web dynamics in a eutrophic lake. Ecology 75(3): 835–846