Aquatic Invasions (2018) Volume 13, Issue 3: 365–378
DOI: https://doi.org/10.3391/ai.2018.13.3.05
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Research Article

Do Singapore's seawalls host non-native marine molluscs?

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Received: 9 March 2018 / Accepted: 8 August 2018 / Published online: 17 September 2018

Handling editor: Cynthia McKenzie

Abstract

Marine urbanization and the construction of artificial coastal structures such as seawalls have been implicated in the spread of non-native marine species for a variety of reasons, the most common being that seawalls provide unoccupied niches for alien colonisation. If urbanisation is accompanied by a concomitant increase in shipping then this may also be a factor, i.e. increased propagule pressure of non-native species due to translocation beyond their native range via the hulls of ships and/or in ballast water. Singapore is potentially highly vulnerable to invasion by non-native marine species as its coastline comprises over 60% seawall and it is one of the world's busiest ports. The aim of this study is to investigate the native, non-native, and cryptogenic molluscs found on Singapore's seawalls. Seven seawall sites around Singapore were surveyed and all specimens found were either Indo-Pacific species or of unknown origin. To determine whether there were potential non-natives from within the Indo-Pacific, a set of attributes concerning the history, biogeography, detectability, human affinity, invasion pathway, biology, ecology, life-history, pre-history, evolution and genetics of mollusc species was collected from available literature. Only one "possibly introduced" species, *Siphonaria guamensis* Quoy and Gaimard, 1833 (Gastropoda), was identified. The remaining species consisted of 41 native to Singapore and 23 cryptogenic species. The results from this study add to the increasing pool of literature showing that, contrary to widespread assumption, there is a very low occurrence of non-native marine species in Singapore.

Key words: intertidal, ecological engineering, urban ecology, invasive species, reconciliation

Introduction

Man-made coastal structures have been associated with the proliferation and establishment of marine non-native species (e.g., Amat et al. 2008; Mineur et al. 2012; Airoldi et al. 2015). They represent novel and "invasible" habitats that tend to display traits such as high levels of disturbance and lack of natural predators, which can facilitate colonization by opportunistic species (Lodge 1993; Mineur et al. 2012). For instance, the pantropical seaweed, *Caulerpa webbiana*, rapidly colonized Horta harbour in Faial in the North-Eastern Atlantic Azores Islands, occurring at highest densities along the seawall of the harbour (Amat et al. 2008). In the North Adriatic Sea, Airoldi et al. (2015) showed that some artificial marine infrastructure, including seawalls and breakwaters, significantly favoured non-native over native marine species as the assemblages were dominated by non-native and cryptogenic species.

As the number of people living within 100 km of the sea increases (Martínez et al. 2007), huge stretches of coastal landscapes are being developed to facilitate a range of economic and social activities (Yeung 2001; Masselink and Gehrels 2014). This process has been exacerbated by the combined threats of sea-level rise and more frequent and intense storms associated with global warming (Bulleri and Chapman 2015)

that necessitate the construction of defences (e.g., seawalls and breakwaters) to provide shoreline protection (Masselink and Gehrels 2014). Seawalls, in particular, are becoming one of the most prevalent man-made features along urban coastlines (Chapman and Bulleri 2003). For instance, seawalls comprise ~ 95% of the coastline in Victoria Harbour in Hong Kong (Lam et al. 2009), while in Sydney Harbour, they represent approximately half of the entire foreshore (Chapman and Bulleri 2003). In Singapore, 63% of the island-nation's coastline is seawall and this is predicted to reach up to 74% in the next 50 years (Lai et al. 2015).

Non-native species can exert wide-ranging impacts in their newly-established habitats; however, it is only when they generate ecological and economic costs, that they are considered invasive (International Union for the Conservation of Nature 2000). For example, serpulid polychaetes such as *Hydroides elegans* (Haswell, 1883) have become a major biofoulant on artificial surfaces throughout the Mediterranean and their control incurs significant costs (Kocak et al. 1999; Streftaris and Zenetos 2006). In Hawaii, the invasive algae *Hypnea musciformis* (Wulfen) J.V.Lamouroux, 1813, forms massive algae blooms with detrimental impacts to coral reefs as well as to tourism and property value (Cesar et al. 2002). It is difficult to predict whether the impact of a non-native species will be neutral, positive or negative, and therefore it is prudent to treat all of them with caution.

Globalization has facilitated the transport of species via a multitude of introduction pathways (Occhipinti-Ambrogi and Savini 2003; Mineur et al. 2012). Shipping, aquaculture, canal construction and the aquarium trade are some of the most common anthropogenic routes of introduction for non-native marine species (Molnar et al. 2008). The intensification of maritime trade, in particular, has played a principal role in accelerating their proliferation, accounting for more than half of global marine bio-invasions (Molnar et al. 2008; Hulme 2009). In light of the importance of shipping activities in the spread of marine species, Seebens et al. (2013) incorporated data on global cargo ship networks to model the risks of marine invasions via release of ballast water. The study identified Singapore as the number one bio-invasion hot spot—facing the highest risk of introductions via shipping ballast (Seebens et al. 2013). However, Jaafar et al. (2012) reported only 17 non-native marine species established in Singapore, with just six of these thought to have been introduced via shipping-mediated pathways. Out of the 17 non-native species reported, two were molluscs, namely *Mytilopsis sallei* and *Brachidontes striatulus*. One additional non-native mussel, *Mytella strigata*, was detected in 2016 and subsequently ascertained to be established in Singapore (Lim et al. 2018). Hence, despite being potentially exposed to high propagule pressure due to shipping activity, the available literature indicates that Singapore hosts a surprisingly low number of non-native marine species, seemingly contradicting Seebens et al.'s (2013) model predictions.

Singapore, nevertheless, remains a major shipping hub that is surrounded by seawalls and other artificial marine structures, thus a targeted investigation into the presence/absence of non-native species is warranted. Based on tonnage, Singapore is currently the second largest port in the world, with over 130,000 ship calls every year (Singapore Department of Statistics 2016). Almost two thirds of Singapore's coastline is seawall: generally grouted or un-grouted granite "rip-rap" armour, i.e. boulders stacked along the coastline at a ~30º slope (Lai et al. 2015). While there have been some surveys of the biodiversity found on local seawalls (Lee and Sin 2009; Lee et al. 2009a; Lee et al. 2009b), the native/non-native status of these inhabitants has never been documented. If the origin of the species remains unknown, it is impossible to assess the extent of any biological invasion and hence devise appropriate management strategies. The present study aimed to document as many non-native species as possible. We focused on molluscs as they are dominant fauna on Singapore's seawalls (Lee et al. 2009a; Loke et al. 2016; Loke and Todd 2016; Loke et al. 2017) and local taxonomic expertise is available. Specific objectives were to add to the number of seawalls surveyed and to produce a comprehensive list of native, non-native, and cryptogenic molluscs on seawalls in Singapore. The findings from this study will provide a much-needed baseline for monitoring of potentially invasive molluscs. The results will also have implications for management strategies and habitat reconciliation efforts for seawalls in Singapore.

Material and methods

Located just over one degree north of the equator, Singapore is a tropical island city-state separated from Peninsular Malaysia by the Straits of Johor in the north, and from Indonesia by the Straits of Singapore in the south. The total land area of Singapore (approximately 719.1 km^2) comprises the main island and over 60 smaller natural and man-made islands (Singapore Department of Statistics 2016). Almost 20% of this area has been reclaimed from the sea during the last 50 years and erosion of this new land is controlled using artificial coastal defences (Singapore Land Authority 2017).

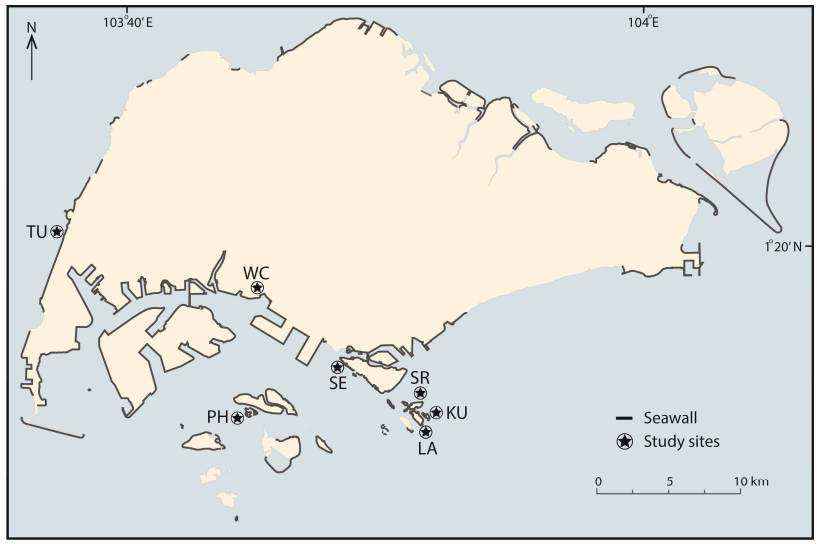

Figure 1. Survey sites in present study. Abbreviations used: KU, Kusu Island; LA, Lazarus Island; PH, Pulau Hantu; SE, Sentosa; SR, Seringat Island; TU, Tuas; WC, West Coast. Map of seawalls in Singapore adapted from Lai et al. (2015).

Sampling sites, survey protocol and species identification

Surveys were conducted at seven seawall sites, two on the western coast of mainland Singapore and five among the Southern Islands of Singapore (Figure 1; Supplementary material Table S1). None of these seven sites had been surveyed before. Results were compared to data from previous seawall studies (i.e. Lee et al. 2009a; Loke and Todd 2016; Loke et al. 2016) conducted at Pasir Ris, Marine Parade, Fort road, Marina South, Labrador park, Tuas, St John's Island, Pulau Tekukor, Sister's Islands, Pulau Hantu, Pulau Satumu and Sultan Shoal.

Temperature, light, slope angle and surface rugosity were measured at all seawalls surveyed to characterise each site (Table S1). Temperature and light were measured using data loggers (HOBO Pendant®), two of which were attached to the substrate at each site for two weeks. Maximum, minimum and average temperature and light readings were obtained for all sites. Slope angle was calculated by measuring the horizontal distance from a virtual point 1.8 m above the base of the seawall to the slope of the seawall (Figure S1). Surface rugosity was measured using the "chain link method" (Luckhurst and Luckhurst 1978), where a steel chain with fixed link length was laid over the substrate surface along a straight transect length perpendicular to the base of the seawall and was made to adhere as closely as possible to the contours and crevices of the seawall. Linear distance of the same transect length was also measured to derive the ratio of surface distance to linear distance as a measure of surface rugosity.

All surveys were conducted during evening spring low tides from November 2014 to January 2015 when the entire seawall is exposed, i.e. at tidal heights of 0.4–0.7 m. At each site, a single 50 m length of wall was demarcated parallel to the shoreline. The entire seawall, comprising a flattened top, a middle sloping surface, a base and in some cases, a horizontal revetment prior to the base, within this 50 m stretch was surveyed for 90 mins by one person (WTT). The survey method was based on the Rapid Assessment Survey (RAS) protocol, one of the five most common survey methods utilised to detect introduced marine species (Campbell et al. 2007). The advantage of the RAS protocol is its inclusion of qualitative sampling methods which are not constrained to any particular sample area or do not collect all material from an area (i.e. complete census) but, rather, are largely based on time-restricted haphazard visual searches standardized by catch effort (e.g., all species collected within one hour at a specific site; Campbell et al. 2007). In the present study the protocol was applied to one taxon only: molluscs. Samples were preserved in 75% ethanol and identified in the laboratory to species level using the following guides and identification keys: Mollusca (Tan and Ng 1988; Poutiers 1998a, b; Tan and Chou 2000), Cerithiidae (Houbrick 1985; Houbrick 1992), Littorinidae (Reid 1984), Muricidae (Tan and Sigurdsson 1990; Tan and Sigurdsson1996; Tan 2000) and Neritidae (Tan and Clements 2008). The species list arising from the current study was merged with previous lists from Lee et al. (2009a) and Loke and Todd (2016) to create the most complete catalogue of mollusc species found on seawalls in Singapore to date.

Determining the status (native/non-native/cryptogenic) of species

Native (or indigenous) species refers to species that occur within their natural range and dispersal potential, i.e. they occur in Singapore naturally without direct or indirect anthropogenic introduction or maintenance (International Union for the Conservation of Nature 2000). Non-native (alien, introduced, or non-indigenous) species are those that occur outside their natural range and dispersal potential, i.e. they are unlikely to occur in Singapore naturally without direct or indirect anthropogenic introduction or maintenance (International Union for the Conservation of Nature 2000). Cryptogenic species are species that cannot be demonstrated to be native or introduced (Carlton 1996).

Criteria used to determine whether a species was native, non-native or cryptogenic to Singapore were adapted from Chapman and Carlton (1991), whereby 10 attributes for introduced species were proposed in the form of testable hypotheses to be validated or disproved. Under an "introduced species hypothesis", positive evidence of an attribute indicates that a species may be introduced to a locale whereas negative evidence implies that a species is native (Chapman and Carlton 1991). A species for which there is insufficient evidence to demonstrate it to be either introduced or native status is regarded as cryptogenic, following the definition by Carlton (1996). The overall correspondence of all attributes of a species being examined is evaluated to determine its introduced status. The specific attributes that were considered following Chapman and Carlton (1991) and adapted to Singapore in the present study are summarised in Table 1.

Attributes 1, 6 and 7 (Appearance in local regions where not found previously, Discontinuous regional distribution, and Discontinuous global distribution, respectively) were first evaluated for all species using a variety of published material, including historical literature, regional checklists of molluscs, taxonomic monographs and "grey literature", to determine the local, regional and global distribution of the species and thereby narrow down the species that are potentially non-native to Singapore. Attribute 5 (Prevalence on or restriction to new or artificial environment(s)) was also examined to assess the prevalence of all species on seawalls in Singapore. Attribute 3 (Association with human mechanism(s) of dispersal) was positive for all the species identified in this study owing to Singapore being a major shipping hub. The remaining attributes were then applied to "potentially introduced" species using species-specific studies where available.

Results

A total of 42 species of mollusc were recorded from the seven sites sampled in this study (Table 2). Thirty-five of these had been recorded previously on Singapore's seawalls (Lee et al. 2009a; Loke and Todd 2016; Loke et al. 2016), while seven species are new records (i.e. previously unrecorded) from the seawalls. Adding these seven species to the previous lists in Lee et al. (2009a) and Loke and Todd (2016) results in a combined total of 65 species. Based on our survey, species richness among the sites ranged from six to 23 (Table 2; Figure 2). West Coast was particularly species-poor, with only six species of molluscs identified; the seawall with the second lowest species richness was Kusu Island with 16 mollusc species. Seringat Island had the highest mollusc species richness with 23 species identified. Not all of the species were common across the sites. Only one species, *Drupella margariticola* (Broderip, 1833) was found at all the seven surveyed seawalls, while four species (i.e. *Siphonaria guamensis* Quoy and Gaimard, 1833, *Monodonta labio* (Linnaeus, 1758), *Nerita undata* Linnaeus, 1758 and *Reishia bitubercularis* (Lamarck, 1822)) were found at six of the seven seawall sites. There were 16 species that were only recorded at a single seawall site (Table 2).

Status of native, non-native and cryptogenic species on Singapore's seawalls

A literature review on the distribution of the mollusc species identified in the present study and those listed in Lee et al. (2009a) and Loke and Todd (2016), revealed that all of the 65 species found on seawalls in Singapore to date occur within the larger realm of the Indo-Pacific (Figure 3).

Variation in the terms used to describe species distribution includes the regions: Indo-West Pacific, Western Pacific, Western-Central Pacific and Indian Ocean (Table 3). As such, there were no obvious non-native mollusc species from the East Pacific, Atlantic coasts or the Mediterranean, for example. However, the Indo-Pacific realm encompasses a vast region of great diversity and species are not necessarily spread homogeneously, i.e. organisms can occur in a discontinuous manner within the Indo-Pacific and be considered native only to a sub-region of the larger Indo-Pacific. Thus, based on the broadly-defined Indo-Pacific distribution of species alone, it is difficult to determine whether there are non-native species from other parts of the Indo-Pacific region occurring on Singapore's seawalls.

Application of the attributes described in Table 1 to all 65 mollusc species revealed that only one species

Table 1. Specific attributes to assess the native/non-native/cryptogenic status of species in the present study. Adapted from Chapman and Carlton (1991) to Singapore's context.

No	Attributes by Chapman and Carlton (1991)	Adaptation to Singapore in the present study
1	Previously unrecorded in local region	This attribute can be assessed by referring to reliable historical surveys of local fauna. In this study, the checklist of Singapore molluscs by Tan and Woo (2010) was the primary reference for this purpose.
2	Range expansion following introduction	This attribute can be assessed only if information regarding the exact location of the first appearance of the species in question and its subsequent range expansion is available. In this study, the location of a species' first record within Singapore was often not available or ambiguous. Therefore, this attribute could not be adequately evaluated.
3	Access to human mechanism(s) of dispersal	Since populations of introduced species usually remain associated with the dispersal mechanisms by which they arrived (Chapman and Carlton 1991), this attribute can be assessed by identifying the possible routes of introduction into a location. Some of the most common human-assisted pathways include shipping, aquaculture and aquarium trade (Molnar et al. 2008). Singapore has been a major centre for global trade ever since its establishment (Buckley 1902). The long maritime history coupled with the voluminous level of shipping activities of Singapore would provide considerable human mechanisms of dispersal of organisms to Singapore (Yeo et al. 2011; Jaafar et al. 2012). It is likely that shipping is a major introduction pathway for any non-native species found on the seawall. Other possible human mechanisms of dispersal include commercial fisheries and the ornamental trade (Yeo et al. 2011; Jaafar et al. 2012).
4	Association with other introduced species	Introduced species tend to co-exist predominantly with other introduced taxa (Chapman and Carlton 1991). This attribute can only be assessed if species-specific ecological studies are available. Also, since the non-native status of many taxa on seawalls in Singapore have yet to be verified prior to this study, it is difficult to adequately evaluate this attribute in this study.
5	Prevalence on or restriction to new or artificial environment(s)	Introduced species often dominate on or are limited to human-created substrates such as coastal defences, rock jetties and buoys (Chapman and Carlton 1991; Mineur et al. 2012). In this study, this attribute was assessed by evaluating the prevalence of the species in question across all the seawalls sites surveyed in this present study as well as in Lee et al. (2009a).
6	Discontinuous or restricted regional distribution	Introduced species tend to have a restricted distribution along a continuous continental margin (Chapman and Carlton 1991). When applied by Chapman and Carlton (1991) and subsequent authors (e.g., Wasson et al. 2000; Toft et al. 2002), the regional distribution of species was evaluated along a continuous coastline, e.g., the North American Atlantic coastline. However, Singapore is a small island and a "continuous continental margin" is limited to that of the island. Therefore, in the present study, the attribute was assessed by determining the presence of the species in Singapore and Peninsular Malaysia, since both Singapore and Peninsular Malaysia belong to the same marine ecoregion (Spalding et al. 2007) so it can be expected that both locales may share similar marine species.
7	Disjunct global distribution	It is rare for marine invertebrates of the northern hemisphere, which have been extensively studied, to have naturally isolated intercontinental or interoceanic populations (Chapman and Carlton 1991). In the present study, this attribute was assessed by looking at the overall distribution of the species in question beyond Singapore and Peninsular Malaysia, and determining whether the known populations form a discontinuous distribution globally.
8, 9	Insufficient (active and passive) dispersal capabilities to account for observed distribution	This attribute can be assessed only if information regarding the life history stages and adaptations for dispersal of the species in question is available.
10	Exotic evolutionary origin	Most introduced species share the closest genetic affinity to species groups occurring elsewhere in the world (Chapman and Carlton 1991). This attribute can be assessed only if there are rigorous phylogenetic analyses of all species in a genus.

Table 2. List of taxa collected and identified from all seven sites. Presence (●) of taxa found at each site is indicated. Please refer to Figure 1 for abbreviations of sites surveyed.

Species	Location						
	WC	SR	LA	KU	SE	TU	PH
Mollusca: Gastropoda							
Cellana radiata (Born, 1778)			●		●		●
Patelloida saccharina (Linnaeus, 1758)	●	●	●	●			
Siphonaria atra Quoy and Gaimard, 1833		●	●	●	●		
Siphonaria guamensis Quoy and Gaimard, 1833	●	●	●	●	●		●
Siphonaria javanica (Lamarck, 1819)			●				
Turbo bruneus (Röding, 1798)		●		●	●		●
Monodonta labio (Linnaeus, 1758)		●	●	●	●	●	●
Trochus maculatus Linnaeus, 1758		●	●	●	●		●
Trochus radiatus Gmelin, 1791					●		
Nerita albicilla Linnaeus, 1758		●	●	●	●		●
Nerita articulata Gould, 1847						●	●
Nerita chameleon Linnaeus, 1758							●
Nerita histrio Linnaeus, 1758						●	●
Nerita undata Linnaeus, 1758		●	●	●	●	●	●
Echinolittorina malaccana (Philippi, 1847)	●	●	●	●	●		
Echinolittorina vidua (Gould, 1859)		●	●	●	●		
Littoraria articulata (Philippi, 1846)	●		●			●	
Littoraria strigata (Philippi, 1846)	●	●	●	●	●		
Planaxis sulcatus (Born, 1778)				●			
Chicoreus capucinus (Lamarck, 1822)						●	
Drupella margariticola (Broderip, 1833)	●	●	●	●	●	●	●
Reishia bitubercularis (Lamarck, 1822)		●	●	●	●	●	●
Reishia clavigera (Küster, 1860)		●	●			●	
Semiricinula fusca (Küster, 1862)		●	●	●	●		●
Tenguella musiva (Kiener, 1835)		●	●	●	●	●	
Pollia fumosa (Dillwyn, 1817)						●	
Euplica scripta (Lamarck, 1822)		●	●		●		●
Pardalinops testudinaria (Link, 1807)		●			●		●
Pictocolumbella ocellata (Link, 1807)			●		●		●
Pseudanachis basedowi (Hedley, 1918)						●	
Gyrineum natator (Röding, 1798)						●	
Laevistrombus turturella (Röding, 1798)						●	
Cerithium coralium Kiener, 1841					●		
Cerithium traillii G. B. Sowerby II, 1855		●					●
Clypeomorus pellucida (Hombron and Jacquinot, 1852)						●	
Clypeomorus batillariaeformis Habe and Kosuge, 1966		●				●	●
Clypeomorus petrosa chemnitziana (Pilsbry, 1901)		●					
Rhinoclavis sinensis (Gmelin, 1791)		●					
Batillaria zonalis (Bruguière, 1792)		●			●		
Nassarius crenoliratus (A. Adams, 1852)					●	●	●
Nassarius livescens (Philippi, 1849)							●
Mollusca: Bivalvia							
Gafrarium divaricatum (Gmelin, 1791)						●	
Perna viridis (Linnaeus, 1758)						●	
Total mollusc species	6	23	20	16	22	19	20

is likely to be non-native to Singapore, *Siphonaria guamensis*. Forty-one species were found to be native and the remaining 23 species were classed as cryptogenic (Table 3). Of the species classified as cryptogenic, 22 have two or less attributes with positive evidence that they may be introduced. One other, *Semiricinula fusca* (Küster, 1862), had three positive attributes supporting a non-native origin, however, as its presence in Singapore was recorded in the early 1970s (Chuang 1973)—suggesting it is native, its status remains ambiguous.

Discussion

This study is the first to examine the origin status of marine molluscs on Singapore's seawalls. Our present surveys produced seven new records for Singapore's seawalls, i.e. these seven taxa were not recorded in previous studies of Singapore seawalls by Lee et al. (2009a) and Loke and Todd (2016). Combining our survey results with the lists in Lee et al. (2009a) and Loke and Todd (2016) yielded a baseline total of 65

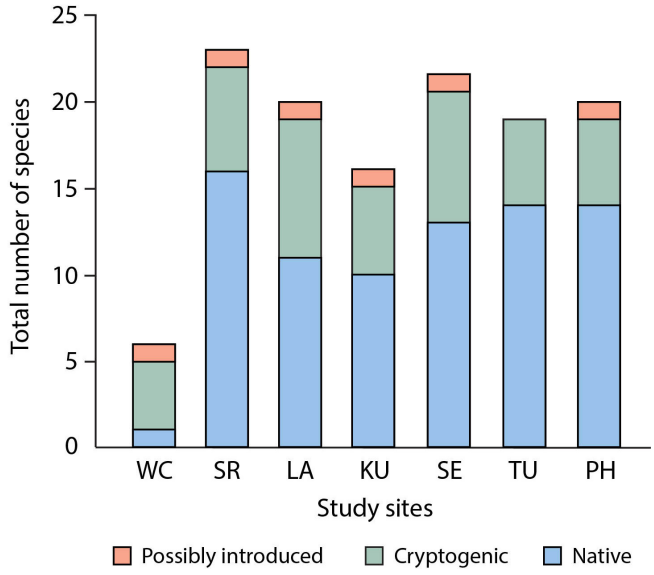

Figure 2. Mollusc richness and proportion of native, cryptogenic and possible introduced species at each of the seven sites surveyed in this study. Abbreviations used: KU, Kusu Island; LA, Lazarus Island; PH, Pulau Hantu; SE, Sentosa; SR, Seringat Island; TU, Tuas; WC, West Coast.

Figure 3. Location of Singapore within the Indo-Pacific region (outlines in green) as defined in Spalding et al. (2007).

species of molluscs now known from Singapore's seawalls. When attributes used by Chapman and Carlton (1991) to assess whether an introduction has occurred were applied to these 65 species, only one was identified as being possibly introduced, *Siphonaria guamensis*. This is an unexpectedly low number when considering that Seebens et al. (2013) proposed Singapore as the top marine bio-invasion risk hotspot, and given the hypothesized association of marine alien species with seawalls (Mineur et al. 2012). Below we expand on how *Siphonaria guamensis* was determined to be "possibly introduced".

Attribute 1: Appearance in local regions where not found previously. — The earliest published record of *Siphonaria guamensis* in Singapore is relatively recent (e.g., Tan and Chou 2000; Goh et al. 2002). Local museum records of the species date back only as far as the late 1980s. The species is absent from earlier historical checklists of molluscs in Singapore (e.g., Chuang 1973; Chou et al. 1994; Way and Purchon 1981), which suggests a possible recent introduction. It is worth noting that *S. guamensis* is very common and abundant on Singapore's seawalls (pers. obs.; Chim and Tan 2009; Lee et al. 2009a). Hence, it is unlikely to have gone unnoticed if it was present historically. Nevertheless, the taxonomy of this family remains problematic and we do not rule out the possibility that the absence of earlier records of this species could be due to misidentification or a lack of means of identification.

Table 3. Distribution and origin status of molluscs found on Singapore's seawalls. Species are marked with "✶" if reported in the following studies: a = Lee et al. 2009a; b = Loke and Todd 2016; c = present study. "+" = positive (i.e. satisfies the criterion); "–" = negative (i.e. does not satisfy the criterion); "0" = insufficient evidence; N = Native; C = cryptogenic; I = possibly introduced.

Sources			Species	Distribution		Attributes				Status
a	b	c		Location	Ref*	1	5	6	7	
Mollusca, Gastropoda										
✶	✶	✶	*Siphonaria guamensis* Quoy and Gaimard, 1833	Indo-West Pacific	1	+	+	+	+	I
✶	✶	✶	*Cellana radiata* (Born, 1778)	Indo-Pacific; Indo-West Pacific	2, 3	–	+	–	+	C
✶	✶	✶	*Patelloida saccharina* (Linnaeus, 1758)	Indo-Pacific; Indo-West Pacific	3, 4	+	+	–	0	C
	✶		*Patelloida pygmaea* (Dunker, 1860)	Indo-West Pacific	3	–	+	0	0	C
✶		✶	*Siphonaria javanica* (Lamarck, 1819)	Indo-West Pacific	1	–	+	+	0	C
		✶	*Trochus radiatus* Gmelin, 1791	Indian Ocean; Red Sea	5	–	–	+	+	C
✶		✶	*Echinolittorina malaccana* (Philippi, 1847)	Indo-West Pacific	6	–	+	–	+	C
✶			*Echinolittorina melanacme* (E. A. Smith, 1876)	Indo-West Pacific	6, 7	+	+	–	–	C
		✶	*Littoraria articulata* (Philippi, 1846)	Indo-West Pacific	7, 8	–	+	–	0	C
✶	✶	✶	*Drupella margariticola* (Broderip, 1833)	Indo-Pacific	9	–	+	–	+	C
✶			*Orania bimucronata* (Reeve, 1846)	Western Central Pacific	9	+	–	+	–	C
✶		✶	*Semiricinula fusca* (Küster, 1862)	Indo-West Pacific: East Africa, Southeast and Northeast Asia	9	–	+	+	+	C
	✶		*Muricodrupa fiscella* (Gmelin, 1791)	Indo-West Pacific	10	–	0	–	0	C
✶		✶	*Reishia bitubercularis* (Lamarck, 1822)	Indo-West Pacific	11	–	+	–	+	C
✶			*Semiricinula squamosa* (Pease, 1868)	Indo-West Pacific	9	+	–	–	+	C
		✶	*Clypeomorus pellucida* (Hombron and Jacquinot, 1852)	Western Pacific	12	–	–	–	+	C
	✶		*Clypeomorus purpurastoma* Houbrick, 1985	Western Pacific and East Indian Ocean	12	–	0	–	0	C
	✶		*Clypeomorus bifasciata* (G. B. Sowerby II, 1855)	Western Pacific and Indian Ocean	12	–	0	–	0	C
		✶	*Batillaria zonalis* (Bruguière, 1792)	Northwest Pacific	9	–	–	–	+	C
	✶	✶	*Nassarius crenoliratus* (A. Adams, 1852)	Indo- Pacific; Western Central Pacific	9, 13	–	–	+	–	C
✶		✶	*Siphonaria atra* Quoy and Gaimard, 1833	Indo-West Pacific	1	–	+	–	+	N
✶	✶	✶	*Turbo bruneus* (Röding, 1798)	Indo-West Pacific	14	–	+	–	0	N
✶	✶	✶	*Monodonta labio* (Linnaeus, 1758)	Indo-Pacific	15	–	+	–	+	N
✶	✶	✶	*Trochus maculatus* Linnaeus, 1758	Indian Ocean; Indo-West Pacific	5, 16, 17	–	+	–	+	N
	✶		*Umbonium vestiarium* (Linnaeus, 1758)	Indo-Pacific	4	–	0	–	–	N
	✶		*Euchelus atratus* (Gmelin, 1791)	South-Western Indian Ocean	18	–	0	–	–	N
✶		✶	*Nerita albicilla* Linnaeus, 1758	Indo-West Pacific	19	–	+	–	+	N
✶		✶	*Nerita articulata* Gould, 1847	Indo-West Pacific	19	–	–	–	+	N
✶	✶	✶	*Nerita chameleon* Linnaeus, 1758	Indo-West Pacific	19	–	+	–	+	N
✶		✶	*Nerita histrio* Linnaeus, 1758	Indo-West Pacific	19	–	–	–	+	N
✶	✶	✶	*Nerita undata* Linnaeus, 1758	Indo-West Pacific	19	–	+	–	+	N
✶		✶	*Echinolittorina vidua* (Gould, 1859)	Indo-West Pacific	6, 7	–	+	–	0	N
		✶	*Littoraria strigata* (Philippi, 1846)	Indo-West Pacific	7, 8	–	+	–	+	N
	✶	✶	*Planaxis sulcatus* (Born, 1778)	Tropical Pacific	20	–	–	–	+	N
		✶	*Chicoreus capucinus* (Lamarck, 1822)	Southeast Asia; Pacific Ocean; Tropical Australia	21	–	–	–	0	N
✶	✶	✶	*Tenguella* musiva (Kiener, 1835)	Indo-West Pacific	11	–	+	–	0	N
✶		✶	*Reishia clavigera* (Küster, 1860)	Indo-West Pacific	11	–	+	–	0	N
✶			*Mancinella echinata* (Blainville, 1832)	Indo-West Pacific	11	–	–	–	0	N
✶			*Indothais gradata* (Jonas, 1846)	Indo-West Pacific	11	–	–	–	0	N
✶			*Reishia jubilaea* (K. S. Tan and Sigurdsson, 1990)	Indo-West Pacific	11	0	–	–	0	N
✶			*Indothais rufotincta* (K. S. Tan and Sigurdsson, 1996)	Indo-West Pacific	11	–	–	–	0	N
✶			*Drupella rugosa* (Born, 1778)	Indo-West Pacific	11	–	–	–	0	N
		✶	*Pollia fumosa* (Dillwyn, 1817)	Western Central Pacific	9	–	–	–	+	N
✶	✶	✶	*Euplica scripta* (Lamarck, 1822)	Indo-Pacific	22	–	–	–	+	N
	✶	✶	*Pardalinops testudinaria* (Link, 1807)	Southwest Pacific and Eastern Indian Ocean	23	–	–	–	+	N
✶	✶	✶	*Pictocolumbella ocellata* (Link, 1807)	Indo-Pacific	9	–	+	–	+	N
✶		✶	*Pseudanachis basedowi* (Hedley, 1918)	Central Indo-West Pacific	24	–	–	–	–	N

Table 3. (continued)

Sources			Species	Distribution		Attributes				Status
a	b	c		Location	Ref*	1	5	6	7	
✶		✶	*Gyrineum natator* (Röding, 1798)	Tropical Indo-West Pacific	25	–	–	–	+	N
		✶	*Laevistrombus turturella* (Röding, 1798)	Southern India to Australia and Melanesia and North to Japan	26	–	–	–	+	N
		✶	*Cerithium coralium* Kiener, 1841	Indo-West Pacific	27	–	–	–	0	N
	✶	✶	*Cerithium traillii* G. B. Sowerby II, 1855	Indo-West Pacific	27	–	–	–	0	N
	✶	✶	*Clypeomorus batillariaeformis* Habe and Kosuge, 1966	Indo-West Pacific	12	–	–	–	+	N
	✶	✶	*Clypeomorus petrosa chemnitziana* (Pilsbry, 1901)	Continental portions of the Western Pacific	12	–	–	–	0	N
		✶	*Rhinoclavis sinensis* (Gmelin, 1791)	Indo-Pacific	9, 16	–	–	–	+	N
	✶	✶	*Nassarius livescens* (Philippi, 1849)	Western Central Pacific	9	–	–	–	0	N
Mollusca, Bivalvia										
	✶		*Gafrarium dispar* (Holten, 1802)	Indo-Pacific	28	–	0	–	0	C
✶	✶		*Isognomon legumen* Gmelin 1971	Indo-West Pacific	9	–	–	+	+	C
	✶		*Arca navicularis* Bruguière, 1789	Indo Pacific, Red Sea	28	–	0	+	0	C
	✶		*Plicatula australis* Lamarck, 1819	East Africa to Japan; Northern Australia	29, 30	–	0	+	+	C
✶			*Musculista senhousia* (Benson, 1842)	Asia	31	–	–	+	+	N
		✶	*Gafrarium divaricatum* (Gmelin, 1791)	Indo-Pacific	32	–	–	–	+	N
	✶		*Septifer bilocularis* (Linnaeus, 1758)	Indo-West Pacific	23	–	0	–	–	N
✶		✶	*Perna viridis* (Linnaeus, 1758)	Indo-Pacific	33	–	–	–	+	N
✶			*Septifer excisus* (Wiegmann, 1837)	Indo-West Pacific	34	–	–	–	+	N
✶			*Saccostrea cucullata* (Born, 1778)	Indo-Pacific	35	–	+	–	+	N

* 1. Dayrat et al. 2014; 2. Balaparameswara Rao and Ganapati 1971; 3. Nakano and Sasaki 2011; 4. Mienis 2004; 5. Tryon et al. 1889; 6. Reid 2007; 7. Williams and Reid 2004; 8. Reid et al. 2010; 9. Palomares and Pauly 2015; 10. Houart and Tröndlé 2008; 11. Claremont et al. 2013; 12. Houbrick 1985; 13. Cernohorsky 1984; 14. Williams 2007; 15. Donald et al. 2005; 16. Poutiers 1998b; 17. Williams et al. 2010; 18. Herbert 2012; 19. Frey and Vermeij 2008; 20. Vermeij 1971; 21. Tan 2000; 22. deMaintenon 1999; 23. deMaintenon 2008; 24. Wilson 1994; 25. The Academy of Natural Sciences 2006; 26. Abbott 1960; 27. Houbrick 1992; 28. Prashad 1932; 29. Huber 2010; 30. Lamprell and Healy 1998; 31. Crooks 1996; 32. Poutiers 1998a; 33. Buddo et al. 2003; 34. Vermeij 1990; 35. Lam and Morton 2006.

Attribute 2: Initial expansion of local range subsequent to introduction. — This attribute was undetermined for *S. guamensis* because its known presence in Singapore is recent, and the specific location of its initial record in Singapore is not known.

Attribute 3: Association with human mechanism(s) of dispersal. — Singapore has been a major centre for global trade since its establishment as a British port in 1819 (Buckley 1902). This long maritime history coupled with the voluminous level of shipping activities represents major human pathways of translocation of organisms to Singapore (Jaafar et al. 2012). Although it is not known if *S. guamensis* is transported by ships, some studies have evoked this vector to account for similar species being found outside of their known geographical occurrence (Zenetos et al. 2005). *Siphonaria guamensis* is neither a typical fouling species or species imported for aquaculture or the aquarium trade in Singapore (Jaafar et al. 2012), but it is possible that it is dispersed via ship ballast water.

Attribute 4: Association with or dependency on other introduced species. — This attribute was undetermined for *S. guamensis*, since the native/non-native status of many coastal marine taxa in Singapore has yet to be documented. There is also a lack of species-specific ecological studies for marine taxa in Singapore's coastal environment.

Attribute 5: Prevalence on or restriction to new or artificial environment(s). — *Siphonaria guamensis* was one of the most commonly-occurring species on the seawalls surveyed, appearing on 18 out of the 19 seawall sites surveyed to date (Lee et al. 2009a; Loke and Todd 2016). In addition, Chim and Tan (2009) found that *S. guamensis* exclusively inhabited seawalls at Sungei Api Api (an estuary in the north-east of Singapore). Hence, *S. guamensis* appears to be prevalent on artificial structures, a characteristic of non-native species (Chapman and Carlton 1991; Mineur et al. 2012).

Attribute 6: Relatively restricted distribution on a continent compared to distributions of native species (i.e. discontinuous regional distribution). — *Siphonaria guamensis* is not observed in Peninsular Malaysia (Way and Purchon 1981; Wong and Arshad 2011) which suggests it has a discontinuous regional distribution.

Attribute 7: Isolated populations on different continents or in isolated oceans (i.e. discontinuous global distribution). — Since its first record on the

island of Guam in 1833 (Quoy and Gaimard 1833), other early records of *S. guamensis* have been limited to the islands of Micronesia on Guam and Palau (Vermeij 1971), and in the Java Sea (Chim and Tan 2009). Records of the species outside of Micronesia are recent and discontinuous, e.g., Singapore (Tan and Chou 2000), Natuna Islands, Indonesia (Tan and Kastoro 2004) and India (Murty et al. 2013) (Table 4).

Attributes 8, 9: Insufficient active/passive dispersal capabilities to account for the observed distribution of the species. — Information regarding the dispersal capability of *S. guamensis* remains limited. *Siphonaria* species generally spawn by producing strings of egg masses attached to a substrate, which may hatch within 4 to 20 days depending on the species (Abe 1940; Huang and Chan 2000). Survival period of the larval stage remains virtually unknown. In Singapore, Chim and Tan (2009) noted that veligers of *S. guamensis* are released within 18 days upon production of the egg masses, so long distance dispersal via natural mechanisms such as rafting would be constrained, but still possible.

Attribute 10: Exotic evolutionary origin. (Most introduced species populations have the closest morphologic and genetic affinities to species groups occurring elsewhere in the world). — Phylogenetic studies of *Siphonaria* are still lacking, possibly since the delineation of *Siphonaria* species based on shell morphology remains challenging and the use of molecular data in *Siphonaria* taxonomy is still in its infancy (Dayrat et al. 2014).

Table 4. Global distribution of *Siphonaria guamensis.*

Location	Source
Asia (South China Sea)	
Singapore	Tan and Chou 2000; Goh et al. 2002.
Natuna Islands, Indonesia	Tan and Kastoro 2004
Asia (Java sea)	
Billiton and Java Sea	Hubendick 1946 (as cited in Chim and Tan 2009)
Asia (Indian Ocean)	
India	Murty et al. 2013
Micronesia (Northwest Pacific)	
Western Caroline Islands, Palau	Vermeij 1971
Mariana Islands, Guam	Vermeij 1971
Guam	Quoy and Gaimard 1833; Hubendick 1946 (as cited in Chim and Tan 2009).

Latitudinal trends in marine invasions and possible contributing factors

Establishing the biogeographic and thereby native status of many tropical marine species remains a challenge due to the paucity of historical biodiversity records as well as the poorly resolved systematics of several tropical taxa (Yeo et al. 2011). Records of species' presence are therefore more robust than records of absence, since the latter may be compounded by differences in survey effort across geographical areas and taxonomic groups (Campbell et al. 2007). Consequently, present-day new records of species in a particular locale may represent either introductions via anthropogenic means of dispersal or discoveries of native species that have escaped detection, and Yeo et al. (2011) suggested that a number of new species found during marine surveys in recent years (referring to the 2000s) "may in fact be considered cryptogenic", pg 405. In this study, 23 species were categorised as cryptogenic because there was insufficient information to suggest they were native to Singapore or potentially non-native. Most of these species have two or less attributes with positive evidence lending support that it may be introduced, with the exception of *Semiricinula fusca* which had three attributes with positive evidence. The attributes (generally attributes 1 and 6) with positive evidence for the cryptogenic species were mainly concerned with historical records in Singapore and regional distribution.

The low occurrence of non-native marine species currently observed in Singapore appears to be part of an emerging pattern in global marine invasions whereby there are fewer successful invasion events in the tropics than in temperate zones (Knops et al. 1999; Freestone et al. 2013). Even though most introduced marine species have been reported in temperate areas, and the lower incidence of invasion events in the tropics may simply be an artefact of less research conducted in the region, recent tropical invasion studies are lending support to the observation that ecosystems in lower latitudes may indeed be more resistant to marine invasion than those in temperate zones (Hutchings et al. 2002; Astudillo et al. 2014).

A combination of abiotic and biotic factors has been proposed to explain the observed latitudinal trend in marine invasions. In order for a non-native species to successfully invade a new locale, it must first overcome the initial "abiotic filter" which affects the extent of compatibility between the native distribution of the species and the new environment in which they find themselves (Hutchings et al. 2002; Olyarnik et al. 2009). Frequently, the environmental conditions in tropical ecosystems are too harsh for non-natives to establish (e.g., Hutchings et al. 2002;

Astudillo et al. 2014). In a study comparing temperate and tropical ports in Australia, Hutchings et al. (2002) proposed that tropical ports in the sub-equatorial latitudes of Australia experienced stronger physical stresses such as irregular fluctuations in temperature, salinity, emersion periods and rainfall. Therefore, tropical ports in Australia appear to have abiotic conditions unsuitable for their temperate counterparts, which could hinder the establishment of non-native species which are not accustomed to the local environment. This lends support to the observation that the 'possibly introduced' species (*S. guamensis*) identified on Singapore's seawalls may be from within the tropical parts of the Indo-Pacific, whereby there is likely to be a greater match in habitats between the source and recipient locale. This is opposed to the scenario in which potentially non-native species were to originate from a source locale outside of the Indo-Pacific where there could be greater disparity in abiotic and biotic conditions.

Unsuitable environmental conditions are a key factor that prevents the establishment of non-native species outside their native range (Lodge 1993). In a review of non-native marine species in Hong Kong, Astudillo et al. (2014) re-examined the status of six non-native species first identified by Morton (1987) with the expectation that they would become more abundant along the coasts of Hong Kong. However, only four of the original six non-native marine species were found, three of which were uncommon (Astudillo et al. 2014). In Singapore, when the tide is low, rock surface temperatures on seawalls regularly exceed 50 °C, which may be beyond the tolerance of non-native species (Table S1; Loke 2015). Limited resource heterogeneity, particularly on artificial seawalls which are less complex than natural rocky shores, is another possible cause of potential failure for establishment as topographically "simple" seawalls provide less available niches for species to utilize (Lodge 1993; Loke and Todd 2016). An alternative, or complementary, hypothesis to explain the latitudinal trend in marine bio-invasions is biotic resistance (Stachowicz et al. 1999, 2002; Freestone et al. 2013). Biotic resistance predicts that species-rich communities typical in the tropics provide stronger community resistance to invasions via a range of potential mechanisms such as the limiting of space as a resource. However, given that the species richness of conventional (unenhanced) seawalls in Singapore is, to begin with, lower than natural rocky shores (i.e. 105 species on seawalls versus 138 species on rocky shores; Lai et al. 2018), biotic resistance may be a less significant factor than abiotic environmental conditions in influencing the type of organisms that inhabit seawalls.

Conclusion

The present study has increased the number of seawalls surveyed in Singapore, expanded the species list of molluscs on Singapore's seawalls with seven new records/previously unrecorded taxa, and highlighted one potentially non-native mollusc species. Our findings contribute to the growing body of literature indicating the occurrence of non-native marine species in Singapore is, in fact, very low. This trend directly contradicts Seebens et al.'s (2013) model predictions about Singapore. A combination of abiotic and biotic factors could prevent the establishment of non-native species on Singapore's seawalls and explain this dichotomy. Even though the results from the present study suggest that there is little in the way of invasion events along Singapore's seawalls, the high shipping volume and connectivity of its port cannot be ignored, and regular monitoring must therefore be instituted as a preventative management strategy for biosecurity.

Acknowledgements

This research was funded by the National Research Foundation, Prime Minister's Office, Singapore under its Marine Science Research and Development Programme (Award No. MSRDP-05) and a National Parks Board CME Grant (number R-154-000-566-490). The authors would like to thank National Parks Board for providing permits for the surveys (NP/RP11-058) and Sentosa Development Corporation for facilitating access to the various field sites. The comments by Fred Wells and two anonymous reviewers greatly improved this paper.

References

Abbott RT (1960) The genus *Strombus* in the Indo-Pacific. *Indo-Pacific Mollusca* 1(2): 33–146

Abe N (1940) The homing, spawning and other habits of a limpet, *Siphonaria japonica* Donovan. Scientific *Reports of Tohoku Imperial University 4th Series (Biology)* 15: 59–95

Airoldi L, Turon X, Perkol-Finkel S, Rius M (2015) Corridors for aliens but not for natives: effects of marine urban sprawl at a regional scale. *Diversity and Distributions* 21: 1–14, https://doi.org/10.1111/ddi.12301

Amat JN, Cardigos F, Santos RS (2008) The recent northern introduction of the seaweed *Caulerpa webbiana* (Caulerpales, Chlorophyta) in Faial, Azores Islands (North-Eastern Atlantic). *Aquatic Invasions* 3: 417–422, https://doi.org/10.3391/ai.2008.3.4.7

Astudillo JC, Wong JCY, Dumont CP, Bonebrake TC, Leung KMY (2014) Status of six non-native marine species in the coastal environment of Hong Kong, 30 years after their first record. *BioInvasions Records* 3: 123–137, https://doi.org/10.3391/bir.2014.3.3.01

Balaparameswara Rao M, Ganapati PN (1971) Ecological studies on a tropical limpet *Cellana radiata*. *Marine Biology* 9: 109–114, https://doi.org/10.1007/BF00348250

Buddo DSA, Steele RD, D'Oyen ER (2003) Distribution of the invasive Indo-Pacific green mussel, *Perna viridis*, in Kingston Harbour, Jamaica. *Bulletin of Marine Science* 73(2): 433–441

Buckley CB (1902) An Anecdotal History of Old Times in Singapore (with Portraits and Illustrations), Volume 1. Fraser & Neave Limited, Singapore, 406 pp

Bulleri F, Chapman MG (2015) Artificial physical structures. In: Crowe TP, Frid CLJ (eds), Marine Ecosystems: Human Impacts on Biodiversity, Functioning and Services, Cambridge University Press, Cambridge, pp 167–201, https://doi.org/10.1017/CBO9781139794763.007

Campbell ML, Gould B, Hewitt CL (2007) Survey evaluations to assess marine bioinvasions. *Marine Pollution Bulletin* 55: 360–378, https://doi.org/10.1016/j.marpolbul.2007.01.015

Carlton JT (1996) Biological invasions and cryptogenic species. *Ecology* 77: 1653–1655, https://doi.org/10.2307/2265767

Cernohorsky WO (1984) Systematics of the family Nassariidae (Mollusca: Gastropoda). *Bulletin of the Auckland Institute and Museum* 14: 1–356

Cesar HSJ, van Beukering PJH, Pintz W, Dierking J (2002) Economic valuation of the coral reefs of Hawai'i. Final Report Submitted to the Hawai'i Coral Reef Initiative, University of Hawai'i, Honolulu, 123 pp

Chapman JW, Carlton JT (1991) A test of criteria for introduced species: the global invasion by the isopod *Synidotea laevidorsalis* (Miers, 1881). *Journal of Crustacean Biology* 11: 386–400, https://doi.org/10.2307/1548465

Chapman MG, Bulleri F (2003) Intertidal seawalls—new features of landscape in intertidal environments. *Landscape and Urban Planning* 62: 159–172, https://doi.org/10.1016/S0169-2046(02)00148-2

Chim CK, Tan KS (2009) Vertical distribution, spawning and recruitment of *Siphonaria guamensis* (Gastropoda: Pulmonata) on a seawall in Singapore. *Raffles Bulletin of Zoology* Supplement 22: 269–278

Chou LM, Ng PKL, Lim KKP (1994) Animalia. In: Wee YC, Ng PKL (eds), A First Look at Biodiversity in Singapore. National Council on the Environment, Singapore, pp 70–106

Chuang SH (1973) Sea shells. In: Chuang SH (ed), Animal Life and Nature in Singapore. Singapore University Press, Singapore, pp 175–201

Claremont M, Vermeij GJ, Williams ST, Reid DG (2013) Global phylogeny and new classification of the Rapaninae (Gastropoda: Muricidae), dominant molluscan predators on tropical rocky seashores. *Molecular Phylogenetics and Evolution* 66: 91–102, https://doi.org/10.1016/j.ympev.2012.09.014

Crooks JA (1996) The population ecology of an exotic mussel, *Musculista senhousia*, in a Southern California bay. *Estuaries* 19: 42–50, https://doi.org/10.2307/1352650

Dayrat B, Goulding TC, White TR (2014) Diversity of Indo-West Pacific *Siphonaria* (Mollusca: Gastropoda: Euthyneura). *Zootaxa* 3779: 246–276, https://doi.org/10.11646/zootaxa.3779.2.7

deMaintenon MJ (1999) Phylogenetic analysis of the Columbellidae (Mollusca: Neogastropoda) and the evolution of herbivory from carnivory. *Invertebrate Biology* 118: 258–288, https://doi.org/10.2307/3226997

deMaintenon MJ (2008) Results of the Rumphius biohistorial expedition to Ambon. Part 14. The Columbellidae (Gastropoda: Neogastropoda) collected at Ambon during the Rumphius biohistorial expedition. *Zoologische Mededelingen* 82(34): 341–374

Donald KM, Kennedy M, Spencer HG (2005) The phylogeny and taxonomy of austral monodontine topshells (Mollusca: Gastropoda: Trochidae), inferred from DNA sequences. *Molecular Phylogenetics and Evolution* 37: 474–483, https://doi.org/10.1016/j.ympev.2005.04.011

Freestone AL, Rutz GM, Torchin ME (2013) Stronger biotic resistance in tropics relative to temperate zone: effects of predation on marine invasion dynamics. *Ecology* 94: 1370–1377, https://doi.org/10.1890/12-1382.1

Frey MA, Vermeij GJ (2008) Molecular phylogenies and historical biogeography of a circumtropical group of gastropods (Genus: *Nerita*): implications for regional diversity patterns in the marine tropics. *Molecular Phylogenetic Evolution* 48: 1067–1086, https://doi.org/10.1016/j.ympev.2008.05.009

Goh BPL, Sodhi NS, Li D, Ho SH, Ng PKL (2002) A Guide to Urban Creatures. Singapore Science Centre, Singapore, 160 pp

Herbert DG (2012) A revision of the Chilodontidae (Gastropoda: Vetigastropoda: Seguenzioidea) of southern Africa and the south-western Indian Ocean. *African Invertebrates* 53: 381–502, https://doi.org/10.5733/afin.053.0209

Houart R, Tröndlé J (2008) Update of Muricidae (excluding Coralliophilinae) from French Polynesia with description of ten new species. *Novapex* 9: 53–93

Houbrick RS (1985) Genus *Clypeomorus* Jousseaume (Cerithiidae: Prosobranchia). *Smithsonian Contributions to Zoology* 403: 1–131, https://doi.org/10.5479/si.00810282.403

Houbrick RS (1992) Monograph of the genus *Cerithium* Bruguière in the Indo-Pacific (Cerithiidae: Prosobranchia). *Smithsonian Contributions to Zoology* 510: 1–211, https://doi.org/10.5479/si.00810282.510

Huang R, Chan BKK (2000) Egg capsules and early development of *Siphonaria japonica* (Gastropoda: Pulmonata). In: Morton B (ed), The marine flora and fauna of Hong Kong and southern China V. Hong Kong University Press, Hong Kong, pp 129–136

Huber M (2010) Compendium of Bivalves. A Full-Color Guide to 3,300 of the World's Marine Bivalves. A Status on Bivalvia after 250 years of research. Conchbooks, Hackenheim, 901 pp

Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology* 46: 10–18, https://doi.org/10.1111/j.1365-2664.2008.01600.x

Hutchings PA, Hilliard RW, Coles SL (2002) Species introduction and potential for marine pest invasions into tropical marine communities, with special reference to the Indo-Pacific. *Pacific Science* 56: 223–233, https://doi.org/10.1353/psc.2002.0017

International Union for the Conservation of Nature (2000) IUCN Guidelines for the Prevention of Biodiversity Loss caused by Alien Invasive Species. IUCN, Gland, Switzerland, 24 pp

Jaafar Z, Yeo DC, Tan HH, O'Riordan RM (2012) Status of estuarine and marine non-indigenous species in Singapore. *The Raffles Bulletin of Zoology* 25: 79–92

Knops JMH, Tilman D, Haddad NM, Naeem S, Mitchell CE, Haarstad J, Ritchie ME, Howe KM, Reich PB, Siemann E, Groth J (1999) Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters* 2: 286–293, https://doi.org/10.1046/j.1461-0248.1999.00083.x

Kocak F, Ergen Z, Çinar ME (1999) Fouling organisms and their developments in a polluted and an unpolluted marina in the Aegean Sea (Turkey). *Ophelia* 50: 1–20, https://doi.org/10.1080/00785326.1999.10409385

Lai S, Loke LHL, Hilton MJ, Bouma TJ, Todd PA (2015) The effects of urbanisation on coastal habitats and the potential for ecological engineering: a Singapore case study. *Ocean and Coastal Management* 103: 78–85, https://doi.org/10.1016/j.ocecoaman.2014.11.006

Lai S, Loke LHL, Bouma TJ, Todd PA (2018) Biodiversity surveys and stable isotope analyses reveal key differences in intertidal assemblages between tropical seawalls and rocky shores. *Marine Ecology Progress Series* 587: 41–53, https://doi.org/10.3354/meps12409

Lam K, Morton B (2006) Morphological and mitochondrial-DNA analysis of the Indo-West Pacific rock oysters (Ostreidae: *Saccostrea* species). *Journal of Molluscan Studies* 72: 235–245, https://doi.org/10.1093/mollus/eyl002

Lam NWY, Huang R, Chan BKK (2009) Variations in intertidal assemblages and zonation patterns between vertical artificial seawalls and natural rocky shores: a case study from Victoria Harbour, Hong Kong. *Zoological Studies* 48(2): 184–195

Lamprell K, Healy J (1998) Bivalves of Australia. Volume 2. Backhuys, Leiden, 288 pp

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, Tan KS, Sin TM (2009a) Intertidal assemblages on coastal defence structures in Singapore I: a faunal study. *Raffles Bulletin of Zoology* 22: 237–254

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

Lim JY, Tay TS, Lim CS, Lee SSC, Teo SL-M, Tan KS (2018) *Mytella strigata* (Bivalvia: Mytilidae): an alien mussel recently introduced to Singapore and spreading rapidly. *Molluscan Research* 38: 170–186, https://doi.org/10.1080/13235818.2018.1423858

Lodge DM (1993) Biological invasions: lessons for ecology. *Trends in Ecology & Evolution* 8: 133–137, https://doi.org/10.1016/0169-5347(93)90025-K

Loke LHL (2015) Enhancing biodiversity on tropical seawalls: how habitat complexity and fragmentation regulate intertidal communities. Unpublished PhD Thesis, National University of Singapore, Singapore, 255 pp

Loke LHL, Todd PA (2016) Structural complexity and component type increase intertidal biodiversity independently of area. *Ecology* 97: 383–393, https://doi.org/10.1890/15-0257.1

Loke LHL, Liao LM, Bouma TJ, Todd PA (2016) Succession of seawall algal communities on artificial substrates. *Raffles Bulletin of Zoology* 32: 1–10

Loke LHL, Bouma TJ, Todd PA (2017) The effects of manipulating microhabitat size and variability on tropical seawall biodiversity: field and flume experiments. *Journal of Experimental Marine Biology and Ecology* 492: 113–120, https://doi.org/10.1016/j.jembe.2017.01.024

Luckhurst BE, Luckhurst K (1978) Analysis of the influence of the substrate variables on coral reef fish communities. *Marine Biology* 49: 317–323, https://doi.org/10.1007/BF00455026

Martínez ML, Intralawan A, Vázquez G, Pérez-Maqueo O, Sutton P, Landgrave R (2007) The coasts of our world: ecological, economic and social importance. *Ecological Economics* 63: 254–272, https://doi.org/10.1016/j.ecolecon.2006.10.022

Masselink G, Gehrels R (2014) Introduction to coastal environments and global change. In: Masselink G, Gehrels R (eds), Coastal Environments and Global Change. John Wiley & Sons, West Sussex, pp 1–27

Mienis HK (2004) New data concerning the presence of Lessepsian and other Indo-Pacific migrants among the molluscs in the Mediterranean Sea with emphasize on the situation in Israel. In: Ozturk B, Salman A (eds), Proceedings 1st National Malacology Congress, 1–3 September 2004, Izmir. *Turkish Journal of Aquatic Life* 2(2): 117–131

Mineur F, Cook EJ, Minchin D, Bohn K, Macleod A, Maggs CA (2012) Changing coasts: marine aliens and artificial structures. *Oceanography and Marine Biology: An Annual Review* 50: 189–234, https://doi.org/10.1201/b12157-5

Molnar JL, Gamboa RL, Revenga C, Spalding MD (2008) Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment* 6: 485–492, https://doi.org/10.1890/070064

Morton B (1987) Recent marine introductions into Hong Kong. *Bulletin of Marine Science* 41(2): 503–513

Murty KVR, Shameem A, Umadevi K (2013) Feeding, anatomy and digestive enzymes of false limpet *Siphonaria guamensis*. *World Journal of Fish and Marine Sciences* 5(1): 104–109

Nakano T, Sasaki T (2011) Recent advances in molecular phylogeny, systematics and evolution of patellogastropod limpets. *Journal of Molluscan Studies* 77: 203–217, https://doi.org/10.1093/mollus/eyr016

Occhipinti-Ambrogi A, Savini D (2003) Biological invasions as a component of global change in stressed marine ecosystems. *Marine Pollution Bulletin* 46: 542–551, https://doi.org/10.1016/S0025-326X(02)00363-6

Olyarnik SV, Bracken MES, Byrnes JE, Hughes AR, Hultgren KM, Stachowicz JJ (2009) Ecological factors affecting community invasibility. In: Rilov G, Crooks JA (eds), Biological Invasions in Marine Ecosystems, Ecological Studies 204, Springer, Verlag Berlin Heidelberg, pp 215–238, https://doi.org/10.1007/978-3-540-79236-9_12

Palomares MLD, Pauly D (2015) SeaLifeBase. http://www.sealifebase.ca/ (accessed 1 October 2014)

Poutiers JM (1998a) Bivalves. In: Carpenter KE, Niem VH (eds), FAO Species Identification Guide for Fishery Purposes. The Living Marine Resources of the Western Central Pacific. Volume 1. Seaweeds, Corals, Bivalves and Gastropods. FAO, Rome, pp 123–362

Poutiers JM (1998b) Gastropods. In: Carpenter KE, Niem VH (eds) FAO Species Identification Guide for Fishery Purposes. The Living Marine Resources of the Western Central Pacific. Volume 1. Seaweeds, Corals, Bivalves and Gastropods. FAO, Rome, pp 363–648

Prashad B (1932) The Lamellibranchia of the Siboga Expedition: Systematic part. 2. Pelecypoda (exclusive of the Pectinidae). *Siboga-expeditie* 53c: 1–353

Quoy JRC, Gaimard JP (1833) Mollusques. Voyage de Découverts de l'Astrolabe, Éxécuté par odre du Roi, pendant les années 1826–1827–1828–1829, sous le commandement de M. J. Dumont d'Urville. Zoologie. Tome second. J. Tatsu, Paris, pp 321–686

Reid DG (1984) The Systematics and Ecology of the Mangrove-dwelling *Littoraria* species (Gastropoda: Littorinidae) in the Indo-Pacific. PhD Thesis, James Cook University of North Queensland, 398 pp

Reid DG (2007) The genus *Echinolittorina* Habe, 1956 (Gastropoda: Littorinidae) in the Indo-West Pacific Ocean. *Zootaxa* 1420: 1–161, https://doi.org/10.11646/zootaxa.1420.1.1

Reid DG, Dyal P, Williams ST (2010) Global diversification of mangrove fauna: a molecular phylogeny of *Littoraria* (Gastropoda: Littorinidae). *Molecular Phylogenetics and Evolution* 55: 185–201, https://doi.org/10.1016/j.ympev.2009.09.036

Seebens H, Gastner MT, Blasius B (2013) The risk of marine bioinvasion caused by global shipping. *Ecology Letters* 16: 782–790, https://doi.org/10.1111/ele.12111

Singapore Department of Statistics (2016) Yearbook of Statistics Singapore 2016. http://www.singstat.gov.sg/publications/publications-and-papers/reference/yoscontents (accessed 1 January 2018)

Singapore Land Authority (2017) Total Land Area of Singapore. https://data.gov.sg/dataset/total-land-area-of-singapore (accessed 1 January 2018)

Spalding MD, Fox HE, Allen GR, Davidson N, Ferdaña ZA, Finlayson M, Halpern BS, Jorge MA, Lombana A, Lourie SA, Martin KD, McManus E, Molnar J, Recchia CA, Robertson J (2007) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *BioScience* 57: 573–583, https://doi.org/10.1641/B570707

Stachowicz JJ, Whitlatch RB, Osman RW (1999) Species diversity and invasion resistance in a marine ecosystem. *Science* 286: 1577–1579, https://doi.org/10.1126/science.286.5444.1577

Stachowicz JJ, Fried H, Osman RW, Whitlatch RB (2002) Biodiversity, invasion resistance, and marine ecosystem function: reconciling pattern and process. *Ecology* 83: 2575–2590, https://doi.org/10.1890/0012-9658(2002)083[2575:BIRAME]2.0.CO;2

Streftaris N, Zenetos A (2006) Alien marine species in the Mediterranean - the 100 'worst invasives' and their impact. *Mediterranean Marine Science* 7: 87–118, https://doi.org/10.12681/mms.180

Tan KS (2000) Species checklist of Muricidae (Mollusca: Gastropoda) in the South China Sea. *Raffles Bulletin of Zoology* 48(8): 495–512

Tan KS, Chou LM (2000) A Guide to the Common Seashells of Singapore. Singapore Science Centre, Singapore, 168 pp

Tan KS, Kastoro WW (2004) A small collection of gastropods and bivalves from the Anambas and Natuna Islands, South China Sea. *Raffles Bulletin of Zoology* Supplement 11: 47–54

Tan KS, Sigurdsson JB (1990) A new species of *Thais* (Gastropoda: Muricidae) from Singapore and Peninsular Malaysia. *Raffles Bulletin of Zooology* 38(2): 205–211

Tan KS, Sigurdsson JB (1996) A new species of *Thais* (Neogastropoda, Muricidae) from Singapore, with a description of *Thais javanica*. *Journal of Molluscan Studies* 62: 517–535, https://doi.org/10.1093/mollus/62.4.517

Tan LWH, Ng PKL (1988) A Guide to Seashore Life. Singapore Science Centre, Singapore, 159 pp

Tan SK, Clements R (2008) Taxonomy and the distribution of the Neritidae (Mollusca: Gastropoda) in Singapore. *Zoological Studies* 47(4): 481–494

Tan SK, Woo HPM (2010) A preliminary checklist of the molluscs of Singapore. Raffles Museum of Biodiversity Research, National University of Singapore, Singapore. http://lkcnhm.nus.edu.sg/nus/pdf/PUBLICATION/LKCNH%20Museum%20Books/LKCNHM%20Books/preliminary_checklist_molluscs_singapore.pdf (accessed 24 October 2014)

The Academy of Natural Sciences (2006) OBIS Indo-Pacific Molluscan Database. The Academy of Natural Sciences, Philadelphia. http://clade.ansp.org/obis/find_mollusk.html (accessed 24 October 2014)

Toft JD, Cordell JR, Fields WC (2002) New records of crustaceans (Amphipoda, Isopoda) in the Sacramento/San Joaquin delta, California, and application of criteria for introduced species. *Journal of Crustacean Biology* 22: 190–200, https://doi.org/10.1163/20021975-99990222

Tryon GW, Pilsbry HA, Sharp B (1889) Manual of Conchology; Structural and Systematic, with illustrations of the species. Volume XI: Trochidae, Stomatidae, Pleurotomariidae, Haliotidae. Academy of Natural Sciences, Philadelphia, 519 pp

Vermeij GJ (1971) Substratum relationships of some tropical Pacific intertidal gastropods. *Marine Biology* 10: 315–320, https://doi.org/10.1007/BF00368091

Vermeij GJ (1990) Tropical Pacific pelecypods and productivity: a hypothesis. *Bulletin of Marine Science* 47(1): 62–67

Wasson K, Holle BV, Toft J, Ruiz G (2000) Detecting invasions of marine organisms: kamptozoan case histories. *Biological Invasions* 2: 59–74, https://doi.org/10.1023/A:1010049907067

Way K, Purchon RD (1981) The marine shelled Mollusca of West Malaysia and Singapore, Part 2. Polyplacophora and Gastropoda. *Journal of Molluscan Studies* 47(3): 313–321

Williams ST (2007) Origins and diversification of Indo-West Pacific marine fauna: evolutionary history and biogeography of turban shells (Gastropoda, Turbinidae). *Biological Journal of the Linnean Society* 92: 573–592, https://doi.org/10.1111/j.1095-8312.2007.00854.x

Williams ST, Reid D (2004) Speciation and diversity on tropical rocky shores: a global phylogeny of snails of the genus *Echinolittorina*. *Evolution* 58: 2227–2251, https://doi.org/10.1111/j.0014-3820.2004.tb01600.x

Williams ST, Donald KM, Spencer HG, Nakano T (2010) Molecular systematics of the marine gastropod families Trochidae and Calliostomatidae (Mollusca: Superfamily Trochoidea). *Molecular Phylogenetics and Evolution* 54: 783–809, https://doi.org/10.1016/j.ympev.2009.11.008

Wilson BR (1994) Australian Marine Shells: Prosobranch Gastropods. Part 2 (Neogastropods). Odyssey Publishing, Western Australia, 370 pp

Wong NLWS, Arshad A (2011) A brief review on marine shelled Mollusca (Gastropoda and Bivalvia) record in Malaysia. *Journal of Fisheries and Aquatic Science* 6: 669–699, https://doi.org/10.3923/jfas.2011.669.699

Yeo DCJ, Carlton JT, Teo SLM, Ng PKL (2011) An incoming flood on a cryptic stage: understanding alien crustacean invasions in Southeast Asia. In: Galil BS, Clark PF, Carlton JT (eds), In the Wrong Place - Alien Marine Crustaceans: Distribution, Biology and Impacts. Invading Nature - Springer Series in Invasion Ecology 6, Springer, The Netherlands, pp 403–417, https://doi.org/10.1007/978-94-007-0591-3_14

Yeung Y (2001) Coastal mega-cities in Asia: transformation, sustainability and management. *Ocean & Coastal Management* 44: 319–333, https://doi.org/10.1016/S0964-5691(01)00053-9

Zenetos A, Koutsoubas D, Vardala-Theodorou E (2005) Origin and vectors of introduction of exotic molluscs in Greek waters. *Belgian Journal of Zoology* 135(2): 279–286

Supplementary material

The following supplementary material is available for this article:

Figure S1. Calculation of slope angle based on horizontal distance from 1.8 m above seawall base to seawall slope.

Table S1. Coordinates of transects at survey sites, with characteristics (i.e. grouting, slope, rugosity, temperature, light and approximate age) of each site.

This material is available as part of online article from:

http://www.aquaticinvasions.net/2018/Supplements/AI_2018_Tan_etal_Figure_S1.pdf

http://www.aquaticinvasions.net/2018/Supplements/AI_2018_Tan_etal_Table_S1.xlsx