



Review

A low number of introduced marine species in the tropics: a case study from Singapore

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Abstract

Non-indigenous marine species (NIMS) are being transported around the world by anthropogenic mechanisms, particularly by vessels in ballast water or as biofouling. A small subset of NIMS become invasive marine species (IMS) and can cause considerable damage to local marine ecosystems. Understanding where NIMS originate, how they are transported, and their effects in the new environments are crucial to the management of IMS. As one of the busiest ports in the world that handles tens of thousands of high invasion-risk vessels annually, Singapore is regarded as being at very high risk for the introduction of NIMS and IMS. However, a compilation of 3,650 marine invertebrates, fishes and plants revealed that only 22 species have been confirmed as NIMS. The results are consistent with a growing dataset that suggests biodiverse marine ecosystems in the tropical Indo-West Pacific are less susceptible to introductions than previously thought.

Key words: introduced marine pests, invasion risk, shipping, biofouling, ballast water, biotic resistance, Pilbara, Western Australia, Southeast Asia, Indo-West Pacific

Introduction

The number of non-indigenous marine species (NIMS) being introduced into new areas as a direct result of human activities—such as global shipping and canal construction, and by deliberate or inadvertent release of species used in aquaculture, fisheries and aquarium trade—has received the attention of the general public (Willan et al. 2000) and caused increasing concern to scientists, agencies and managers who are working with the marine environment (Dommissiee and Hough 2004). The area of greatest known marine introductions is the Mediterranean Sea, with 821 species, largely a result of Lessepsian migration through the Suez Canal (Zenetos et al. 2017). Other areas with high numbers of NIMS are within the Hawaiian Islands, USA (343 species; DeFelice et al. 2001); the state of California, USA (307 species), including in San Francisco Bay (190 species; Foss 2008);

and Port Philip Bay, Melbourne, Australia (99 species; Hewitt et al. 2004). There have been a number of surveys of ports and adjacent habitats in Australia that have recorded introduced species (Hewitt and Martin 2001; Hewitt 2002). It must be noted that there have been large components of the biota that have not been identified or are cryptogenic (Bishop and Hutchings 2011), so the number of introduced species is probably significantly underestimated. It is not a coincidence that marine hotspots of introduced species are often in and around ports, as shipping movements are a primary vector of NIMS, either through ballast water (Carlton 1985) or biofouling (Carlton 1996; Hewitt 2002; Hewitt et al. 2004; Yeo et al. 2010; Jaafar et al. 2012).

Only a small proportion of NIMS become invasive marine species (IMS, also referred to as introduced marine pests), that cause harm by modifying local ecosystems, threatening commercial fisheries, introducing diseases, and fouling industrial structures (Carlton 2001; Hayes et al. 2005; Wells et al. 2009). For example, the Pacific lionfish species, *Pterois volitans* (Linnaeus, 1758) and *P. miles* (Bennett, 1828), were introduced to Florida in the 1990s and now occur widely in the Caribbean Sea (Albins and Hixon 2008). They are thought to compete with, and prey on, native species, thus causing significant ecosystem changes (Albins and Hixon 2008; Hackerott et al. 2013; Côté et al. 2013). The Asian green mussel *Perna viridis* Linnaeus, 1758, was introduced to Trinidad, West Indies, in about 1990 (Agard et al. 1992). It has subsequently been recorded in Kingston, Jamaica (Buddo et al. 2003), and Florida and Georgia in the United States (SCAISTF 2007). There are concerns that *P. viridis* in Tampa Bay will outcompete the native mussel *Brachidontes exustus* (Linnaeus, 1758) (Barber et al. 2005) and American oyster (*Crassostrea virginica*) (McFarland et al. 2015). Economically, *P. viridis* reduces the effectiveness of cooling systems and fouls navigation buoys, floating docks, piers and pilings. It also accumulates toxins and is a cause of shellfish poisoning in humans (NIMPIS 2017). Overall, IMS are widely considered to be a key threat to the marine environment (Johnson and Chapman 2007; Molnar et al. 2008; Katsanevakis et al. 2014; Crowe and Frid 2015).

As a major transport hub with links to hundreds of ports worldwide and extensive artificial marine habitats, Singapore is considered to be at considerable risk for the introduction of exotic marine species (Yeo et al. 2011; Seebens et al. 2013; Lim et al. 2017). The history of international trade in Singapore dates back to the 1300s, with European vessels first arriving in the 1500s; trade increased rapidly in the early 1800s when Singapore became a British colony (Yeo et al. 2011). Singapore is now one of the busiest ports in the world with direct access to all Asian countries and is a hub for vessels trading between Europe and Asia. The port is connected to over 600 others in 120 countries worldwide (MPA 2017a). It

has 70% of the world's jack-up rig-building market and over 65% of the global floating production storage and offloading (FPSO) conversion market by dollar value. In addition to construction, servicing of these vessels in Singapore means there are numerous high invasion-risk vessels (Yeo et al. 2010) in port for prolonged periods. At any moment there are approximately 1,000 vessels in Singapore's port. In 2016 there were 138,998 vessel arrivals involving a total of 593 million tonnes of cargo and a million passengers. Arrivals included a large number of high-risk vessels, such as 9,496 barges and 11,343 tugboats that remain in port areas for long periods (MPA 2017a). There were also extensive movements of dredgers, oil rigs, and other similar vessels, but these numbers are not published. Following the global financial crisis of 2008 and the downturn in international shipping, many laid up vessels remained in port without work for months, increasing the risk of biofouling and subsequent transport of marine species into new habitats (Floerl and Coutts 2009).

While there has been no comprehensive NIMS survey in Singapore, several studies have contributed to available knowledge. The most extensive to date (Jaafar et al. 2012) recorded only 17 NIMS: 12 fishes, 2 molluscs, 2 dinoflagellates and 1 polychaete. In another important study, Lim et al. (2017) analysed vessel movements in the Keppel Terminal. They found that > 92% of vessels remained in the terminal for < 7 days. The data were combined with biogeographic information on the last port of call to construct an assessment matrix to estimate the risk of introduction of NIMS by biofouling.

However, the results obtained by Lim et al. (2017) cannot be extrapolated to Singapore as a whole. Container ships are considered to be low risk vessels for IMS and are in port for short periods, as the study documented. In contrast, other vessel types such as tugboats, barges, dredgers and drilling rigs present a much greater risk as they often remain in port for prolonged periods (Floerl and Coutts 2009). Also, because these vessels are in close contact with the bottom and other structures, there is a tendency for the antifouling coating to be scraped off. Usage of bulkers and tankers fluctuates with global demand in the charter market and charter rates vary (Floerl and Coutts 2009). This negates the cost benefits of using premium antifouling systems. An example of the high risk effects of such vessels was provided by Yeo et al. (2010), who made a snapshot survey of decapod and malacostracan crustaceans on a drilling rig being cleaned in Singapore and found 14 species not previously encountered in Singapore. In contrast to the short turnaround of commercial shipping vessels at the Keppel Terminal (Lim et al. 2017), drilling rigs and other high-risk vessels can remain alongside or in anchorage for months while they are serviced or wait for new contracts. In addition, the close proximity of Singapore to ports in Batam Island, Indonesia (20 km away shore to shore), and southern

Johor, Malaysia, means that even though they are in three separate countries, they are essentially operating as one contiguous port area, with vessels frequently moving from one port to another (Wells, *pers. obs.*).

Singapore is a signatory to the “International Convention for the Control and Management of Ships Ballast Water and Sediments”, which came into force on 8 September 2017. Accordingly, all vessels covered by the convention are required to report their ballast water management status to the Maritime and Port Authority of Singapore 24 hours prior to their arrival in Singapore (MPA 2017b, 2017c). Singapore also requires that best practice procedures be followed for the removal of tributyltin (TBT) based antifouling systems from vessels (MPA 2008), but there are as yet no requirements for biofouling management. Vessel hull cleaning is extensively undertaken both in water and in drydock in Singapore, but there are no requirements for the management of material cleaned from vessels although indiscriminate disposal of such material could conceivably be policed under Singapore’s Prevention of Pollution of the Sea Act. The Agri-food and Veterinary Authority (AVA; soon to be devolved into the Singapore Food Agency with some of their responsibilities moved to National Parks Board in April 2019) regulates aquaculture practices in Singapore, and are responsible for any introduced food species for culture, as well as the import of animals in the pet trade, which includes marine organisms. Seebens et al. (2013) evaluated the NIMS risk of ports worldwide based on shipping traffic and ballast water release and concluded that Singapore had the greatest risk of NIMS introductions. Papers and information cited above support this hypothesis, but the biological evidence of only 17 NIMS known in Singapore—of which only six (two dinoflagellates, two bivalves, one polychaete, and one fish) were believed to have been introduced via shipping activities (Jaafar et al. 2012)—contradicts the high-risk evaluation. Distinguishing shipping-mediated invasions from those caused by other pathways (e.g., aquaculture) can be challenging; resolving specific responsible vectors such as ballast water and hull fouling within a general pathway such as shipping even more so. The present paper seeks to test the hypothesis that Singapore is in fact at high risk of NIMS introduction.

Materials and methods

A comprehensive literature search was undertaken on the shallow water (≤ 50 m) marine taxa of Singapore, including all macroscopic invertebrates, fishes and marine plants. Marine birds, mammals, reptiles and microscopic species (apart from dinoflagellates) were excluded. All supplements and regular issues from 1980 of *The Raffles Bulletin of Zoology*, published by the National University of Singapore (NUS), were examined. Three marine biological workshops have been held to document the marine flora and

fauna of Singapore (Tan 2013; Tan and Goh 2015, 2016), where specialists in a diverse range of taxa collected at the workshops and reported on specimens in their area of expertise. Field collections from the workshops were supplemented for the workshop reports by specimens held at the Lee Kong Chian Natural History Museum of NUS. Other publications by NUS (e.g., *Nature in Singapore* and *Singapore Biodiversity Records*) were also searched, and the literature cited in these studies has provided additional species records. Of particular interest was a symposium on the ecology and conservation of Southeast Asian marine and freshwater environments (Sasekumar et al. 1994). Overall, approximately 90 papers were found recording marine species present in Singapore.

There is no comprehensive list of NIMS in Singapore. However, there have been several works on NIMS in Singapore published in recent years: Tan and Tan (2003), Puthia et al. (2010), Yeo et al. (2010), Yeo and Chia (2010), Yeo et al. (2011), Jaafar et al. (2012) and Tan et al. (2018). These papers and associated taxonomic work were searched for references to species that have been introduced to Singapore.

Results

In total, 3,650 shallow water marine species have been recorded in Singapore (Table 1; Figure 1), indicating considerable biodiversity in a small area. The list is dominated by molluscs (1151 species), fishes (618), crustaceans (302), marine algae (302), corals (255) and sponges (250+). Groups such as echinoderms (141 species), polychaetes (136), bryozoans (103) and ascidians (50) are known to be well represented elsewhere in terms of NIMS but have not been as well studied in Singapore. There are undoubtedly other species in these groups that are yet to be recorded. Several groups such as flatworms and marine mites have been examined briefly by one or a few studies and what records there are probably do not reflect the full diversity in Singapore. Some groups, such as hydroids, have not been examined at all in Singapore.

Our findings raise the number of marine species recorded as having been introduced to Singapore from 17 (Jaafar et al. 2012) to 33 (Table 2). Fourteen of the introduced species are fishes. In contrast to the other groups that have largely been introduced via ballast water or as biofouling on vessels, most of the fishes were introduced through the freshwater aquarium trade or the aquaculture industry. Only three of the fish species (*Larimichthys crocea*, *Sciaenops ocellatus* and *Podocercus brasiliensis*) are listed in the World Register of Marine Species (WoRMS 2017) and the World Register of Introduced Marine Species (WRiMS; Ahyong et al. 2018) as characteristically being in marine environments (Table 2). Many of the remaining species are cichlids, a predominantly freshwater family but with euryhaline species commonly found in coastal areas; four are not listed as

Table 1. Numbers of species recorded in various taxonomic groups in Singapore, and the primary sources of information.

Taxonomic group	Number of species	Primary sources of information
Marine algae	302	Lee et al. (2013a, b), Loke et al. (2016), Ng et al. (2015b), Phang et al. (2016), Song et al. (2015).
Seagrasses	12	McKenzie et al. (2016), Yaakub et al. (2013).
Marine angiosperms	36	Yang et al. (2013).
Sponges	250+	Lim (2015), Lim et al. (2012), Lim et al. (2016), Lim and Tan (2016), Lim et al. (2013), de Voogd and Cleary (2013).
Corals	255	Hoeksema (2013), Hoeksema and Koh (2013), Huang et al. (2013).
Other cnidarians	40	Goh and Chou (1996), Fautin and Tan (2016), Fautin et al. (2015), Fautin et al. (2013), Reimer and Todd (2013), Sih and Chou (2013).
Flatworms	18	Bolaños et al. (2016), Chim et al. (2015).
Nemerteans	4	Ng et al. (2011).
Polychaetes	136	Chan (2013), Eeckhaut et al. (1994), Lee and Glasby (2015a, 2015b), Glasby et al. (2016), Tan and Chou (1993, 1994, 1996, 1998).
Echiurians	1	Chuang (1962).
Nematodes	2	Chen et al. (2015).
Phoronids	1	Ng et al. (2011).
Sipunculans	19	Hsueh and Tan (2016).
Bryozoans	103	Gordon (2016), Tilbrook and Gordon (2015, 2016).
Entoprocts	1	Tilbrook and Gordon (2016).
Mites	35	Bartsch (2013, 2015), Smit (2013).
Arachnids	1	Ng et al. (2011).
Crustaceans	472	Ahyong (2016), Anker and de Grave (2016), Bruce and Wong (2015), Bruce et al. (2016), Gan and Li (2017), Hughes (2016), Jones and Hosie (2016), Koh and Ng (2008), Lee et al. (2015), Lin and Osawa (2016), Low et al. (2009), Markham (2013), Ng (2015), Ng and Chuang (1996), Ng and Komatsu (2016), Ng et al. (2015c), Ng and Richer de Forges (2015), Osawa and Ng (2016), Rahayu (2015), Rahayu et al. (2016), Uyeno (2015), Upanoi (2015), Wee and Ng (1995), White (2015).
Other arthropods	2	Ng et al. (2011).
Echinoderms	141	Fujita (2016), Fujita and Irimura (2015), Messing and Tay (2016), O'Loughlin and Ong (2015), Ong et al. (2016), Ong and Wong (2015), Tay and Low (2016).
Molluscs	1,151	Glover et al. (2016), Jensen (2013, 2015), Jensen and Ong (2015), Norman et al. (2016), Sanpanich and Tan (2016), Tan and Woo (2010), Tan et al. (2018).
Ascidians	50	Lee et al. (2016).
Fishes	618	Kottelat (2013), Larson et al. (2016), Ng et al. (2015a). Toh et al. (2016).
Total	3,650	Total

marine species in WoRMS (2017) and eight species (including the *Cichlosoma urophthalmus* × *Parachromis managuensis* hybrid) are listed as occurring in fresh and brackish water. These were introduced into Singapore through the freshwater aquarium trade. Three species of *Oreochromis* (tilapia) are freshwater species raised commercially for human consumption; they may enter the upper reaches of estuaries. If these essentially fresh and brackish water species are disregarded, the number of marine species introduced into Singapore waters is reduced to 22.

Discussion

Singapore lies in close proximity to the megadiverse coral triangle that stretches from Malaysia and the Philippines east to Papua New Guinea and the Solomon Islands (Hoegh-Guldberg 2009), evidenced by the high number of macroscopic marine invertebrates, plants and fish species reported in its territorial waters. Three marine biodiversity workshops conducted since 2006 (Tan 2013; Tan and Goh 2015, 2016) resulted in extensive species lists, suggesting that considerable biodiversity persists despite

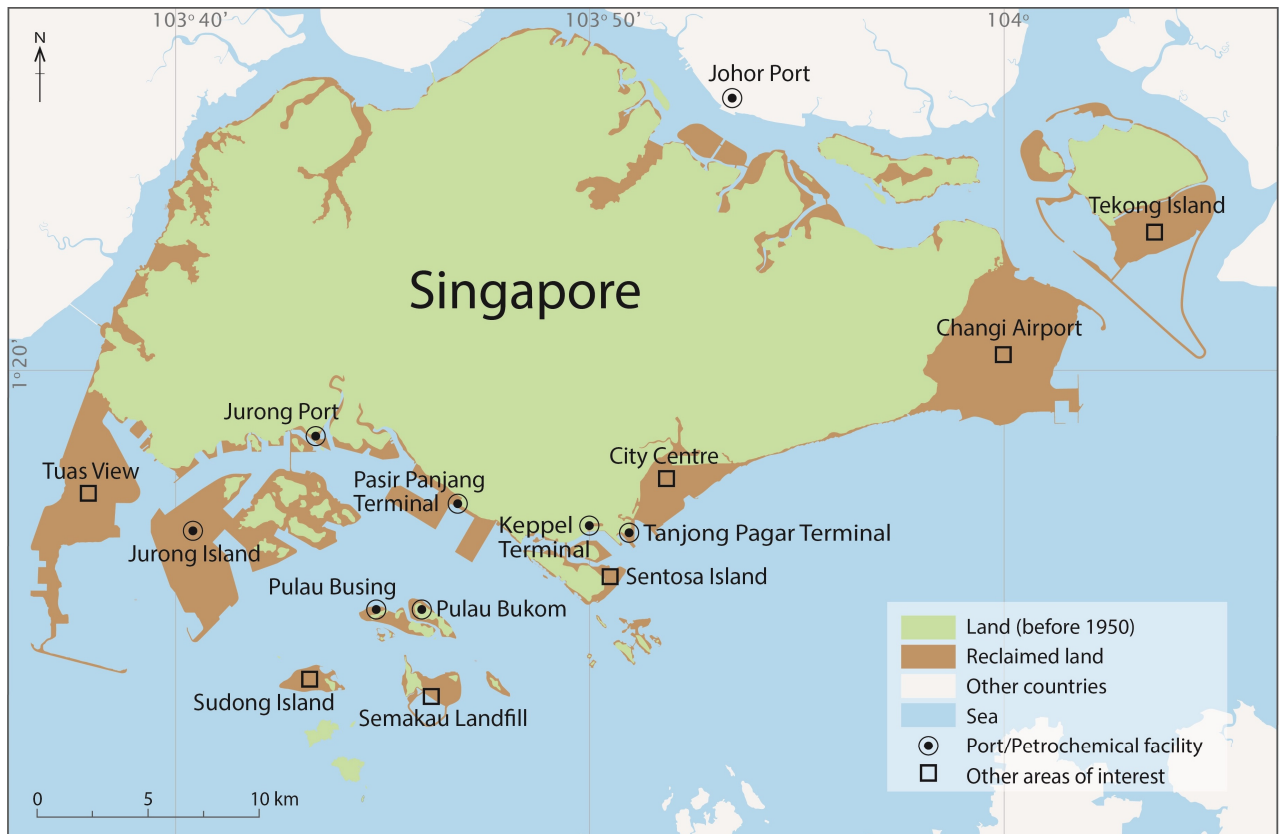


Figure 1. Map of Singapore showing localities mentioned in the text and the amount of land reclaimed since 1950.

extensive urbanization of the marine environment. Although 3,650 marine species have been reported to date, many taxa were addressed in only one or a few papers, while some taxa have never been assessed. New records are continually found, even in groups with the greatest known diversity such as molluscs (1,151 recorded species) and fishes (618), so the actual marine biodiversity in Singapore waters is undoubtedly greater than presently known. Further investigations are required for many of the taxonomic groups, particularly those which are likely to include NIMS.

With its long history as a major transport hub, prodigious vessel traffic (including numerous high-risk vessels such as oil rigs, dredgers, barges and tugboats), and extensive artificial habitats (e.g., seawalls, swimming lagoons, buoys), Singapore has been considered a high-risk port for the introduction of NIMS (Yeo et al. 2011; Lim et al. 2017). A predictive modelling study by Seebens et al. (2013) ranked Singapore as the number one port in the world for the risk of marine bioinvasions. Citing an almost complete lack of available data for Asia, Seebens et al. (2013) did not validate their model for tropical Singapore; the study only provided theoretical support to the long-held academic assumptions about this global shipping hub. Our results, however, show that only 22 fully marine NIMS have been recorded as introduced to Singapore's waters. This is compelling evidence that the worldwide number one ranking of Singapore for potential NIMS introductions (Seebens et al. 2013) is not supported. The questions are then: Is Singapore

Table 2. Known introduced marine and estuarine species in Singapore. WRiMS = World Register of Introduced Marine Species.

Group/Species	Report	Source	WRiMS
Dinoflagellates			
<i>Alexandrium affine</i> (Inoue and Fukuyo) Balech, 1995	Tan et al. (2016b); Lim et al. (2017)	Shipping	Yes
<i>Gymnodinium catenatum</i> Graham, 1943	Holmes and Teo (2002); Jaafar et al. (2012); Tan et al. (2016b); Lim et al. (2017)	Shipping	Yes
<i>Gymnodinium impudicum</i> (Fraga and Bravo) Gert Hansen and Moestrup, 2000	Holmes and Teo (2002); Jaafar et al. (2012)	Shipping	Yes
Marine algae			
<i>Bryopsis pennata</i> Lamouroux, 1809	Lim et al. (2017)	Shipping	Yes
<i>Cladophora sericea</i> (Hudson) Kützing, 1843	Lim et al. (2017)	Shipping	Yes
<i>Hypnea musciformis</i> (Wulfen) Lamouroux, 1813	Lim et al. (2017)	Shipping	Yes
Cnidarian			
<i>Diadumene lineata</i> (Verrill, 1869)	Fautin et al. (2009)	Shipping	Yes
Polychaete			
<i>Hydroides sanctaerucis</i> Krøyer in Mörch, 1863	Lewis et al. (2006); Jaafar et al. (2012)	Shipping	Yes
Crustaceans			
<i>Amphibalanus amphitrite</i> (Darwin, 1854)	Lim et al. (2017)	Shipping	Yes
<i>Amphibalanus improvisus</i> (Darwin, 1854)	Lim et al. (2017)	Shipping	Yes
<i>Podocerus brasiliensis</i> (Dana, 1853)	Hughes (2015)	Shipping	No
Molluscs			
<i>Magallana gigas</i> (Thunberg, 1793)	Baven et al. (2007)	Aquaculture	Yes
<i>Brachidontes striatulus</i> (Hanley, 1843)	Morton and Tan (2006); Jaafar et al. (2012)	Shipping	No
<i>Mytella strigata</i> (Hanley, 1843)	Lim et al. (2018)	Shipping	Yes
<i>Mytilopsis sallei</i> (Récluz, 1849)	Tan and Chou (2000); Tan and Morton (2006); Wong et al. (2010); Jaafar et al. (2012)	Shipping	Yes
Bryozoans			
<i>Bugula neritina</i> (Linnaeus, 1758)	Tilbrook and Gordon (2016)	Shipping	Yes
<i>Watersipora arcuata</i> Banta, 1969	Lim et al. (2017)	Shipping	Yes
<i>Watersipora subatra</i> (Ortmann, 1890)	Tilbrook and Gordon (2016)	Shipping	No
<i>Biflustra perambulata</i> Louis and Menon, 2009	Tilbrook and Gordon (2016)	Shipping	No
<i>Hippoporina indica</i> Madhavan Pillai, 1978	Tilbrook and Gordon (2016)	Shipping	Yes
Fish			
<i>Mayaheros urophthalmus</i> (Günther, 1862)	Tan and Tan (2003); Jaafar et al. (2012)	Aquarium trade	Yes
<i>Mayaheros urophthalmus</i> × <i>Parachromis managuensis</i> (hybrid)	Jaafar et al. (2012)	Aquarium trade	brackish, fresh No
<i>Eetroplus suratensis</i> (Bloch, 1790)	Ng and Tan (2010); Jaafar et al. (2012); Ng et al. (2015)	Aquarium trade	No
<i>Herichthys carpintis</i> (Jordan and Snyder, 1899)	Jaafar et al. (2012)	Aquarium trade	No
<i>Larimichthys crocea</i> (Richardson, 1846)	Jaafar et al. (2012); Ng et al. (2015)	Aquaculture	No
<i>Oreochromis aureus</i> (Steindacher, 1864)	Smith et al., 1983; Jaafar et al. (2012)	Aquaculture	Yes brackish, fresh
<i>Oreochromis mossambicus</i> (Peters, 1852)	Harrison and Tham, 1973; Jaafar et al. (2012); Ng et al. (2015)	Aquaculture	Yes brackish, fresh
<i>Oreochromis niloticus</i> (Linnaeus, 1758)	Smith et al., 1983; Jaafar et al. (2012)	Aquaculture	Yes brackish, fresh fresh
<i>Paraneetroplus melanurus</i> (Günther, 1862)	Ng et al. (2015)	Aquarium trade	No
<i>Poecilia sphenops</i> Valenciennes, 1846	Goh et al. (2002); Jaafar et al. (2012); Ng et al. (2015)	Aquarium trade	No
<i>Sciaenops ocellatus</i> (Linnaeus, 1766)	Jaafar et al. (2012); Ng et al. (2015)	Aquaculture	Yes
<i>Veija</i> spp.	Jaafar et al. (2012)	Aquarium trade	No
<i>Yongeichthys virgatulus</i> (Jordan and Snyder, 1901)	Jaafar et al. (2012); Larson et al. (2016)	Shipping	No

in fact at high risk, but we are not detecting NIMS that have become established in the Singapore marine environment? Is Singapore not at high risk and if not, why not? There have been several studies that provide evidence that the risk of NIMS in Singapore through shipping activities is not as high as previously suggested (Yeo et al. 2011; Seebens et al. 2013; Lim et al. 2017).

Lim et al. (2017) examined shipping patterns at the Keppel-Pasir Panjang Terminal container port in Singapore over three one-month periods, and developed a list of 66 species that could be introduced to Singapore through the container port. The potentially introduced benthic species are all in groups that have been studied in Singapore (Table 1). Planktonic dinoflagellates were compared with the report on phytoplankton in Singapore by Tan et al. (2016b) and planktonic crustaceans were compared to the zooplankton report by Schmoker et al. (2014). Only 17 of the 66 possible introduced species listed by Lim et al. (2017) have been recorded in Singapore. The top three ports by vessel traffic were from nearby Malaysia, Thailand and Indonesia (Lim et al. 2017). Three species (the alga *Caulerpa taxifolia* and the bivalve molluscs *Arcuatula senhousia* and *Ruditapes philippinarum*) could have been introduced from one or more of these ports but are believed to be native to Singapore, as their geographic range incorporates Singapore. This reduces the known number of introduced species to Singapore on the list provided by Lim et al. (2017) to 14. Note that the general concern over invasive *C. taxifolia* involves an aquarium strain released into the Mediterranean Sea where it is causing considerable damage (e.g., Jousson et al. 1998). The strain has also been introduced into Australia (Creese et al. 2004; Wiltshire and Deveney 2017). It is not the Indo-West Pacific wildtype populations that occurs in Singapore.

Until recently, there were no surveys in Singapore specifically targeting NIMS (but see below for surveys of artificial habitats). In contrast, freshwater habitats in Singapore have been better studied in recent years for the introduction of exotic species. There have been a number of reports on the presence of these species and the potential adverse effects in the freshwater environment (e.g., Ng et al. 1993; Ah Yong and Yeo 2007; Ng and Tan 2010; Ng et al. 2013; Liew et al. 2013; Kwik et al. 2013; Ng et al. 2016; Liew et al. 2018). Many of the freshwater studies have been conducted, at least in part, by trained taxonomists who also work in the Singapore marine environment and are aware of the issues of NIMS. These taxonomists would have been looking for NIMS in their marine studies but have found very few. For example, both Peter Ng and Darren Yeo are crustacean taxonomists who have reported extensively on freshwater crustaceans in Singapore (e.g., Ng 1997; Yeo 2010), but they have not

recorded any marine crustaceans from Singapore waters that are NIMS (Ng et al. 2011; Yeo et al. 2011).

NIMS are thought to be concentrated in artificial habitats (Glasby and Connell 1999; Glasby et al. 2007), and there have been a number of ecological studies of artificial marine habitats in Singapore. Lee and Sin (2013), Lee et al. (2013a, b), Chim and Tan (2013). Lai et al. (2015) and Tan et al. (2016a) reported that most of the Singapore shoreline is now composed of coastal defence structures (seawalls and breakwaters) that have replaced natural rocky shores as the most common intertidal hard substratum. As habitat variability is lower on the seawalls, the biota present is mostly (> 80%) a subset of species that can be found on nearby natural rocky shores (Lai et al. 2018). Tan et al. (2018) surveyed Singapore's seawalls specifically for non-indigenous molluscs, but found only evidence of one “possibly introduced” species. In addition, Lim et al. (2009) examined sponges fouling navigation buoys; Loke et al. (2016) examined succession patterns of seawall algal communities on artificial substrates; Toh et al. (2016) recorded 105 species of fish from 48 families in three recreational marinas in Singapore; and during two seawall-enhancement experiments (i.e. Loke and Todd 2016; Loke et al. 2017) over 58,000 individuals were collected and identified. However, none of these papers reported NIMS, further evidence that the paucity of NIMS in Singapore marine waters—even in artificial/modified habitats commonly colonised by NIMS—is real.

Yeo et al. (2011) hypothesised that species presently in Singapore may have been the result of anthropogenic transfers at some time in the past. Given the long history of vessel movements in the Singapore region and the short distances to other countries, this is a very real possibility. Yeo et al. (2011) developed a list of 127 species of crabs that could possibly have been distributed in the past by human vectors and suggested that detailed analysis of their distributions, including genetic analysis, might elucidate previous introductions by anthropogenic mechanisms. Dias et al. (2018) analysed the genetics of the Asian green mussel, *Perna viridis*, and found population clusters in three regions: USA/Caribbean, India and Southeast Asia. The level of detail and breadth of geographic coverage required for this work illustrates the challenge of using the technique for a broad range of taxa such as the 127 crab species suggested by Yeo et al. (2011).

There is mounting evidence that the paucity of NIMS in biodiverse areas such as Singapore, and other locales within the tropical Indo-West Pacific, may be a general feature. A number of papers have reported that there are fewer NIMS in tropical Indo-Pacific waters, and even fewer of these become invasive (Coles and Eldredge 2002; Hewitt 2002; Huisman et al. 2008; Freestone et al. 2011). Briggs (2012, 2013) argued that invasions from more diverse to less diverse ecosystems is a natural, continuing process

which has been accelerated by shipping activities. Some of the invaders have proved to be pests, indicating that such anthropogenic movements need to be controlled. The low number of NIMS recorded in Singapore is consistent with Briggs' hypothesis as the area already has considerable marine biodiversity.

Extensive studies in Guam in the tropical Pacific have reported > 5,500 species, but only 85 of these are regarded as NIMS, and only 23% of the introduced species are known from outside Apra harbour (Paulay et al. 2002). With 343 species, Hawaii is the exception to the lack of NIMS in the Indo-West Pacific tropical waters (DeFelice et al. 2001). Ironically, Pearl Harbor, Hawaii, the only tropical port out of four that Seebens et al. (2013) used to validate their predictive model, was not among the top 20 high marine bioinvasion-risk ports identified in that study. Hawaii is also on the margins of the Indo-West Pacific, and has less diverse biota compared to areas closer to the coral triangle (Hutchings et al. 2002).

There have been a number of studies of NIMS in Australia. NIMPIS (2017) records over 250 NIMS in Australian waters. The extensive coastline of Western Australia extends from the temperate south coast, through a transition zone on the west coast to the tropical north coast. Huisman et al. (2008) surveyed all available reports on NIMS in Western Australia and regarded 60 species as having established populations. There was a clear distinction between 37 species that lived only in the temperate south and six in the tropics; 17 occurred in both areas. Only three species were on the Australian national IMS list (NIMPCG 2009a, 2009b), and all of these were in temperate habitats. Two additional IMS were later reported from temperate habitats (Wells 2018). Hewitt (2002) addressed the question of whether there were fewer introduced species in the tropics by surveying four Australian ports, two tropical and two temperate, using standardised methods. Forty-eight of the 58 NIMS found were in the two temperate ports, but only 28 were in the tropical ports. However, there were a number of species that were cryptogenic or were not identified to species.

In a study similar to the present report, Wells (2018) recorded 5,532 species of marine invertebrates, fishes and marine plants in the 800 km coastline of the tropical Pilbara region of northwestern Australia. He also detailed the extensive IMS surveys that have been undertaken in the area. It is probably the most intensively surveyed region of such a size in the world, but only one IMS, the ascidian *Didemnum perlucidum* Monnoit, 1983, has been found during the surveys of soft sediments as well as encrusting species. The species was first recorded in Western Australia (WA) from the temperate Fremantle marine area in 2010 (Smale and Childs 2011) but is now known from all regions of WA and also the Northern Territory (Bridgwood et al. 2014). The apparent lack of IMS in tropical Australian waters is not limited to WA, but is true for the entire continent. DAFF

(2017) presents an interactive map of IMS from 28 ports. None are shown at the 12 northern ports (the presence of *D. perlucidum* in Dampier was reported after the map was last updated). In contrast, 11 IMS are recorded from the 16 temperate ports. However, the mapping is based on incomplete data as many of the species in the port surveys were not fully identified (Bishop and Hutchings 2011).

In reporting on the low number of NIMS in Singapore, Yeo et al. (2011) suggested that part of the explanation may be that species were introduced in centuries before marine studies began, and present distributions do not reflect the native range of the species. This hypothesis is soundly based in Singapore, with its history of centuries as a major transport hub, including wooden boats with no antifouling protection. Currently there are nearly 140,000 vessel arrivals in Singapore annually, with numerous high-risk vessels arriving from all over the world. This contrasts sharply with the Pilbara region of northern Western Australia, which has 5,532 known species, only 24 NIMS, of which only one is a known IMS (Wells 2018). Unlike Singapore, until recently there has been little vessel traffic into the Pilbara. Historically, Indonesian sea cucumber (*bêche-de-mer*) fishermen visited the Kimberley and Northern Territory to the north, but few, if any, ventured as far south as the Pilbara coast. The first European vessel reached the Pilbara in 1699. Coastal towns later developed but there was little vessel traffic until the iron ore industry started exporting in the 1960s. Vessel movements grew rapidly with the advent of a major resources boom in the early 2000s (Wells 2018). However, for the year 2011, the most recent for which data have been compiled, only 8,195 vessels entered ports along the entire north coast of WA (Bridgwood and McDonald 2014). Combined, the Pilbara and Singapore studies present strong evidence that the relatively low number of NIMS in the Indo-West Pacific tropics is neither due to a lack of knowledge nor an absence of sampling, but rather that there must be one or more underlying biological and/or environmental factors causing the relative lack of invasion success (Hewitt 2002). The question then is: What mechanism(s) prevent NIMS from being introduced into tropical habitats?

The niche size hypothesis (Hutchings et al. 2002) perhaps offers an explanation for the lack of NIMS in tropical waters. For Singapore and Pilbara at least, there is a strong possibility that the low numbers of marine non-indigenous species are driven by biotic resistance in the recipient communities. Lower incidences of marine invasion in tropical ports/areas such as Singapore (this study) and Pilbara (Wells 2018) compared to temperate environments such as San Francisco Bay (Foss 2008) and Melbourne (Hewitt et al. 2004) have been attributed to their relatively (compared to subtropical/temperate localities) higher diversity and therefore more complex community interactions, which include greater

interspecific competition leading to reduced niche availability (Hutchings et al. 2002). In this hypothesis the higher diversity of tropical communities increases interactions between the species towards invasion resistance (Hewitt 2002). Specifically, a number of potential mechanisms have been proposed. Working with terrestrial plant plots, Kennedy et al. (2002) demonstrated that greater species richness increases density and crowding, decreasing invader establishment and success. They concluded that decreasing diversity, such as by installing artificial structures or disturbing habitats, would increase invasion success. Stachowicz et al. (1999) manipulated marine communities in Long Island Sound in the north-eastern United States and found more diverse communities had more resistance to invasions by the ascidian *Botrylloides diegensis* Ritter and Forsyth, 1917. In Hawaii, Zabin and Hadfield (2002) showed that the Caribbean barnacle *Chthamalus proteus* Dando and Southward, 1980, lives at a higher shore level than the native *Nesochthamalus intertextus* (Darwin, 1854) and the two are ecologically separated. Another mechanism was suggested by Freestone et al. (2011, 2013) who demonstrated experimentally that, at least in their study sites, greater predation pressure on introduced species in tropical communities when compared to temperate ones could explain the inability of species to invade tropical environments. Clearly then, with such explicative processes occurring, we suggest that baseline studies of the existing marine biota and incorporation of actual data be made priorities for validation and refinement of predictive models of bioinvasion risk. It is also important to lodge voucher material in a recognised museum, such as the Lee Kong Chian Natural History Museum in Singapore so the material can be re-examined by future researchers.

The next question is what impacts do the 22 known NIMS have on the Singapore marine environment? There has been relatively little work on this aspect, but several studies have been made. The most recent was by Lim et al. (2018) on the American mussel *Mytella strigata*, in which they demonstrated is an earlier name for the species previously known as *M. charruana* (d'Orbigny, 1846). The mussel dramatically invaded the shores of the Johor Strait, between Singapore and Malaysia. Extensive populations have been established on mudflats, in and around mangrove areas, and on artificial surfaces along the coast of Singapore in the four years since the species was first detected. Densities in excess of 10,000 per 100 cm⁻² have been recorded on floating fish farms, where *M. strigata* has excluded the native *P. viridis* (Lim et al. 2018). A second bivalve, the Caribbean dreissenid *Mytilopsis sallei*, was first discovered in Singapore in the 1980s. By the early 2000s the species was widely distributed in low salinity areas of the upper reaches of monsoonal canals throughout Singapore, with densities of up to 830 individuals per 100 cm² (Tan and Morton 2006). *Mytilopsis sallei* has also been reported in the Songkhla

Lagoon (also known as Songkhla Lake) of southern Thailand (as *Mytilopsis adamsi* Morrison, 1946 in Wangkulangkul 2018), where it has developed dense populations; however, these are restricted to the low salinity waters near the mouths of rivers flowing into the lagoon. The introduced mussel *Brachidontes striatulus* was reported by Morton and Tan (2006) at much lower densities (up to 75 individuals per 100 cm²), nested among the byssal threads of *M. sallei*. The species was expected to spread more widely in Singapore (Morton and Tan 2006), but there have been no subsequent publications on the mussel. There have been no analyses of the potential effects of the other NIMS recorded in Singapore.

Conclusion

Increasing coastal urbanisation, coupled with intensification of maritime activities, will continue to exert considerable pressure on tropical coastal marine ecosystems that may result in further introductions and invasions in the future. It is timely that global prevention efforts such as the International Maritime Organization (IMO) Ballast Water Management Convention, which Singapore is a signatory of, have recently come into force. The new GloFouling Partnership, launched in 2018, was developed to promote understanding and uptake of the guidelines in developing areas.

Evidence presented alludes to biological/environmental factors affecting establishment and proliferation of NIMS. It is our responsibility to develop new data sets so that invasion science evolves to address current discrepancies, especially if the current understanding impedes informed management of coastal/marine areas/resources. With the increasing number of NIMS being reported in the marine environment, it is imperative that we increase our understanding of introductions in tropical marine systems. We need comprehensive studies to document the resident flora and fauna, including describing native undescribed species, to underpin our understanding of the actual number of NIMS in local marine environments. These studies should concentrate on taxa such as polychaetes, bryozoans and ascidians that are known to have significant numbers of NIMS. A detailed understanding is required of the invasion success of NIMS in a variety of geographical areas to build on the results obtained in the Singapore and Pilbara studies, and to inform/validate prevention and management strategies, including those based on predictive modelling approaches.

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