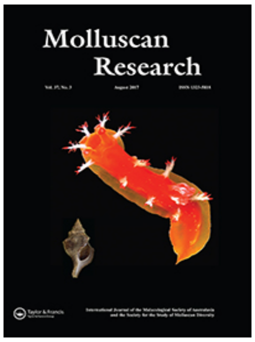

Molluscan Research

ISSN: 1323-5818 (Print) 1448-6067 (Online) Journal homepage: https://www.tandfonline.com/loi/tmos20

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To cite this article: Fred E. Wells (2017) If the Asian green mussel, *Perna viridis* (Linnaeus, 1758), poses the greatest invasive marine species threat to Australia, why has it not invaded?, Molluscan Research, 37:3, 167-174, DOI: 10.1080/13235818.2017.1322676

To link to this article: https://doi.org/10.1080/13235818.2017.1322676

Published online: 16 May 2017.

MOLLUSCAN RESEARCH, 2017
VOL. 37, NO. 3, 167–174
https://doi.org/10.1080/13235818.2017.1322676

If the Asian green mussel, *Perna viridis* (Linnaeus, 1758), poses the greatest invasive marine species threat to Australia, why has it not invaded?

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ABSTRACT

A national approach has been developed to the problem of invasive marine species (IMS) in the Australian marine environment. Fifty-five species were listed as posing significant threats to Australia. A 2005 analysis of the scientific literature concluded that the Asian green mussel *Perna viridis* (Linnaeus, 1758) poses the greatest threat to Australia. The mussel has in fact successfully invaded many areas of the world's oceans. Despite the numerous and varied opportunities for *P. viridis* to be distributed to northern Australia it has not established a known population on the continent, perhaps suggesting there are biological factors inhibiting its establishment. The invasion success of *P. viridis* in many parts of the world and its failure so far to establish in Australia make the species ideal for testing theories of the factors determining invasion success. Such research will allow a reconsideration of the invasion threat the species poses to the Australian marine environment.

ARTICLE HISTORY
Received 6 June 2016
Final version received 25 January 2017

KEYWORDS
Ballast water; biofouling; distribution; marine pest; molluscs; veliger

Introduction

During the 1990s there were a number of incidents in Australia involving invasive marine species (IMS; also, known as introduced marine pests) that were widely discussed by regulators and the general public. Two of these stand out. Firstly, the north Pacific seastar *Asterias amurensis* Lutken, 1871 was found in the Derwent River estuary at Hobart, Tasmania where it threatened lucrative abalone fisheries. It later spread to Port Philip Bay, Victoria where a scallop fishery was threatened (Turner 1992; Coggin 1998). Secondly, an IMS survey in Darwin in March 1999 uncovered a massive infestation of the black striped mussel *Mytilopsis sallei* (Récluz, 1849) that was centred in the Cullen Bay marina, where densities of up to 23,650 m^{-2} were recorded. The Northern Territory government declared an environmental emergency and the species was successfully eradicated (Ferguson 2000; Russell and Hewitt 2000; Willan et al. 2000; Bax et al. 2002).

In response to these and other issues, the National Introduced Marine Pests Coordinating Group (NIMPCG, since replaced by the Marine Pests Sectoral Committee) was formed to develop a National System for the Prevention and Management of Marine Pest Incursions (NIMPCG 2009a, 2009b). As part of this process, the Commonwealth Scientific and Industrial Research Organisation (CSIRO) was contracted to undertake a comprehensive search of the scientific literature on IMS. A database was developed with information on 1582 marine species that had been distributed through human activities worldwide and the effects of the introductions, which had largely been overseas (Hayes et al. 2002, 2005; Hayes and Sliwa 2003). The list was reduced to a national IMS list of 55 species considered to present the greatest threat to the Australian marine environment. Included were a wide range of plant and animal groups, comprising both holoplanktonic and benthic species: dinoflagellates, diatoms, macroalgae, cnidarians, polychaetes, an echinoderm, fish, molluscs (bivalves and gastropods) and crustaceans (copepods, barnacles and crabs). Hayes et al. (2005) analysed the risks to Australia of the 55 IMS species in two successive years; in both cases the Asian green mussel *Perna viridis* (Linnaeus, 1758) was classified as the only high priority species.

There has been a considerable increase in our knowledge of the IMS issue in the years since Hayes et al. (2005) was published. The present article brings together our current knowledge of the invasion capabilities of *P. viridis* to Australia and argues that a re-evaluation of the threat posed by the mussel is warranted.

Invasion capability of *Perna viridis*

In general, the life history traits that make a successful invader are: a short life span, rapid growth rate, rapid sexual maturity, high fecundity, ability to colonise a wide range of habitats, wide physiological tolerances, gregarious behaviour, suspension feeding and ability

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Published online 16 May 2017

to repopulate following a population crash (Morton 1997); all of these traits apply to *P. viridis*. Specifically, in terms of mussels, Bayne (1976) attributed their competitive superiority to their rapid recruitment and growth, their ability to detach and re-attach with a byssus and their ability to quickly migrate to vacant spaces created by natural forces. It is obvious that *P. viridis* is endowed with several characteristics that qualify it to be a successful invader (Rajagopal et al. 2006).

Many of the above characteristics also apply to aquaculture species. *Perna viridis* is widely used for human consumption in South East Asia and in other regions. Originally it was a wild caught species. The wild caught fishery peaked in 1971, when 165,500 tonnes were landed. The wild caught fishery has since declined to minimal levels and been replaced by aquaculture production, which peaked at 312,607 tonnes in 2002 and then declined to 159,474 tonnes by 2014 (FAO 2016).

The native range of *P. viridis* extends across a wide swath of the Indo-Pacific from the Philippines to the Persian Gulf, including the Malaysian peninsula and the islands of Sumatra, Java and Sulawesi in Indonesia (Siddall 1980). Although it is native to tropical Asian waters, *P. viridis* has become widely distributed in the Indian, Pacific and Atlantic Oceans accidentally and also deliberately for use as an aquaculture species (NIMPIS 2015; FAO 2016). For example, *P. viridis* has been introduced to New Caledonia, Fiji, Tahiti, Tonga and Samoa (Baker et al. 2007). It was accidentally introduced to Trinidad, West Indies in about 1991 and spread to Venezuela by 1993. In 1999 it was discovered in Tampa Bay, Florida, where it obstructed cooling water intakes at several power plants. It then increased its range to northeastern Florida, and by the end of 2003 had extended northward into Georgia (SCAISTF 2007). However, the Georgia population is apparently restricted by the tidal range and winter mortalities (MAREX 2017).

Barber et al. (2005) concluded that *P. viridis* in Tampa Bay had a higher fecundity than the native mussel *Brachidontes exustus* (Linnaeus, 1758) because *P. viridis* had a faster growth rate and reached a greater maximum size. They speculated that this may result in the displacement of native bivalves in Tampa Bay, including *B. exustus*. Firth et al. (2011) reported a series of winter mortalities of *P. viridis* on intertidal shorelines in Tampa Bay caused by low air temperatures that might halt the northward spread of the species. However, over time global warming trends might lessen the impacts of winter temperatures in this area. SCAISTF (2007) reported that because of its large size, rapid growth rate and early maturity, *P. viridis* is a nuisance species even within its native range. The impacts of this species are potentially severe. Ecologically it can displace native American oysters (*Crassostrea virginica*) on intertidal oyster reefs in the southern United States and reduce the density of juvenile oysters (McFarland et al. 2015). Economically it reduces the effectiveness of cooling systems and fouls navigation buoys, floating docks, piers and pilings. Densities can reach 35,000 m^{-2} (Rajagopal et al. 1991). *Perna viridis* also accumulates toxins and is a cause of shellfish poisoning in humans (NIMPIS 2015).

This mussel caused concern in Australia when it was introduced to Cairns, Queensland in 2001 by an apprehended illegal fishing vessel, the MV *Wing Sang 108*. A small breeding population was established but died out after a few years (Neil et al. 2005; Stafford et al. 2007).

Economic costs of combatting invasive marine species

Mitigating the risk posed by *P. viridis* is not simply a scientific question of academic interest—it has a substantial financial cost. In 2002 the dredge *Leonardo da Vinci* entered Geraldton Harbour, Western Australia (WA) to work on a major harbour enhancement project. The dredge came directly to Geraldton from Jamaica in the West Indies. Parts of the dredge were heavily fouled with a variety of species, including potential IMS species. Fortunately, mitigation measures prevented the species from spreading into the harbour (Wells et al. 2009b). Since the 2002 incident all assessments of major development projects by the WA Environmental Protection Authority (EPA) have recommended that the Minister for the Environment impose legally binding ministerial conditions that require developers to minimise the risk of their vessels introducing IMS to WA waters. The measures include risk assessments of construction vessels, IMS inspections of medium and high risk vessels entering WA waters from overseas and interstate, and IMS monitoring programs at the construction sites. Similar procedures are required by the Northern Territory as a result of the *M. sallei* incident.

Although WA awareness of IMS issues was raised by the 2002 incident, the lead time for project development by the proponent and EPA assessment meant that it was several years before the requirements became effective for major projects. Most vessel assessments and inspections have occurred since 2010. The largest single project has been the Gorgon liquefied natural gas (LNG) plant at Barrow Island, which has risk assessed and/or inspected 641 vessels since 2010 (S. McKirdy, Chevron Australia, pers. comm. 2016). Another major company, Woodside Energy Ltd, also developed a risk assessment and inspection methodology used to assess and minimise the IMS risk posed by its vessels (Woodside 2016). By October 2016, 363 IMS assessments had been carried out by Woodside.

Of these 22% (or 78) were assessed as a 'high' or 'uncertain' risk and required additional management measures such as IMS inspections, cleaning or other treatment to minimise the risk of introducing IMS (T. Box, Woodside, pers. comm. 2016). Other companies have adopted similar protocols that have assessed smaller numbers of vessels.

The inspections themselves have had a substantial cost, but there have also been costs caused by consequent delays to mobilisation and cleaning where IMS have been detected. *Perna viridis* is by far the most commonly detected species; most of the detections reported to the WA Department of Fisheries (DoF) have been a result of these inspections. Almost all of the *P. viridis* detected were juveniles that were not in reproductive condition. In some instances, when the vessel was to remain in WA waters for a few days it was allowed to complete its mission and depart. However, many of the vessels were remaining in the state for prolonged periods. The floating drydock at Henderson, WA is capable of handling vessels up to 100 m long. Facilities at Henderson, Dampier and Darwin can haul smaller vessels out of the water for cleaning and application of antifouling. These facilities were used when possible to clean the vessels, but they were not always available, and many ships were too large to be handled. These vessels went to Singapore or Batam, Indonesia for cleaning. The journey requires approximately a week each way, plus the time in drydock. Unfortunately, there are only anecdotal estimates of the costs involved in these activities.

Arthur et al. (2015) estimated the Australian costs of ballast water management for IMS. They recognised biofouling as a major pathway for the introduction of IMS but excluded it from their study for two reasons: firstly, they considered the primary driver of biofouling management to be reduction in fuel costs and increasing vessel safety; and, secondly, the lack of an Australian national management program for biofouling management for IMS. They estimated the annual costs of IMS prevention through ballast water management at AU$36.2 million a year for exchange and AU $0.8 million a year for compliance monitoring. The costs of eradication attempts, which presumably would also apply to biofouling species, were estimated at AU$5–20 million with a 5%–20% chance of successful eradication. The costs of an IMS established in the environment were estimated at AU$4–1000 million per incursion.

Possible *Perna viridis* transport to Australian waters

As noted above, *P. viridis* is the species most consistently detected on vessels inspected in WA. In the 20 months of January 2014 through August 2015, the latest period for which data are available, 15 of 19 detections of listed IMS species entering WA waters from overseas were *P. viridis* (R. Adams, DoF, presentation to IMS workshop at DoF in August 2015). Most of the detections were on construction vessels such as barges, dredges and offshore support vessels (seagoing tugs) that were inspected as required for vessels working on projects subject to EPA ministerial conditions. To some extent this reflects the higher risk of these vessels which have been targeted, but *P. viridis* has also been detected on naval vessels, a cruise liner, a private yacht and a bulk cargo vessel inspected by DoF. However, it should be noted that many vessels of high risk types enter WA and are not inspected as they are not working on projects subject to ministerial conditions. It is not known how many of these uninspected vessels carried *P. viridis*.

These numerous detections of *P. viridis* since 2010, and the lack of known populations having become established and survived in Australian waters, raises the question of whether the risk posed to the Australian marine environment by *P. viridis* is as high as previously thought and why the species has not invaded Australian waters? There have been numerous opportunities and pathways for *P. viridis* to have reached northern Australia over a substantial time frame, yet the species is not known to have become established long-term in Australian waters.

Pathways for *Perna viridis* introduction to Australia

The veliger larvae of *P. viridis* can remain for 3 to 4 weeks in the plankton before settling (Rajagopal et al. 2006), implying a substantial distribution capability. However, Gilg et al. (2014) examined settlement patterns of *P. viridis* in the Intracoastal Waterway (ICW) in northeastern Florida. Most settlement occurred within the main ICW channel and not in adjacent feeder creeks. Most larvae settled within 10 km, but some were at least 18 km from a potential source population. Their model projections suggested that dispersal distance along the open coast could often exceed 100 km, but this is not sufficient for dispersal to occur from most of Indonesia to northern Australia.

There is a marine biogeographical break between western Indonesia (Sunda Shelf, Makassar Strait and Lombok Strait) and eastern Indonesia (Flores Sea, Banda Sea and Sahul Shelf) (Nuryanto and Kochzius 2009). *Perna viridis* occurs naturally in western Indonesia but not in eastern Indonesia (Huhn et al. 2015). The species has been recorded on the south coast of the island of New Guinea (FAO 2016), but this record needs confirmation, as the area is east of the distribution gap reported by Huhn et al. (2015) and New Guinea was not on their list of known Indonesian populations of *P. viridis*. If *P. viridis* is in fact in southern New Guinea, Torres Strait, between southern New Guinea and northern Queensland, is only 150 km wide at its narrowest point, and there are numerous intermediate islands that could serve as stepping stones for movement of *P. viridis* into northern Queensland.

Whether or not 'natural' larval dispersal is a possibility, there are a variety of human-mediated mechanisms which would enhance the possibilities for *P. viridis* reaching northern Australia.

As described above, a small breeding population became established at Cairns, Queensland in 2001, but subsequently died out naturally (Stafford et al. 2007). Similarly, a population of approximately two dozen mature New Zealand green mussels, *Perna canalicula* (Gmelin, 1791), was found in the Outer Harbour, Adelaide, South Australia in 1996 and was successfully eradicated (Wiltshire et al. 2010). An alternative hypothesis is that *P. canalicula* failed to establish because of natural mechanisms. McDonald (2012) found a small population of *P. viridis* on two naval vessels in Cockburn Sound that had apparently spawned during a marine heat wave in the area. The vessels were cleaned and no individuals have been found in the local marine environment.

Perna viridis occurs in Sulawesi (Siddall 1980; Yaqin et al. 2011; Huhn et al. 2015). In the early 1800s between 30 and 60 praus from Macassar (now known as Sulawesi), Indonesia, visited the Northern Territory annually to collect sea cucumbers and other species. The trade existed from at least the 1700s, and possibly earlier, until the early 20th century (Clark and May 2013). Even today wooden Indonesian praus are allowed to fish in the waters offshore of northern Australia in areas such as Ashmore Reef and Scott Reef. Some of the boats have fished illegally and have been found to have *P. viridis* attached (Wells et al. 2009a).

Early European explorers in the region also used wooden boats and moved between Singapore and other Asian ports and northern Australia. The earliest settlements on the Australian north coast were serviced by wooden boats. More recently shipping has developed rapidly along the coast of northern Australia. Mining accelerated in the 1960s with the commencement of large scale shipments of iron ore and other minerals from Pilbara ports, including Port Hedland, Dampier and Cape Lambert. LNG shipments from the North-West Shelf began in the 1980s. Bridgwood and McDonald (2014) analysed the risk of IMS introductions into WA by commercial vessels. They recorded 8195 vessel visits on the north coast of WA in 2011 alone: over half of these were rated as low risk vessels (4858 or 59.3%); vessels with a moderate risk rating accounted for 3221 visits (39.3%); and vessels with a high risk rating accounted for 116 visits (1.4%). Many of these vessels were from South East Asian ports where *P. viridis* is present, suggesting there have been many undetected incursions even in recent years.

Heersink et al. (2014) assessed the risk posed by *P. viridis* by addressing two questions: can *P. viridis* establish in Australia; and, if *P. viridis* can establish, what is the likelihood of this happening? The questions were addressed with a two-stage Bayesian model that incorporated the estimated approach rate of vessels fouled with *P. viridis* in the last 50 years and an analysis of temperature tolerances of the species. They estimated that tens to hundreds of fouled vessels arrived in Australian ports annually over the last half a century. *Perna viridis* would be able to survive the temperature regime in ports in the northern half of Australia, as happened in Cairns. Based on a statistical analysis of the estimated rate of fouled vessels arriving in Australia and the lack (except for Cairns) of any populations developing, Heersink et al. (2014) concluded that the probability that the environment is suitable for *P. viridis* establishment is low both in WA (c. 2%) and Northern Territory ports (c. 12%). Assuming the port environment to be suitable, the estimated probability of entry per fouled vessel entry ranged from c. 0.1% in WA and Queensland to c. 0.4% in the Northern Territory. These estimates were combined with vessel numbers for each state for 2013, the year examined. The establishment probability varied from c. 0.13% in WA to c. 10% in Queensland. Heersink et al. (2014) pointed out that the estimates were conservative, as they do not include natural dispersal mechanisms. The conclusion of Heersink et al. (2014) is that the threat posed to the Australian marine environment by *P. viridis* may be lower than previously thought.

Huhn et al. (2015) recorded the introduction of *P. viridis* into Ambon in eastern Indonesia, east of its previously known range. The introduction is thought to have occurred recently as biofouling on two ferries (KM *Tidar* and KM *Kelimutu*) that operate from ports in western Indonesia where *P. viridis* is known to be present; *P. viridis* was present as biofouling on the two vessels. Investigations showed that the body condition index (BCI) of *P. viridis* collected from the ferries was significantly lower than in similar-sized individuals from three different populations in western Indonesia. The ferries spend most of their time in open oligotrophic oceanic waters where the mussels are food limited, resulting in their lowered BCI. Huhn et al. (2017) hypothesise that the lowered BCI of *P. viridis* restricts their invasion capability and is the reason *P. viridis* has not been introduced into Australia by modern vessels. If this hypothesis is correct it could also explain why the species was not introduced into northern Australia by Macassan fishermen.

Relative lack of IMS introductions in tropical waters

The invasion capabilities of *P. viridis* in Australian waters can also be considered in a broader marine biogeographical context.

Relatively few marine introductions have been detected in tropical waters, and even fewer marine pest species (Coles and Eldredge 2002; Hewitt 2002; Freestone et al. 2011). The tendency for IMS to occur in temperate, rather than tropical, Australian marine waters is well established. Huisman et al. (2008) recorded 60 introduced marine species in WA that were believed to have become established; most (37) were temperate species that occur south from Geraldton, six were tropical species that occur from Shark Bay north, and 17 occurred in both regions. The three species classified as marine pests were all found in the temperate waters from Fremantle south. The national IMS database includes an interactive map of IMS records from 28 localities (DAFF 2017). No IMS are shown at the 12 northern localities. Eleven IMS species are shown at the 16 temperate localities, the most northern of which are Newcastle, New South Wales in the east and Fremantle, WA in the west. However, the database was last updated in 2014 and does not show the invasive ascidian *Didemnum perlucidum* (Monnoit, 1983) along the northwest coast. This species is unique in being the only IMS that spans the entire coastline of WA from the temperate south to the tropical north; it is also found in Darwin (Bridgwood et al. 2014).

A number of reasons have been proposed for the relative lack of introduced species in tropical waters, including 'the higher diversity of native tropical communities conferring an increased resistance to invasions through an increase in biotic interactions' (Hewitt 2002: 213). Alternatively, tropical waters have been less surveyed resulting in less detections, or our taxonomic knowledge of the biodiverse tropics may result in introduced species remaining undetected. Hewitt (2002) analysed results of eight surveys of Australian ports, four tropical and four temperate, conducted with standardised methodology and concluded that in these ports there was no difference in the proportion of introduced species caused by a lack of taxonomic knowledge. Freestone et al. (2011) demonstrated experimentally that, at least in their study sites, predation pressure could explain the inability of species to invade tropical environments.

The outbreak of *Mytilopsis sallei* in Darwin demonstrates that tropical IMS invasions can occur rapidly. However, it is important to note that, unlike *P. viridis*, *M. sallei* is a Caribbean species that does not naturally occur in the region to which it was introduced.

Potential changes to invasion patterns

There are a number of features that restrict our ability to predict the invasion capabilities of individual species including, but not limited to, *P. viridis*.

For example, there may be increases in the number of arrivals of a single species in an area. These may be due to human activities, such as the increase in vessel movements from South East Asia to northwestern Australia in recent years (Bridgwood and McDonald 2014). Heersink et al. (2014) documented the increased propagule pressure of the increased vessel traffic to Australia in the last half a century. There may also be natural causes of increased propagule pressure such as a successful spawning period in the native environment that results in increased numbers of larvae arriving in a new area. This may have happened with *P. viridis*. Barges were routinely moving between Indonesia and the Pilbara without incident when four barges were detected in the Pilbara in April and May 2013 with small numbers of juvenile *P. viridis*. The barges had all undergone inspections prior to departing from Indonesia and were routinely reinspected after 90 days, when the mussels were found. As the mussels were juveniles there was no risk of them spawning (M. Massam, DoF, pers. comm. 2013). It may be that a major natural spawning event in Indonesia had resulted in the barges becoming contaminated.

There can be a substantial time lag between the introduction of a species into a new region before it becomes a recognised IMS. The Suez Canal was opened in 1869 to provide a transport link between the eastern Mediterranean Sea and the Red Sea. Nearly 1000 species have transited through the canal and become established at the other end; most of these Lessepsian migrations have been from the Red Sea to the Mediterranean Sea (Cilia and Deidun 2012). One of the earliest species to transit the canal was the Red Sea mussel *Brachidontes pharaonis* (P. Fischer, 1870), which was first recorded at Port Said, Egypt in 1876 (Dogan et al. 2007). The mussel was found in Israel in 1937, and was still rare in the early 1970s, 100 years after the first Mediterranean detection. However, by the early 2000s *B. pharaonis* dominated local rocky shores (Bogi and Galil 2013). It has since become widespread in the eastern Mediterranean (Cilia and Deidun 2012).

A little understood phenomenon is that there may be different genetic strains of a species, some of which have greater colonising abilities than others. The Australian mussel *Xenostrobus securis* (Lamarck, 1819) has become invasive in Asia and Europe. Colgan and da Costa (2013) investigated the population genetics of the species and reported finding a number of clades, only two of which are invasive. Similarly, the European green crab, *Carcinus maenas* (Linnaeus, 1758) has been introduced into the east coast of North America and many other parts of the world, including Australia. Populations on the east coast of North America date back to the 1800s, but there was also a cold water invasion with different genetics in the late 1900s. A population of *C. maenus* became established in Placentia Bay, Newfoundland around 2002. Crabs in the area have a mixture of warm and cold water genetic characteristics (Blakeslee et al. 2010).

The impacts of climate change are now being documented at an increasing rate worldwide. In Australia, there have been numerous examples of southward range extensions of tropical species. Such range extensions have been recorded along the entire east coast as far south as Tasmania (Ling et al. 2009). On the west coast of WA, a major marine heatwave increased sea surface temperatures by 3–5 °C during the summer of 2011, causing extensive changes to the marine biota (Wernberg et al. 2016). Temperate reef communities are dominated by kelp forests (*Ecklonia radiata* (C. Agardh) J. Agardh) that contracted 100 km to the south and were replaced by persistent seaweed turfs. The temperate biota was replaced by tropical and temperate seaweeds, invertebrates, corals and fishes. The community-wide tropicalisation fundamentally altered key ecological processes which suppressed the recovery of kelp forests.

The southward movement of marine biota on the two Australian coasts increases the area that can be colonised by tropical IMS species such as *P. viridis*. Additionally, extensive habitat disruptions such as the one in WA may increase the susceptibility of the marine environment to invasions by IMS.

In conclusion, the numerous and varied opportunities for *P. viridis* to be distributed to northern Australia, and the fact that it has not established a known population on the continent, suggests that there are one or more biological reasons currently inhibiting its establishment (Heersink et al. 2014), such as the suggestion by Huhn et al. (in press) that *P. viridis* transported as biofouling across the open sea are in poor condition, restricting their ability to colonise new areas. Alternatively, as with *Xenostrobus* (Colgan and da Costa 2013), some lineages may be more invasive than others and invasive lineages have not yet been transmitted to Australian waters. The factors determining the success or failure of a species to become an IMS in a particular area are poorly understood. The invasion success of *P. viridis* in many parts of the world and its failure so far to establish in Australia make the species ideal for testing theories of the factors determining invasion success. Such research will allow a reconsideration of the invasion threat the species poses to the Australian marine environment.

Acknowledgements

I thank Dr Justin McDonald of the WA Department of Fisheries and Dr Tan Koh-Siang of the National University of Singapore for their thoughtful comments on an early draft of the manuscript, and two anonymous reviewers for comments on a later draft.

Disclosure statement

No potential conflict of interest was reported by the author.

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