

Research Article

Biotic and abiotic factors affecting the Tasmanian distribution and density of the introduced New Zealand porcelain crab *Petrolisthes elongatus*

Liam P. Gregory^{1*}, Marnie L. Campbell^{1,2}, Carmen Primo¹ and Chad L. Hewitt^{1,2}

¹ National Centre for Marine Conservation and Resource Sustainability, University of Tasmania, Locked Bag 1370, Launceston 7250 Tasmania, Australia

² Central Queensland University, Bryan Jordan Drive, PO Box 1319, Gladstone 4680 Queensland, Australia

E-mail: lpg@utas.edu.au (LPG), m.campbell@cqu.edu.au (MLC), c.primo@amc.edu.au (CP), c.hewitt@cqu.edu.au (CLH)

*Corresponding author

Received: 9 March 2012 / Accepted: 11 July 2012 / Published online: 25 July 2012

Handling editor: Mark Hanson, Fisheries and Oceans Canada, Canada

Abstract

Petrolisthes elongatus (Milne-Edwards, 1837) was first introduced into southern Tasmania in the late 19th century putatively associated with live-oyster transfers from New Zealand. In the last century *P. elongatus* populations have expanded, inoculating rocky intertidal zones around Tasmania. We initially identified the scope of *P. elongatus* introduced range around Tasmania by visiting 57 sites to identify presence. Density of *P. elongatus* and populations of two native grapsid crab species was assessed at 12 sites around Tasmania to identify any biotic resistance. Abiotic factors including substrate availability and preference, and wave stress, were identified at each of the 57 sites. Our results indicate that *P. elongatus* has successfully invaded a large proportion of the southern and northern coasts of Tasmania, with a small number of sites on the east and none on the west coast supporting *P. elongatus* populations. Densities were found to be higher in southern Tasmania compared to the eastern and northern coastlines. *Petrolisthes elongatus* presence was found to be positively correlated with native grapsid crab presence, however, no statistically significant relationship was found between densities at scales of site or quadrat. Abiotic factors have been identified as the primary drivers of *Petrolisthes* distribution patterns.

Key words: marine; introduced species; population density; biotic resistance; habitat preference

Introduction

Non-indigenous species (NIS) are an increasing threat to biodiversity worldwide (e.g., Lubchenco et al. 1993). NIS have the ability to alter native assemblages and cause permanent and ongoing damage to the ecosystems they inoculate (Carlton and Geller 1993; Ricciardi et al. 1997; Parker et al. 1999). The competing influence of a range of biotic and abiotic mechanisms determines NIS invasion success and includes characteristics of both invading species and the invaded ecosystem. It is hypothesised that the characteristics of invading species, such as fecundity, mobility, and physiological plasticity, contribute to invasion success (e.g., Lodge 1993; Hayes and Sliwa 2003). The characteristics of receiving (invaded) ecosystems are also considered to influence NIS invasion success. For example, the absence of competitors, parasites and predators can contribute to the successful establishment and

subsequent spread of novel species (e.g., Torchin et al. 2001; Shea and Chesson 2002; Torchin et al. 2003; Dunstan and Johnson 2007). However, favourable abiotic conditions (suitable habitat) can be even more important than biotic factors in some cases (e.g., Moyle and Light 1996; Holway et al. 2002).

Two *Petrolisthes* species (commonly known as porcelain crabs) have successfully invaded intertidal systems globally. *Petrolisthes armatus* (Gibbes, 1850) is a species native to Brazil that has successfully invaded North America (Florida to North Carolina), South America (north-west of Brazil to Venezuela), Bermuda, West Indies, the Caribbean and tropical West Africa (Gore 1972; Hollebone and Hay 2007). Previous studies of the invading *P. armatus* have commonly focused on the distribution and abundance, effects on native biodiversity and the possible negative impacts this NIS can have on bivalve fisheries along the south-eastern seaboard of America (Walton et al. 2002;

Hollebone and Hay 2007). These impacts include the over-population of oyster reef communities, which subsequently pushed juvenile and mature native mud crabs (native predator) out of their native ecosystem (Hollebone and Hay 2007). Furthermore, as a filter feeder that attains high densities (4,000 to 11,000 individuals m^{-2}) *P. armatus* may have negative effects on the other filter feeders, including oysters (Haig 1960; Hollebone and Hay 2007).

The second species, *Petrolisthes elongatus* (Milne-Edwards, 1837), is native to New Zealand and has been introduced into Tasmania (Australia). This sedentary filter feeder commonly inhabits the lower intertidal zone where it is found under rocky substrate (Haig 1960; Jones 1976; Jones and Greenwood 1982; Pellegrino 1984). Distribution and tolerance studies on *P. elongatus* in New Zealand reveal the need for rocky substrate as a suitable habitat for shelter and feeding (Jones 1976). Furthermore, studies of *P. elongatus* in its native range (e.g., Jones 1977; Jones and Greenwood 1982; Pellegrino 1984) focused on the factors that affect its abundance and distribution, such as intertidal zonation, desiccation and distribution limitations. However, unlike *P. armatus*, limited ecological research has been conducted on *P. elongatus* in its introduced range of Tasmania (e.g., King 1997).

Petrolisthes elongatus was first introduced into south Tasmania from New Zealand in the late 19th century in ships' dry ballast during the transport of timber and fruit and as a hitchhiker during the transfer of live Bluff oysters, *Ostrea chilensis* (Philippi, 1845) (Lodder 1902; McLay 1988; King 1997). *Petrolisthes elongatus* has since expanded up the eastern and onto the northern coasts of Tasmania (Aquenal 2001); and mainland Australia (unconfirmed sighting) (Species Bank 2007).

Despite its high abundance in parts of Tasmania, the lack of research on *P. elongatus* makes it difficult to determine the negative impacts on native biodiversity similar to findings identified for *P. armatus* (see above; Hollebone and Hay 2007). *Petrolisthes elongatus* is included as a non-target species within Tasmanian introduced species reports (see Aquenal 2001, 2002; Whitehead 2008), however, there have been no management actions taken to control the abundance and spread of this species.

Biotic factors that may affect the distribution and density of *P. elongatus* include possible competitive and predator-prey interactions with

the dominant native grapsid crabs. Research conducted on the native *Petrolisthes cincipes* (Randall, 1840) and *Petrolisthes eriomerus* Stimpson, 1871 on the west coast of the United States indicates that competition and predation affect the distribution of these species along the intertidal gradient (Jensen and Armstrong 1991). As well, abiotic factors such as availability of suitable habitat and exposure to wave energy could also affect the distribution of *P. elongatus* around Tasmania (Jensen and Armstrong 1991; Stillman 2002; Empananza 2007). Thus the goals of this study were to assess the distribution and density of *P. elongatus* populations along Tasmania's coastline, and to evaluate the possible effects of Grapsid crab presence, substrate type, and exposure to wave energy.

Materials and methods

Distribution and Density

An initial visual survey of sites at various locations around Tasmania, (west [Strahan to Marawah], north [Smithton to Little Musselroe Bay], east [Musselroe Bay to Triabunna] and south [Port Arthur to Recherche Bay]) was conducted to qualitatively evaluate the distribution of *P. elongatus*, and the native grapsid crabs *Paragrapsus quadridentatus* (Milne-Edwards, 1837) and *Paragrapsus laevis* (Dana, 1851) (Figure 1, Appendix 1). A total of 57 sites were visited during low tide between December 2010 and January 2011 (austral summer) where a search for the target species presence was conducted from the low tide to the high tide mark. A 30 minute timed search targeting the preferable habitat of these crabs (rocky substrate) was used with presence/absence of the target species being noted (Jones 1976).

Five sites on the north coast, two sites on the east coast, and five sites on the south coast were selected for more detailed sampling. A stratified sampling regime based on tidal height was implemented at each site. Three transect lines (10 m apart along the shoreline) were laid vertically from the low tide mark and extending to the upper limits of the *P. elongatus* population. Transects were placed randomly within the intertidal zone where rocky substrate was present. Each transect line was sampled at three points using a laser level to identify tidal heights for the placement of quadrats: Q1 at the lowest tidal point (0 m above sea level); Q3 at

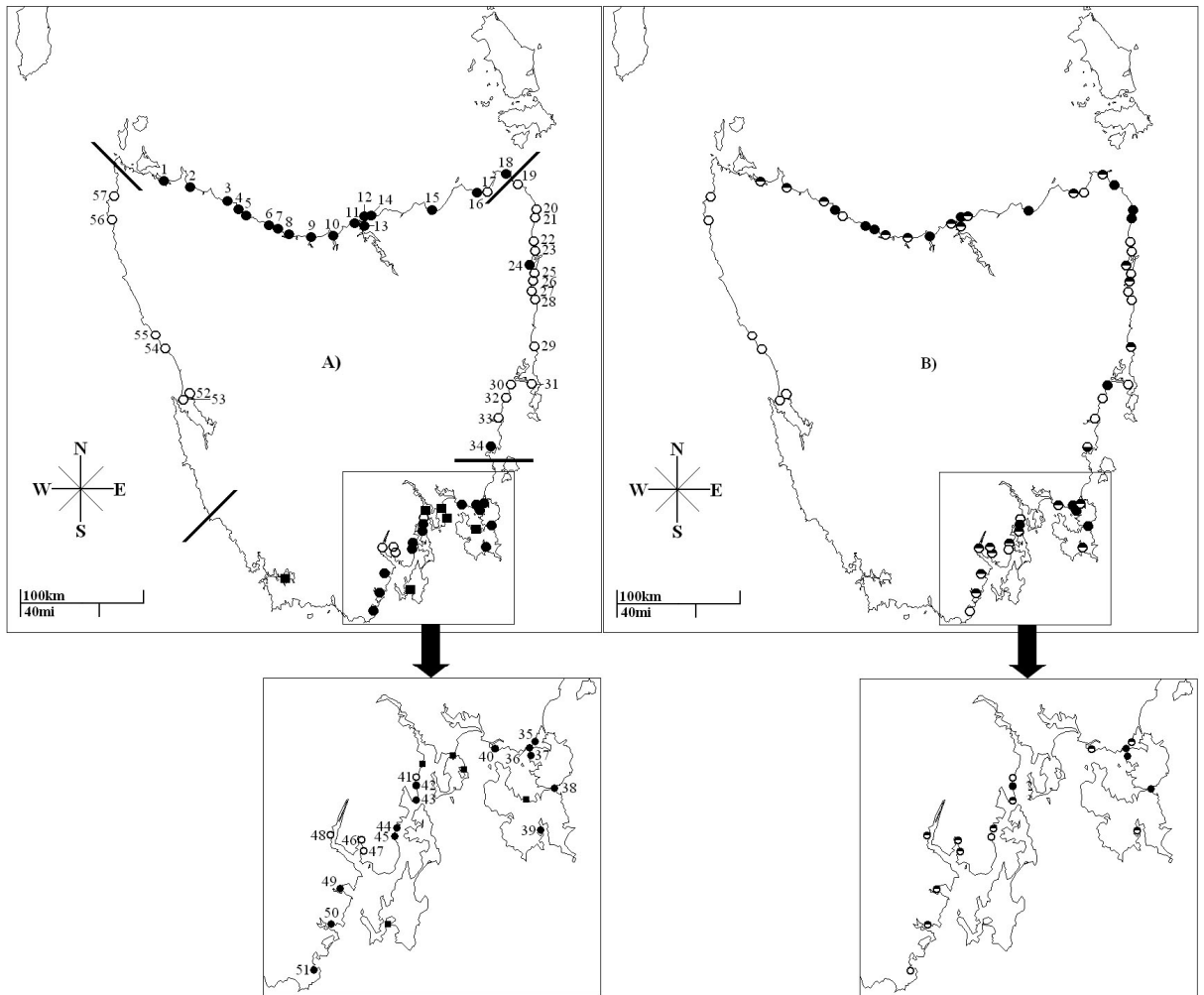


Figure 1. **A)** Tasmanian distribution of *Petrolisthes elongatus* (introduced species). Filled shapes represent presence; open circles represent absence; squares represent sites found through literature with *P. elongatus* presence. Black bars represent the separation of north, south, east and west. **B)** Tasmanian distribution of *Paragrapsus quadridentatus* and *Paragrapsus laevis* (native species). Filled circles represent the presence of both *Paragrapsus* species; top half-filled circles represent the presence of *P. quadridentatus* only; bottom half-filled circles represent the presence of *P. laevis* only; open circles represent absence of *Paragrapsus* species. See Appendix 1 for additional information.

the upper limit of *P. elongatus* population; and Q2 half of the elevation difference between 0 m above sea level and the height measured at the upper limit of the population. Each quadrat was composed of a bottomless bucket (similar to a box core) of 300 mm diameter (providing a quadrat area of 0.071 m²). The use of high-walled quadrats helped to reduce the likelihood of crabs escaping the quadrat area (Empananza 2007). At Kettering (south coast), equipment failure (laser sensor malfunction) resulted in the inability to use tidal heights. Instead, a length

measurement was taken along the intertidal from low tide (Q1) to the point of highest distribution (Q3) and Q2 was placed at the middle point.

All *P. elongatus* individuals within each quadrat were collected, placed in quadrat specific marked zip lock bags, and then stored on ice until euthanised and preserved in 70% ethanol. The density of the two native grapsid crabs (*Paragrapsus quadridentatus* and *Paragrapsus laevis*) was recorded *in situ*. Density was expressed as the total number of individuals per square metre.

Biotic Factors

A chi-square test of independence was carried out to identify a relationship between the presence of *P. elongatus* and the presence of two native grapsid crabs at all 57 sites visited.

A Kruskal-Wallis non-parametric test was applied (as a result of the data violating the assumption of normal distribution) to identify significant differences between the *P. elongatus* and grapsid crab species densities. In addition, a Spearman's correlation coefficient was used to test for a correlation between species densities across sites and within sites at a quadrat scale in order to evaluate the hypothesis that *P. elongatus* and native grapsids compete for space and that native grapsids influence *P. elongatus* distribution due to predatory behaviour. Data was scarce for *Paragrapsus laevis* therefore; the data for both native grapsid species were pooled for this analysis.

Abiotic Factors

Physical characteristics (abiotic information) were evaluated at each of the 57 sites. Substrate type was classified using the Wentworth Scale (1922) summarised as: mud (1/256 - 1/16 mm), very fine sand (1/16mm - 1/8mm), fine sand (1/8 - 1/4 mm), medium sand (1/4mm - 1/2mm), coarse sand (1/2 - 1 mm), very coarse sand (1mm - 2mm), granules (2mm - 4mm), fine gravel (4mm - 8mm), medium gravel (8mm - 16mm), coarse gravel (16mm - 32mm), very coarse gravel (32mm - 64mm), cobble (64 - 256 mm), and boulder (256 - 2048 mm). A Spearman's rank correlation coefficient was used to identify any relationships between the presence of *P. elongatus* and the type of substrate at sites surveyed around Tasmania.

Also, wave energy (low, moderate, high) were characterised based on a Tasmanian environmental report providing a map of wave exposure (Tasmanian Planning Commission 2009). To determine whether or not wave energy influences the distribution and presence of *P. elongatus*, a chi-square test of independence was used.

Results

Distribution and Density Patterns

Petrolisthes elongatus has successfully invaded a large proportion of the Tasmanian coastline, although it is more prevalent in the north and

south shores (Figure 1A). At the time of the study, *P. elongatus* was present in 32 out of 57 sites sampled along the Tasmanian coastline (Figure 1A), and was also found through reviewed literature in Bathurst Harbour (Hirst et al. 2007), South Bruny Island (unconfirmed sightings), Tarooma, Cremorne, Norfolk Bay and Lauderdale (King 1997), resulting in a total of 39 sites with *P. elongatus*. *Paragrapsus quadridentatus* was present in 37 out of 57 sites, while *Paragrapsus laevis* was present in 15 out of 57 sites surveyed (Figure 1B).

Higher densities of *P. elongatus* are more prevalent within the south coast of Tasmania (Figure 2). Four out of five of the southern sites where research was conducted returned >150 individuals/m², in contrast to <50 individuals/m² per site seen in all sites within the other two coastlines (north and east), showing the latitudinal difference of population numbers.

Biotic Factors

The presence of *P. elongatus* was found to be significantly associated with the presence of native grapsid crabs ($\chi^2_{[2]} = 23.786$; $P < 0.001$) (Figure 3). Almost 94% of sites visited around Tasmania with *P. elongatus* presence (n=32) also had grapsid crab populations (n=30).

The density of *P. elongatus* was significantly higher than that of the native grapsids ($H_{[1]} = 7.593$; $P < 0.01$) (Figure 2). The density levels of *P. elongatus* are minimal in northern and eastern sites compared to the large densities within southern sites (Figure 2). In contrast, the density levels of native grapsid crabs from north Tasmania to south Tasmania is similar, with density levels only spiking in Wynyard and Tinderbox (Figure 2). The correlation between densities of *Petrolisthes* and *Paragrapsus* at both site and quadrat scale was, however, non-significant (Figure 4).

Abiotic Factors

A statistically significant correlation was found between the presence of *P. elongatus* and some substrate types, including coarse sand ($\rho = 0.439$, $P < 0.01$), rocky cobble ($\rho = 0.294$, $P < 0.05$) and small rocks ($\rho = 0.587$, $P < 0.01$) (Figure 5). Around 76% of all intertidal sites with *P. elongatus* presence visited contained small rocks. Simultaneously, *P. elongatus* were present at 84% and 83% of sites containing rocky cobble and coarse sand respectively. In contrast,

Figure 2. Density of *Petrolisthes elongatus* (black bars) and native grapsid crabs (grey bars) at Tasmanian sites.

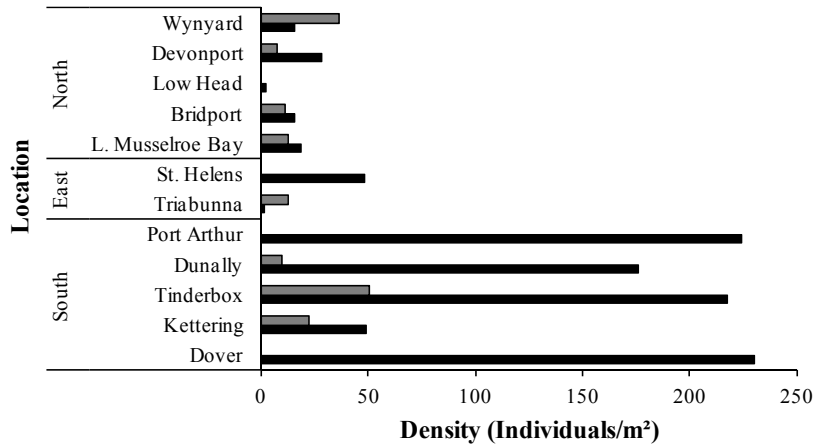
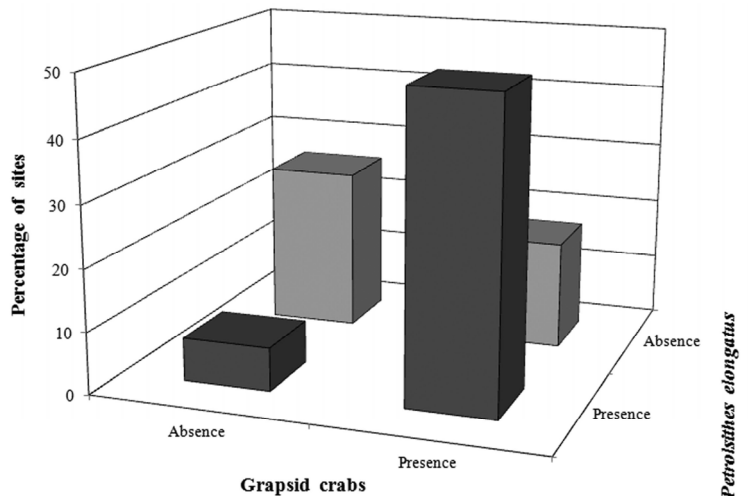


Figure 3. Percentage of Tasmanian sites (n = 57) illustrating the presence or absence of *Petrolisthes elongatus* and the native grapsid crabs *Paragrapsus quadridentatus* and *Paragrapsus laevis*.



P. elongatus absence was statistically correlated with the presence of fine sand ($\rho = -0.464$, $P < 0.05$), and large immovable rocks ($\rho = -0.447$, $P < 0.05$) (Figure 5).

Wave energy (low) significantly influenced the presence of *P. elongatus* ($\chi^2_{[2]} = 11.993$; $P < 0.05$; Figure 6), with it being absent at sites with high wave energy. *Petrolisthes elongatus* exhibited a higher preference for areas with low to moderate wave energy (contributing to 56.2% of *P. elongatus* presence around Tasmania).

Discussion

Introduced species are a threat to global biodiversity (Carlton 1996; Bax et al. 2003; Hewitt 2003; Hewitt et al. 2004). Our research explicitly focused on the distribution and density

of *P. elongatus* around Tasmania with an assessment of biotic and abiotic factors that contribute to the current range of this introduced crab. The rarity of *P. elongatus* along the east coast its absence on the west coast of Tasmania, and its putative initial inoculation site on the southern coast presents a conundrum: what mechanism(s) of dispersal inoculated this large proportion of the north coastline? The wide-spread and disjunct distribution suggests either a suite of inoculation events in disparate locations, or subsequent spread.

Two potential hitchhiker pathways have resulted in the Tasmanian invasion of *P. elongatus*: i) the live Bluff oyster, *O. chilensis*, trade from southern New Zealand to southern Tasmania (Port Davey, Bathurst Harbour, and Recherche Bay) and potentially to northern sites;

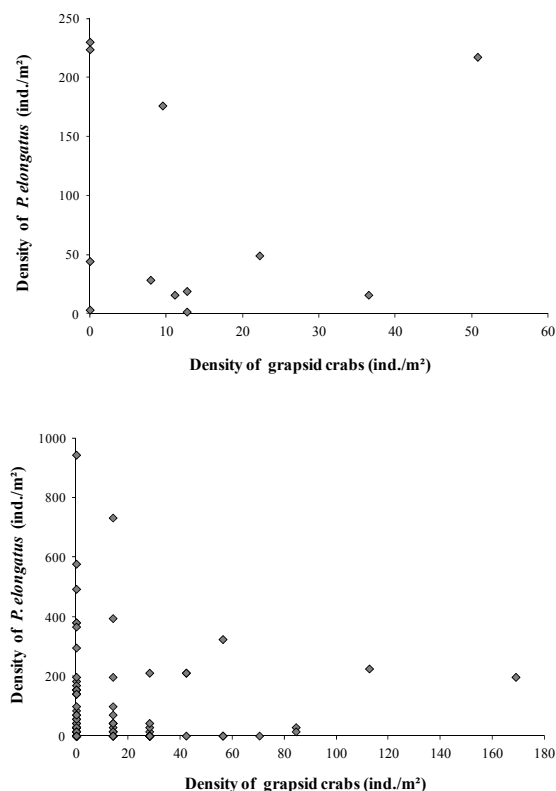


Figure 4. Density of *Petrolisthes elongatus* (y-axis) vs. density of grapsid crabs (x-axis) at site scale (upper chart) and at quadrat scale (lower chart).

and ii) dry-ballast of early trading vessels between Tasmania and New Zealand. These two vectors are the likely mechanisms for the introduction of the suite of New Zealand benthic invertebrates to Tasmania, including the seastars *Astrostele scabra* (Hutton, 1872) (Mallick and Driessen 2009) and *Patriella regularis* (Verrill, 1897) (Dartnall 1969; Waters and Roy 2004); the chiton *Chiton glaucus* Gray, 1828 (Bax et al. 2003); the mollusc *Maoricolpus roseus* (Quoy and Gaimard, 1834) (Mallick and Driessen 2009), as well as the porcelain crab *P. elongatus* (Furlani 1996; King 1997; Bax et al. 2003), with significant populations in the south.

Our results rule out the natural dispersal of mature *P. elongatus* along the Tasmanian coastlines, because of a lack of suitable habitat. Larval dispersal around Tasmania may be explained by nearshore currents (Grosholz and Ruiz 1995; Largier 2003). The currents that

surround Tasmania show a south to north movement with a resulting flow into Bass Strait along the north coast. Yet, the behaviour of *P. elongatus* larvae refutes larval dispersal of *P. elongatus* to new sites. Ulloa and Palma (1998), in their study in Valparaiso Bay (Chile), suggest that *Petrolisthes* larvae do not relocate or easily disperse to new locations. However, others argue that the retention of larvae is explained by eddies and the sheltered nature of Valparaiso Bay, which limits the release of larvae (Johnson et al. 1980; Aiken et al. 2008). The continuous presence of ovigerous females throughout the year may provide a constant supply of recruits that can maintain a population of crabs in an occupied area (Antezana et al. 1965) which may facilitate the spread of *P. elongatus*. This aspect is currently being investigated.

An alternative notion is that larval dispersal is facilitated by human mediated movement from southern to northern sites in Tasmania, through domestic shipping and recreational marine activities. Recreational boat users can act as potential vectors of introduced species (e.g., Hewitt and Campbell 2001; Johnson et al. 2001; Ashton et al. 2006). For example, secondary transfers could have occurred via the Huon pine timber and apple trade between southern and northern Tasmania (Campbell and Hewitt 1999). Similarly, multiple vectors may be operating (Floerl and Inglis 2005), or new inoculations could have occurred via direct shipping from New Zealand.

Molecular analysis is a useful tool to identify multiple vector events such as invasions of European green crab *Carcinus maenas* (Linnaeus, 1758) populations in Nova Scotia (Roman and Palumbi 2004; Roman 2006; Roman and Darling 2007; Darling et al. 2008), Tasmania, and North America (Roman and Palumbi 2004; Roman 2006; Roman and Darling 2007; Darling et al. 2008). Similarly, in New Zealand the varying haplotype groups of the introduced populations of the macroalga *Undaria pinnatifida* (Harvey) Suringar, 1873 have been used to identify source populations from northern Japan, Korea and China (Uwai et al. 2006). In addition, the local spread of the haplotype group on the north island of New Zealand is thought to be linked to recreational and commercial vessels (Uwai et al. 2006). Thus, future research on the distribution of *Petrolisthes* in Tasmania could focus on molecular analysis to determine if there have been multiple invasions events.

Figure 5. Presence of *Petrolisthes elongatus* in relation to substrate type. Black bars represent the percent of sites with presence of *Petrolisthes elongatus* in relation to presence of substrate types; grey bars represent the percent of sites with certain substrate types.

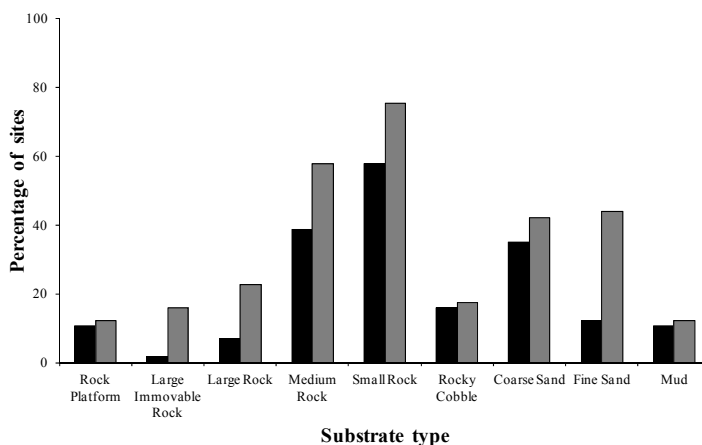
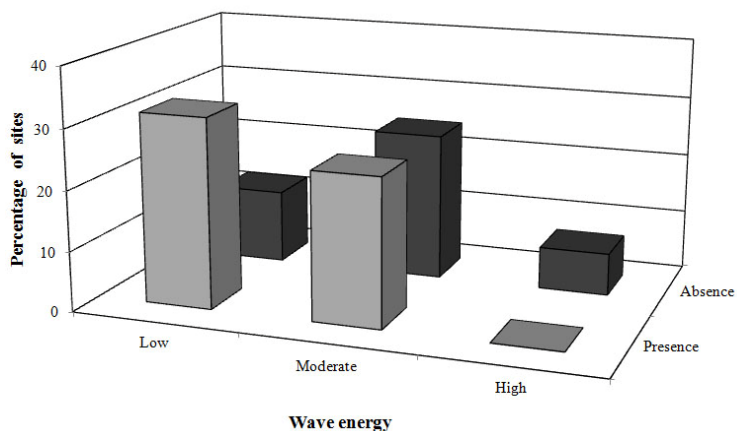


Figure 6. Percentage of sites with *Petrolisthes elongatus* presence and absence in relation to wave exposure levels.



The density of *P. elongatus* is greater within the southern coastal zones of Tasmania compared to the east and north coasts. This supports the concept of an initial incursion and establishment in southern Tasmania (Lodder 1902; McLay 1988). An introduced species' population within close range to the primary hypothesised invasion point may produce a more robust introduced population (more fecund, high larval and juvenile survival rates). Simultaneously, this may be a factor of an introduced population having adapted to recipient communities over a longer period of time, which aligns with the Abundant Centre Hypothesis (ACH; Rivadeneira et al. 2010). The ACH theory however, does not consider potential multiple invasions.

Competition and predation can influence the success (or failure) of introduced species'

establishment and spread within receiving intertidal communities (Grosholz and Ruiz 1995; Bax et al. 2003; Thresher et al. 2003). No significant competitive or predatory relationship exists between *P. elongatus* and grapsid crabs. Similarly, in North America, the distribution and density of *P. armatus* are not impacted by native mud crabs (predators) (Hollebone 2006; Hollebone and Hay 2007). The lack of impact described by Hollebone (2006) and Hollebone and Hay (2007) was attributed to the sedentary nature of *P. armatus*.

Petrolisthes elongatus is typically detected under rocky substrate within the low tide (Figure 5). Sheltering under rocks is a common strategy used by less aggressive crabs (Viviani et al. 2010) such as *Allopetrolisthes punctatus* (Guérin, 1835) (Eastern Pacific porcelain crab). This

strategy enables crabs to maintain high densities (swarms) of individuals that effectively reduce predation pressure. Competition over food resources is unlikely between the introduced and native crabs as the native grapsid crabs are omnivorous (Bishop and Kelaher 2008) and *P. elongatus* is a filter feeder (Steger and Gardner 2007).

The prevalence of *P. elongatus* was found to be highest along the north and south coasts of Tasmania and supports the concept of a relationship between the presence of *P. elongatus* and the type of substrate within sites. This may also explain why there is a lack of prevalence on the east and west coasts of Tasmania. Consistent suitable substrate types can act as suitable pathways for introduced species inoculation and further distribution (Jensen et al. 2002). Sites within the northern and southern coastlines of Tasmania have a preferred consistent-substrate type (small rocks and rocky cobble) for *P. elongatus*. Consistent substrate types between coastal zones may act as stepping stones and contribute to the successful establishment of *P. elongatus*. The east coast of Tasmania provides suitable intertidal habitats (St. Helens, Bicheno, Swansea and Triabunna) for *P. elongatus* to inhabit, however harsh open coastal regions, with minimal shelter, exist between these sites and may act as a barrier to natural dispersal.

Weather exposure plays a role in the distribution of intertidal species, and the inoculation success and population density of introduced marine species (Menge 1978; Jensen et al. 2002; Shanks et al. 2003). *Petrolisthes elongatus* is a prime example of the relationship between exposure to weather and the success of inoculating intertidal zones. *Petrolisthes elongatus* was present in intertidal zones that have a low to moderate wave energy but was absent from locations with high wave energy (Figure 6). High wave energy coastlines are known to disrupt filter feeding and to displace shelter (Jensen and Armstrong 1991). Jensen and Armstrong (1991) found that *P. cinctipes* and *P. eriomerus* have reduced feeding efficiency in high wave energy locations because of the inability of fine sediments to settle out of suspension (Osborne and Rooker 1999). Furthermore, high concentrations of sediments in the water column have been shown to increase energy consumption during filter feeding in *P. elongatus* (Steger and Gardner 2007).

Abiotic stress such as the inability or difficulty to filter feed contributes to the absence of

P. elongatus within high energy intertidal zones. High wave energy coastlines can displace important *P. elongatus* food items such as macroalgae and phytoplankton (Vadas et al. 1990; Jensen and Armstrong 1991). Thus, potentially high energy coastlines offer reduced shelter, reduced ability to filter feed, and as food resources are removed, all of which would impact upon *P. elongatus*. However, it is important to note that this inference of high energy coastlines restricting the natural dispersal and inoculation success of *P. elongatus* is not apparent in its native range in New Zealand (located in coastal zones of high energy including Wellington Harbour, Taranaki coast, Wanganui and others) (see Jones 1977). The difference seen between native and invaded coastlines is potentially explained by founder effects. It is possible the individuals transported to Tasmania were from a population sheltered from high energy coastlines (phenotypically and genetically less hardy individuals), thus the Tasmanian populations of *P. elongatus* may contain these traits. However, further research is needed to determine whether these potential genetic differences exist.

Introduced species have adapted to survive and expand in suitable new environments regardless of the resistance met from native species and abiotic factors (Torchin et al 2001, 2003; Shea and Chesson 2002; Dunstan and Johnson 2007). Since the initial invasion of *P. elongatus*, this species has extended its range to most of the habitable intertidal ecosystems around Tasmania. However, this study suggests that there are still uninvaded intertidal zones within Tasmania that consist of suitable substrate and exposure levels. The range expansion of this species in Tasmania over the last century suggests that inevitable uptake into the remaining suitable intertidal zones will occur. Therefore, this preliminary research provides a framework to guide more detailed future research on *P. elongatus* including the identification of ecological impacts. Furthermore, this study provides important ecological information for the management and prevention of further spread of this species. We have highlighted an important relationship between the presence of *P. elongatus* with suitable substrate availability and wave exposure within sites and now further research is needed to determine the vectors that have led to the disjunct populations that are evident.

Acknowledgements

This work was completed in partial fulfillment of the Masters of Applied Science degree at the University of Tasmania (LG). We would like to thank the volunteers who gave up their time to help our observations and collections in the field including staff and RHD students from the National Centre for Marine Conservation and Resource Sustainability at the University of Tasmania. Furthermore, external help in the field from friends was greatly appreciated. We thank the anonymous reviewers whose comments have made this a stronger article.

References

- Aiken CM, Castillo MI, Navarrete SA (2008) A simulation of the Chilean coastal current and associated topographic upwelling near Valparaiso, Chile. *Continental Shelf Research* 28: 2371–2381, <http://dx.doi.org/10.1016/j.csr.2008.05.006>
- Antezana T, Fagetii E, Lopez MT (1965) Observaciones bioecologicas en decapodos communes de Valparaiso. *Revista de Biología Marina de Valparaiso (Chile)* 12: 1–60
- Aquenal (2001) Exotic marine pests survey, Port of Launceston, Tasmania. For Port of Launceston, Tasmania. Report to DPIPWE, Aquenal Pty Ltd, Hobart
- Aquenal (2002) Exotic marine pests survey, Port of Hobart, Tasmania. Report to DPIPWE, Aquenal Pty Ltd, Hobart
- Ashton G, Boos K, Shucksmith R, Cook E (2006) Risk assessment of hull fouling as a vector for marine non-natives in Scotland. *Aquatic Invasions* 1(4): 214–218, <http://dx.doi.org/10.3391/ai.2006.1.4.4>
- Bax N, Williamson A, Aguero M, Gonzalez E, Geeves W (2003) Marine invasive alien species: a threat to global biodiversity. *Marine Policy* 27(4): 313–323, [http://dx.doi.org/10.1016/S0308-597X\(03\)00041-1](http://dx.doi.org/10.1016/S0308-597X(03)00041-1)
- Bishop MJ, Kelaher BP (2008) Non-additive, identity-dependent effects of detrital species mixing on soft-sediment communities. *Oikos* 117(4): 531–542, <http://dx.doi.org/10.1111/j.0030-1299.2008.16418.x>
- Campbell ML, Hewitt CL (1999) Vectors, shipping and trade. In: Hewitt CL, Campbell ML, Thresher RE, Martin RB (eds), *The introduced species of Port Phillip Bay, Victoria*. Centre for Research on Introduced Marine Pests Technical Report No. 20. CSIRO Marine Research, Hobart, pp 45–60
- Carlton JT, Geller JB (1993) Ecological roulette: the global transport of non indigenous marine organisms. *Science* 261: 78–82, <http://dx.doi.org/10.1126/science.261.5117.78>
- Carlton JT (1996) Biological invasions and cryptogenic species. *Ecology* 77(6): 1653–1655, <http://dx.doi.org/10.2307/2265767>
- Darling JA, Bagley MJ, Roman J, Tepolt CK, Geller JB (2008) Genetic patterns across multiple introductions of the globally invasive crab genus *Carcinus*. *Molecular Ecology* 17: 4992–5007, <http://dx.doi.org/10.1111/j.1365-294X.2008.03978.x>
- Dartnall AJ (1969) New Zealand sea stars in Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* 103:53–55
- Dunstan PK, Johnson CR (2007) Mechanisms of invasions: can the recipient community influence invasion rates? *Botanica Marina* 50(5–6): 361–372, <http://dx.doi.org/10.1515/BOT.2007.041>
- Empananza EJM (2007) Patterns of distribution of dominant porcelain crabs (Decapoda: Porcellanidae) under boulders in the intertidal of Northern Chile. *Journal of the Marine Biological Association of the United Kingdom* 87: 523–531, <http://dx.doi.org/10.1017/S0025315407053611>
- Furlani DM (1996) A guide to the introduced marine species in Australian waters. Centre for Research on Introduced Marine Pests, CSIRO, Division of Fisheries, Hobart, Australia. Technical report #5
- Floerl O, Inglis GJ (2005) Starting the invasion pathway: the interaction between source populations and human transport vectors. *Biological Invasions* 7: 589–606, <http://dx.doi.org/10.1007/s10530-004-0952-8>
- Gore RH (1972) *Petrolisthes armatus* (Gibbes, 1850): The development under laboratory conditions of larvae from a Pacific specimen (Decapoda, Porcellanidae). *Crustaceana* 22(1): 67–83, <http://dx.doi.org/10.1163/156854072X00688>
- Greenwood JG (1965) The larval development of *Petrolisthes elongatus* (H. Milne Edwards) and *Petrolisthes novaezelandiae* Filhol (Anomura, Porcellanidae) with notes on breeding. *Crustaceana* 8(3): 285–307, <http://dx.doi.org/10.1163/156854065X00488>
- Grosholz ED, Ruiz GM (1995) Spread and potential impact of the recently introduced European green crab *Carcinus maenas*, in central California. *Marine Biology* 122(2): 239–247
- Haig J (1960) The Porcellanidae (Crustacea Anomura) of the Eastern Pacific. *Allan Hancock Pacific Expeditions* 24:1–440
- Hayes KR, Sliwa C (2003) Identifying potential marine pests – a deductive approach applied to Australia. *Marine Pollution Bulletin* 46(1): 91–98, [http://dx.doi.org/10.1016/S0025-326X\(02\)00321-1](http://dx.doi.org/10.1016/S0025-326X(02)00321-1)
- Hewitt CL, Campbell ML (2001) The Australian distribution of the introduced sphaeromatid isopod, *Paracerceis sculpta*. *Crustaceana* 74(9): 925–936, <http://dx.doi.org/10.1163/15685400152682674>
- Hewitt CL (2003) The diversity of likely impacts of introduced marine species in Australian waters. *Records of the South Australian Museum Monograph Series* 7: 3–10
- Hewitt CL, Willing J, Bauckham A, Cassidy AM, Cox CMS, Jones L, Wotton DM (2004) New Zealand marine biosecurity: delivering outcomes in a fluid environment. *New Zealand Journal of Marine and Freshwater Research* 38(3): 429–438, <http://dx.doi.org/10.1080/00288330.2004.9517250>
- Hirst A, Barrett N, Meyer L, Reid C (2007) A detailed benthic faunal and introduced marine species survey of Port Davey, Bathurst Channel and Bathurst Harbour in SW Tasmania. NRM Final Report, Tasmanian Aquaculture and Fisheries Institute, p 6
- Hollebone AL (2006) An invasive crab in the South Atlantic Bight: friend or foe? PhD Thesis, Georgia Institute of Technology, Atlanta, Georgia, United States of America, 114 pp
- Hollebone AL, Hay ME (2007) Propagule pressure of an invasive crab overwhelms native biotic resistance. *Marine Ecology Progress Series* 342: 191–196, <http://dx.doi.org/10.3354/meps342191>
- Holway DA, Suarez AV, Case TJ (2002) Role of abiotic factors in governing susceptibility to invasion: a test with Argentine ants. *Ecology* 83(6): 1610–1619, [http://dx.doi.org/10.1890/0012-9658\(2002\)083\[1610:ROAFIG\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2002)083[1610:ROAFIG]2.0.CO;2)
- Jensen GC, Armstrong DA (1991) Intertidal zonation among congeners: factors regulating distribution of porcelain crabs *Petrolisthes* spp. (Anomura: Porcellanidae). *Marine Ecology Progress Series* 73: 47–60, <http://dx.doi.org/10.3354/meps073047>
- Jensen GC, McDonald PS, Armstrong DA (2002) East meets west: competitive interactions between green crab *Carcinus maenas*, and native and introduced shore crab *Hemigrapsus* spp. *Marine Ecology Progress Series* 225: 251–262, <http://dx.doi.org/10.3354/meps225251>
- Johnson WR, Fonseca T, Sievers H (1980) Upwelling in the Humboldt Coastal Current near Valparaiso, Chile. *Journal of Marine Research* 38(1): 1–15
- Johnson LE, Ricciardi A, Carlton JT (2001) Overland dispersal of aquatic invasive species: a risk assessment of transient recreational boating. *Ecological Applications* 11(6): 1789–1799, [http://dx.doi.org/10.1890/1051-0761\(2001\)011\[1789:OD OAIS\]2.0.CO;2](http://dx.doi.org/10.1890/1051-0761(2001)011[1789:OD OAIS]2.0.CO;2)

- Jones MB (1976) Limiting factors in the distribution of intertidal crabs (Crustacea: Decapoda) in the Avon-Heathcote Estuary, Christchurch. *New Zealand Journal of Marine and Freshwater Research* 10: 577–587, <http://dx.doi.org/10.1080/00288330.1976.9515641>
- Jones MB (1977) Breeding and seasonal population changes of *Petrolisthes elongatus* (Crustacea, Decapoda, Anomura) at Kaikoura, New Zealand. *Journal of the Royal Society of New Zealand* 7(3): 259–272, <http://dx.doi.org/10.1080/03036758.1977.10419428>
- Jones MB, Greenwood JG (1982) Water loss of a porcelain crab, *Petrolisthes elongatus* (Milne Edwards, 1837) (Decapoda, Anomura) during atmospheric exposure. *Comparative Biochemistry and Physiology* 72A(4): 631–636, [http://dx.doi.org/10.1016/0300-9629\(82\)90140-2](http://dx.doi.org/10.1016/0300-9629(82)90140-2)
- King R (1997) Systematic relationships between Tasmanian and New Zealand populations of *Petrolisthes elongatus*. BSc Honours Thesis, University of Melbourne, Melbourne, Australia, 37 pp
- Largier JL (2003) Considerations in estimating larval dispersal distances from oceanographic data. *Ecological Applications* 13(1): 71–89, [http://dx.doi.org/10.1890/1051-0761\(2003\)013\[0071:CIELDD\]2.0.CO;2](http://dx.doi.org/10.1890/1051-0761(2003)013[0071:CIELDD]2.0.CO;2)
- Lodder M (1902) The recent mollusc of Tasmania. *Australian Association for the Australian Museum* 9: 321–353
- Lodge DM (1993) Biological invasions: lessons for ecology. *Trends in Ecology and Evolution* 8(4): 133–136, [http://dx.doi.org/10.1016/0169-5347\(93\)90025-K](http://dx.doi.org/10.1016/0169-5347(93)90025-K)
- Lubchenco J, Navarrete SA, Tissot BN, Castilla JC (1993) Possible ecological responses to global climate change: nearshore benthic biota of north eastern Pacific coastal ecosystems. In: Mooney HA, Fuentes ER, Kronberg BI (eds), *Earth system responses to global change: contrasts between North and South America*. Academic, San Diego, California, USA, pp 147–166
- Mallick SA, Driessen MM (2009) Review, risk assessment and management of introduced animals in the Tasmanian wilderness world heritage area. Nature Conservation Report 10/01. Department of Primary Industries, Parks, Water and Environment, Tasmania, pages 9, 34–35
- Menge BA (1978) Predation intensity in a rocky intertidal community. Effect of an algal canopy, wave action and desiccation on predator feeding rates. *Oecologia* 34(1): 17–35, <http://dx.doi.org/10.1007/BF00346238>
- McLay CL (1988) Brachyura and crab-like Anomura of New Zealand [Crabs of New Zealand]. *Leigh Laboratory Bulletin* 22: 1–403
- Meyer-Rochow VB, Meha WP (2010) Tidal rhythm and the role of vision in shelter-seeking behaviour of the half-crab *Petrolisthes elongatus* (Crustacea; Anomura; Pocellanidae). *Journal of the Royal Society of New Zealand* 24(4): 423–427, <http://dx.doi.org/10.1080/03014223.1994.9517477>
- Moyle PB, Light T (1996) Fish invasions in California: do abiotic factors determine success? *Ecology* 77(6): 1666–1670, <http://dx.doi.org/10.2307/2265770>
- Osborne PD, Rooker GA (1999) Sand re-suspension events in a high energy infragravity swash zone. *Journal of Coastal Research* 15(1): 74–86
- Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* 1: 3–19, <http://dx.doi.org/10.1023/A:101034312781>
- Pellegrino CR (1984) The role of desiccation pressures and surface area/volume relationships on seasonal zonation and size distribution of four intertidal decapods crustacea from New Zealand: Implications for adaptations to land. *Crustaceana* 47(3): 251–268, <http://dx.doi.org/10.1163/156854084X00513>
- Ricciardi A, Whoriskey FG, Rasmussen JB (1997) The role of the zebra mussel (*Dreissena polymorpha*) in structuring macroinvertebrate communities on hard substrata. *Canadian Journal of Fish Aquatic Science* 54: 2596–2608, <http://dx.doi.org/10.1139/cjfas-54-11-2596>
- Rivadeneira MM, Hernandez P, Antonio Baeza J, Boltana S, Cifuentes M, Correa C, Cuevas A, Del Valle E, Hinojosa I, Ulrich N (2010) Testing the abundant centre hypothesis using intertidal porcelain crabs along the Chilean coast: linking abundance and life history variation. *Journal of Biogeography* 37: 486–498, <http://dx.doi.org/10.1111/j.1365-2699.2009.02224.x>
- Roman J, Palumbi SR (2004) A global invader at home: population structure of the green crab, *Carcinus maenas*, in Europe. *Molecular Ecology* 13: 2891–2898, <http://dx.doi.org/10.1111/j.1365-294X.2004.02255.x>
- Roman J (2006) Diluting the founder effect: cryptic invasions expand a marine invader's range. *Proceedings of the Royal Society B: Biological Sciences*, 273(1600): 2453–2459, <http://dx.doi.org/10.1098/rspb.2006.3597>
- Roman J, Darling JA (2007) Paradox lost: genetic diversity and the success of aquatic invasions. *Trends in Ecology and Evolution* 22: 454–464, <http://dx.doi.org/10.1016/j.tree.2007.07.002>
- Shanks AL, Grantham BA, Carr MH (2003) Propagule dispersal distance and the size and spacing of marine reserves. *Ecological Applications* 13: 159–169, [http://dx.doi.org/10.1890/1051-0761\(2003\)013\[0159:PDDATS\]2.0.CO;2](http://dx.doi.org/10.1890/1051-0761(2003)013[0159:PDDATS]2.0.CO;2)
- Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution* 17(4): 170–176, [http://dx.doi.org/10.1016/S0169-5347\(02\)02495-3](http://dx.doi.org/10.1016/S0169-5347(02)02495-3)
- Species Bank (2007) *Petrolisthes elongatus*. Online profile in Species Bank. Department of the Environment, Water, Heritage and the Arts. <http://www.deh.gov.au/cgi-bin/species-bank/sbank-treatment.pl?id=78805> (Accessed 10th May 2012)
- Steger KK, Gardner JPA (2007) Laboratory experiments on the effects of variable suspended sediment concentrations on the ecophysiology of the porcelain crab *Petrolisthes elongatus* (Milne Edwards, 1837). *Journal of Experimental Marine Biology and Ecology* 344(2): 181–192, <http://dx.doi.org/10.1016/j.jembe.2007.01.004>
- Stillman JH (2002) Causes and consequences of thermal tolerance limits in rocky intertidal porcelain crabs, Genus *Petrolisthes*. *Integrative and Comparative Biology* 42(4): 790–796, <http://dx.doi.org/10.1093/icb/42.4.790>
- Tasmanian Planning Commission (2009) State of the Environment Report: Tasmania. <http://soer.justice.tas.gov.au/2009/image/948/index.php> (Accessed 19th January 2011)
- Thresher R, Proctor C, Ruiz G, Gurney R, MacKinnon C, Walton W, Rodriguez L, Bax N (2003) Invasion dynamics of the European shore crab, *Carcinus maenas*, in Australia. *Marine Biology* 142: 867–876
- Torchin ME, Lafferty KD, Kuris AM (2001) Release from parasites as natural enemies: increased performance of a globally introduced marine crab. *Biological Invasions* 3: 333–345, <http://dx.doi.org/10.1023/A:1015855019360>
- Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ, Kuris AM (2003) Introduced species and their missing parasites. *Nature* 421: 628–630, <http://dx.doi.org/10.1038/nature01346>
- Ulloa R, Palma S (1998) Distribution larval de *Petrolisthes violaceus*, *P. laevigatus* y *Allopetrolisthes angulosus* en el plancton de la bahia de Valparaiso (Crustacea, Anomura, Porcellanidae). *Revista de Biología Marina y Oceanografía* 33(1): 125–138

- Uwai S, Nelson W, Neill K, Wang W, Aguilar-Rosas L, Min Boo S, Kitayama T, Kawai H (2006) Genetic diversity in *Undaria pinnatifida* (Laminariales, Phaeophyceae) deduced from mitochondria genes – origins and succession of introduced populations. *Phycologia* 45(6): 687–695, <http://dx.doi.org/10.2216/05-66.1>
- Vadas RL, Wright WA, Miller SL (1990) Recruitment of *Ascophyllum nodosum*: wave action as a source of mortality. *Marine Ecology Progress Series* 61: 263–272, <http://dx.doi.org/10.3354/meps061263>
- Viviani CA, Hiller A, Werding B (2010) Swarming in open space in the rocky intertidal: a new population-settlement strategy in the Eastern Pacific porcellanid crab, *Allopetrolisthes punctatus* (Decapoda, Anomura, Porcellanidae). *Crustaceana* 83(4): 435–442, <http://dx.doi.org/10.1163/001121610X489395>
- Walton WC, MacKinnon C, Rodriguez LF, Proctor C, Ruiz GA (2002) Effect of an invasive crab upon a marine fishery: green crab, *Carcinus maenas*, predation upon a venerid clam, *Katelysia scalarina*, in Tasmania (Australia). *Journal of Experimental Marine Biology and Ecology* 272: 171–189, [http://dx.doi.org/10.1016/S0022-0981\(02\)00127-2](http://dx.doi.org/10.1016/S0022-0981(02)00127-2)
- Waters JM, Roy MS (2004) Phylogeography of a high-dispersal New Zealand sea-star: does upwelling block gene-flow? *Molecular Ecology* 13(9): 2797–2806, <http://dx.doi.org/10.1111/j.1365-294X.2004.02282.x>
- Whitehead J (2008) Derwent estuary introduced marine and intertidal species: Review of distribution, issues, recent actions and management options. Derwent Estuary Program, Tasmania, Australia

Supplementary material

The following supplementary material is available for this article.

Appendix 1. Geo-referenced species record information obtained during present survey.

This material is available as part of online article from:

http://www.aquaticinvasions.net/2012/Supplements/AI_2012_Gregory_etal_Supplement.pdf