

An invasive crustacean in Tasmania, Australia: A study on the introduced porcelain crab

Petrolisthes elongatus

Liam Gregory

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The following people and institutions contributed to the publication of work undertaken as part of the thesis:

Candidate: Liam P Gregory - University of Tasmania

Author 2: Marnie L Campbell – Central Queensland University and University of Tasmania

Author 3: Carmen Primo – University of Tasmania

Author 4: Chad L Hewitt – Central Queensland University and University of Tasmania

Paper 1: Biotic and abiotic factors affecting the Tasmanian distribution and density of the introduced New Zealand porcelain crab *Petrolisthes elongatus*

Located in chapter 2

Candidate was the primary author and with authors 2 and 4 contributed to the idea, its formalisation and development. Author 2, 3 and 4 assisted with refinement and presentation. Author 3 assisted in the field.

Signed:

Prof Chad L Hewitt

Supervisor

National Centre for

Marine Conservation

and Resource Sustainability

University of Tasmania

A/Prof John Purser

Director

National Centre for

Marine Conservation

and Resource Sustainability

University of Tasmania

Date: 15/9/2014

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ABSTRACT

Petrolisthes elongatus (Family: Porcellanidae) was introduced into Tasmania over a century ago from New Zealand, most probably via the dry and semi-dry ballast vector as well as associated with the live oyster trade. Since its initial introduction, *P. elongatus* has invaded new intertidal zones across the north, east, and southern coastlines of Tasmania and attains densities of over 200 individuals per m². There is a lack of literature that documents the impacts associated with the invasion of *P. elongatus* and the interactions occurring in the occupied intertidal ecosystems. This project examined the distribution and densities of *P. elongatus* around Tasmania's coastline and examined how these metrics related to native grapsid crabs distribution and density (biotic) and environmental stress (abiotic) to determine if these factors influenced the range and densities of *P. elongatus*. Furthermore, *P. elongatus* carapace length between sites and coastlines was examined to determine if there were differences in morphology across the introduced range, while also examining ovigerous females and sex ratios between sites and coastlines. A monthly quadrat study from February 2012 to January 2013 was conducted at one site, Low Head in the north of Tasmania, to determine seasonal changes in morphology, ovigerous females, and sex ratios within the population.

The introduced range of *P. elongatus* in Tasmania extends from the northwest, down along the east coast and into the southeast, with more individuals found along the north and south coast than the east coast, no individuals were observed on the west coast. Densities were found to be higher in populations along the southern coast of Tasmania when compared to northern and eastern sites. *P. elongatus* were observed colonising small to medium sized rocks on coastlines with low to moderate wave energy.

No direct interaction was found between densities of *P. elongatus* and two native grapsid crabs *Paragrapsus quadridentatus* and *Paragrapsus laevis* at either the site or quadrat scales.

Morphology between coastlines of Tasmania revealed larger carapace lengths at northern sites ($U_{[1]} = -7.57, p < 0.001$); furthermore sex ratios were found to be equal at all sites except for Dunalley and Dover (south Tasmania). Northern sites produced a higher proportion of ovigerous females compared to southern sites ($\chi^2_{[10]} = 42.4; p < 0.001$). Potential seasonal changes were evident within the Low Head (north Tasmania) population with larger carapace lengths in the warmer months ($F_{[1,10]} = 26.394; p < 0.001$). Rapid declines in ovigerous females were observed during winter with large increases into warmer months. Sex ratios become more female dominated into spring and summer. This study begins our understanding of the demography of this introduced crustacean, revealing its ability to successfully invade and produce high densities of individuals in recipient ecosystems. The need for continued research is important to further develop our understanding on the possible impacts and future spread of *Petrolisthes elongatus* in Tasmania and mainland Australia.

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Chapter 1

Marine introductions focusing on Crustaceans

Introduction

Non-indigenous marine species (NIMS) are an increasing threat to native biodiversity worldwide (e.g., Lubchenco et al. 1993; Davis 2003; Millennium Ecosystem Assessment 2003; Molnar et al. 2008). NIMS have the ability to alter native assemblages through predation, competition and parasitism; often causing permanent and ongoing damage to the ecosystems they invade (Carlton and Geller 1993; Ricciardi et al. 1997; Parker et al. 1999; Molnar et al. 2008). The human mediated introduction of NIMS has been a factor for centuries in both the terrestrial and marine environment (Crosby 1986; Carlton 2001; Bax et al. 2003; Hulme 2009). Accidental transfers of NIMS are considered one of the major factors influencing the destruction of native ecosystem and environment.

In a terrestrial context, non-indigenous species can be introduced via air freight cargo, in ornamental pieces, or food transferred by passengers across international borders (Work et al. 2005; Hulme 2009). The ability for pest species to bore into, or be accidentally collected in food goods or natural packaging from overseas is high and can have disastrous results on native biodiversity if not contained at the point of introduction. In recognition of the various methods of transport and the impacts terrestrial pests, pathogens and weeds can have on valued production systems, national quarantine systems provide protection against these unwanted pests (Hewitt et al. 2009a).

In contrast, recognition of NIMS introductions is a relatively recent phenomenon both scientifically and from a quarantine or biosecurity management context (see Hewitt et al 2009a,

b). NIMS introductions are mediated by anthropogenic transfer through accidental mechanisms (which are referred to as vectors), such as shipping (ballast water, hull biofouling, sea chests; e.g., Gollasch 2002; Bax et al. 2003; Coutts et al. 2003; Hewitt et al. 2004a, b; Hewitt et al. 2007); the aquarium trade (Boudouresque 2002; Padilla and Williams 2004; Semmens et al. 2004; Rixon et al. 2005); and intentional introduction through aquaculture and fisheries stock enhancements (Ruiz et al. 1997; Gollasch 2002; Simberloff et al. 2005; Hewitt et al. 2006, 2007; Arthur et al. 2010). Several vectors were of significant relevance historically (e.g., dry and semi-dry ballast, ecosystem transplants associated with oyster aquaculture, wood vessel boring organisms), however have either reduced activity or been eliminated completely in the modern era (Campbell and Hewitt 1999).

Inoculation frequency and abundance, also known as propagule pressure (Williamson and Fritter 1996; Lockwood et al. 2005), are considered to be strong contributing factors to successful establishment in both the marine and terrestrial environments. Species characteristics such as high fecundity and rapid maturation rates are identified as factors which aid invasion success through creation of a continual and self-regulating supply of propagules (Hollebone and Hay 2007). These factors can help overcome founder effects and native species resistance by overwhelming native species resistance (Williamson and Fritter 1996; Lockwood et al. 2005). Once introduced, further range expansion can occur via the same vectors that operated in the initial introduction as well as differing avenues such as natural propagule dispersal in the water column or hitchhiking on recreational vessels (Lockwood et al. 2005).

Shipping is ever increasing as consumerism worldwide increases exponentially. Ten years ago, more than 80% of global trade movement was serviced by freight vessels (Bax et al. 2003). In 2013, the global trade by vessels has increased to more than 90% (IMO Maritime Knowledge Centre 2012). Furthermore, the larger size and speed (including the efficiency of new trade routes) of ships decreases the amount of time between ports and time at sea while subsequently increasing the chance of accidental transfers and successful establishment and spread of NIMS (explain succinctly) (Bax et al 2003; Minchin and Gollasch 2003). Due to an overwhelming number of vessels operating at a global scale, this vector is a main driver of marine species introductions and spread (Gollasch 2002; Bax et al. 2003; Coutts et al. 2003; Hewitt et al. 2004a, b; Hewitt and Campbell 2010).

Ballast

Ballast has been used in trading vessels for centuries, either in the form of dry, semi-dry or water to stabilise the vessel while it is underway (Carlton 1989; Griffiths et al. 2009). Dry and semi-dry ballast is more commonly associated with trade during the 1800's in which sand, cobbles and rocks were collected from the intertidal and placed in barrels and transferred to the vessel bilge (Campbell and Hewitt 1999). This dry and semi-dry ballast was typically maintained in moist environments and, upon arrival in the destination port, discharged to environments similar to the ones from which they were collected. These materials would have also collected and discharged numerous intertidal organisms either as epifaunal or infaunal benthos (King 1997; Hewitt et al. 2004a).

Dry and semi-dry ballast was largely replaced by water ballast in the late 1800s with the development of steel hulled vessels and pumps capable of loading dedicated ballast tanks with sea water (Carlton 1989; Hutchings 1992; King 1997; Campbell and Hewitt 1999). However, in Australia, the use of ballast water only became prevalent after World War II (Campbell and Hewitt 1999). Much like dry and semi-dry ballast, ballast water is pumped on board from harbour water in one port when ships are not carrying cargo and typically discharged before loading in another port. Ballast from around the globe has had the potential to transport species to new environments and creates interactions between previously separated species, sometimes resulting in deleterious outcomes (Ruiz et al. 1997; Ruiz et al. 2000; Bax et al. 2003). Ballast treatment (e.g., exposure of ballast water to heating, ozone, or filtration to kill organisms in the ballast water) and also offshore release and uptake aids in minimising the accidental transfer of NIMS (Oemcke and Leeuwen 2004; Mimura et al. 2005; Perrins et al. 2006). Offshore release and uptake of ballast water aids in minimising accidental transfers of hitchhiking species, this is due to the release of ballast in open waters where the hitchhiking species have a reduced chance of survival and spread than in the intended coastal zone where they would have previously been released (Oemcke and Leeuwen 2004; Mimura et al. 2005; Perrins et al. 2006).

Hull Fouling

Hull fouling (also known as biofouling) by encrusting species, such as bryozoans, ascidians and mussels, also allows for the translocation of species to new environments (Gollasch 2002; Bax et al. 2003; Godwin 2003; Lewis et al. 2003; Drake and Lodge 2007). Once in new environments, the difference in water temperatures, salinity or other marine factors can cause encrusting introduced species to release propagules as a mechanism to ensure survival of the population

(Apte et al. 2000). As a consequence, non-indigenous populations can settle within days and inoculate new locations (Apte et al. 2000).

Over the past couple of decades, and more recently, research into stopping or reducing the number of introduced species attaching to hulls has increased, mainly due to the banning of antifouling tributyltin (TBT) paints. TBT paints are an effective method in reducing hull fouling, but have toxic secondary effects on native marine organisms (Alzieu 1991; Dowson et al 1993; Smith 1996; Evans et al. 2000; Santos et al. 2002;), which led to its banning under the International Convention on the Control of Harmful Anti-Fouling Systems on Ships (AFS Treaty; IMO 2001) by 2008.

There are multiple methods currently used to reduce the effects of hull fouling, including the continued use of biocidal paints consisting of chemicals such as mercury and arsenic (Chambers et al. 2006). Examples of biocidal paints include soluble matrix paints, which slowly release chemicals at the surface of the paint, and contact leaching paints, which release a higher content of biocide from the surface of the paint, and as paint erodes, from deeper in the coating (Callow and Callow 2002; Yebra et al. 2004; Chambers et al. 2006). Self-polishing paints are a non-toxic alternative to biocide paints that create a relatively smooth surface on the hull which when exposed to turbulent waters (such as during transit) that ensure that hitchhiking organisms are sloughed off (Callow and Callow 2002; Yebra et al. 2004; Chambers et al. 2006; Almeida et al. 2007).

Secondary Spread

Once introduced in a new region, NIMS can also utilise the natural environment to aid in the dispersal and establishment of new populations through ocean currents and winds (Johnson and Padilla 1996; Carlton 2001; Ricciardi 2007; Hulme 2009; Wilson et al. 2009). In the case of crustaceans; propagules can spend weeks in the water column, dispersing along coastlines until they are mature enough to metamorphose and settle onto benthic habitats (Kinlan and Gaines 2003; Shanks et al. 2003; Johnston et al. 2009). Mature non-indigenous individuals can also move to new environments via migration along the intertidal. Furthermore, the search for food and shelter can lead to the discovery and inoculation of new niche environments, successful establishment and further spread (Herbold and Moyle 1986; Ruiz et al. 1997; Wilson et al. 2009). Mitigation and eradication of introduced marine and intertidal species is a difficult process due to the theory of enemy release in that an introduced species has a physiological and/or reproductive advantage in new environments as it lacks predation and parasites from its native range. This is thought to enable NIMS to thrive in new locations by achieving high densities and growth rates exceeding that of their native range (Torchin et al. 2003; Wotton et al. 2004; Gribben et al. 2013).

Impacts

As alluded to above, the introduction of NIMS into marine environments can have direct impacts upon the native flora and fauna in the ecosystems they co-inhabit. However, these environmental impacts can also indirectly impact a country's or localised community's economic, cultural and social sustainability and values (Pimentel et al. 2000; Walton et al. 2002; Nunes and van den Bergh 2004; Campbell 2008). Of further concern is that impacts are often missed or not noticed

until it becomes too difficult, logistically or economically, to control the invasion (Davidson and Hewitt 2013).

Environmental impacts

Native marine and intertidal communities are typically structured community assemblages. These assemblages have evolved to regulate species interactions and biomass within the ecosystem through primary producers and keystone predators forming the building blocks of complex food webs, this allows for the regulation of resources without depletion from an overabundance of any one species (Paine 1969; Pimm 1982; Glynn 2004; Bascompte and Melián 2005). The introduction of NIMS, whether it be “lower order” bryozoans or “higher order” predatory crustaceans, can directly or indirectly remove keystone species via predation, competition or displacement from the community (Molnar et al. 2008). As a result, these alterations can potentially cause top-down or bottom-up trophic cascades (Navarrete and Menge 1996; Sala et al. 1998; Bascompte and Melián 2005; Wallentinus and Nyberg 2007; Heithaus et al. 2008), which can have a detrimental follow-on effect to all levels of the ecosystem (Foster and Schiel 1988; Sala et al. 1998). Trussell et al. (2008) revealed the effects of an introduced predator (*Carcinus maenas*) on native rocky intertidal pools: their results show the decrease in the densities of the marine snail *Littorina littorea* that ultimately resulted in deleterious flow on effects to the developing algal species.

Intentional species introduction for aquaculture and other anthropogenic means can result in unintentional spread of hitchhikers, either free living or parasitic, and possible native ecosystem degradation (Naylor et al. 2001; Ruiz et al. 1997; Molnar et al. 2008; Savini et al. 2010). In

Europe, there are multiple species that have successfully spread to other countries and impact upon biodiversity, such as the rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792). Further examples are predatory crustaceans such as the crayfish *Procambarus clarkii* (Girard, 1852) and *Pacifastacus leniusculus* (Dana, 1852) that have been noted to cause multiple negative impacts upon native biodiversity and ecosystems (Savini et al. 2010)

Another example of NIMS affecting multiple areas of a native ecosystem is in the Chesapeake Bay, the largest estuary in the United States, where multiple introductions have been cited and studied (e.g., Ruiz et al. 1997; Ruiz et al. 2000). Two of these NIMS are the pathogens *Haplosporidium nelsoni* Haskin, Stauer and Mackin, 1966 and *Perkinsus marinus* (Mackin, Owen and Collier) Levine, 1978 that are thought to have been accidentally introduced as hitchhikers in other NIMS (e.g., Andrews 1984; Lauckner 1983; Sindermann 1990; Wonham and Carlton 2005; Occhipinti-Ambrogi 2007). These pathogens have been noted to negatively impact native oyster communities (*Crassostrea virginica* (Gmelin, 1971)), causing a reduction of more than 90% in the native oyster population density since the pathogens were introduced (e.g., Andrews 1979; Lauckner 1983; Sindermann 1990).

Although the primary impact of these introduced pathogens is the depletion of the oysters themselves, the effects of these introductions impact both benthic and planktonic species that utilise these oysters as a prey or shelter (Ruiz et al. 1999).

Economic and socio-cultural impacts

The global human population is heavily reliant on coastal waters for a multitude of social, cultural and economic reasons (Vitousek et al. 1997; Hugo et al. 2013). For example more than 82% of Australia's population live within 50km of coastlines (Hugo et al. 2013). . NIMS have the potential to negatively impact any one of these values, possibly leading to effect to other values. The ecosystems impacts caused by NIMS can affect economic values, including the reduction of tourism due to the destruction of the environmental aesthetics (Campbell 2008; Kuhar et al 2009; Campbell and Hewitt 2013); furthermore, NIMS can have deleterious effects on the aquaculture industry via hitchhikers, parasites or pathogens associated with intentional introductions (Perez et al. 2003; Thresher and Kuris 2004; Savini et al 2010).

Introduced dinoflagellates can directly the affect anthropogenic values of an area, including human health. Harmful algal blooms (HABs) can negatively impact pelagic and benthic native ecosystems while also, in certain circumstances, causing harm to humans via direct contact in the water or consuming through local seafood that has been in contact with the toxic bloom (Hallegraeff and Steffenson 1988; Hallegraeff 1998; Codd et al. 1999; Hallegraeff 2003). Social values including recreation (family activities, boating, swimming and tourism and more) and aesthetic and cultural values including beliefs and spiritual connection could be negatively impacted as a result of decreasing aesthetic values of an ecosystem, the perceived removal of native flora and fauna, or a change in the environment that individuals and communities observe (Campbell 2008; Kuhar et al 2009; Campbell and Hewitt 2013).

Management

Pre-border, border and post-border management efforts have been implemented in different countries around the world (e.g. Australia and New Zealand) with the aim of reducing the amount of NIMS successfully entering, establishing and spreading into recipient environments (Bax et al. 2003; Wotton and Hewitt 2004; Hewitt and Campbell 2007). As previously mentioned, management aimed at pre-border and border control of marine species is conducted mainly via new anti-fouling technology and ballast water treatment to minimise the propagule pressure of NIMS while also increasing the probability of detection and surveillance of NIMS at the point of introduction (i.e. ports) (Hewitt et al. 2004b). However, new introductions are still likely (Ricciardi and Rasmussen 1998; Hewitt et al., 2004b; Faasse and Ligthart 2007).

Introduced NIMS spread to new environments and can successfully establish large populations most often before they are detected and reported (Ruiz et al. 1997; Hewitt et al. 2004b; Minchin et al. 2006; Floerl et al. 2009). In such circumstances, post-border management (to detect, eradicate or mitigate NIMS impacts) is difficult. The response time to react to a detected incursion (if action is taken) is often long, and during that time the introduced population can successfully establish in the new environments. There have been occasions when introductions occur, are detected and eradicated within 6-7 months, such as the black striped mussel invasion in Darwin Harbour (Willan et al. 2000), but these successful detection and eradications are rare events.

Successful eradication of an introduced species requires early response and fast action (Willan et al. 2000; Wotton et al. 2004). A further example of this is the introduction of the macroalgae

Undaria pinnatifida to the Chatham Islands, New Zealand, and its subsequent eradication (Wotton et al. 2004). In this instance, *U. pinnatifida* was detected fairly early, and managerial processes to mitigate the invasion were implemented, ultimately resulting in the successful outcome of eradicating this NIMS (Wotton et al. 2004). In this instance, areas containing the invasive macroalgae were exposed to elevated water temperature, with no signs of new populations of *Undaria* appearing three years after the eradication (Wotton et al. 2004). Continued surveying and monitoring of ecosystems that have are susceptible to NIMS introductions, especially those areas in a mitigation/eradication process, is critical to enable rapid response if re-introduction or spread has occurred to minimise the potential impact of NIMS and monitor the recovery of native biodiversity and ecosystems (Bax et al. 2003; Hewitt et al. 2004b; Campbell et al. 2007).

Crab Invasions

Crabs are among the most successful groups of introduced marine organisms globally (Ruiz et al. 1997) associated with both intentional and accidental transfer mechanisms. For example, the European green crab *Carcinus maenas* (Linnaeus, 1758) has successfully inoculated and established populations in North America, South America, Africa, Australia, New Zealand and north-east Asia (e.g., Le Roux et al. 1990; Grosholz and Ruiz 1996; Thresher et al. 2003). The voraciousness of this carnivorous species has also contributed to its success, allowing it to overrun native predators and dominate native community assemblages (Grosholz and Ruiz 1995).

Other introduced crustaceans have also successfully invaded intertidal zones. The Chinese mitten crab, *Eriocheir sinensis*, has established populations in European waters (UK, Germany and France) and also in the United States where it was intentionally introduced as an aquaculture import, however their spread along the east coast has since caused deleterious effects on native biodiversity (Cohen and Carlton 1997; Bentley 2011). The omnivorous Asian shore crab *Hemigrapsus sanguineus* (De Haan, 1835) has invaded North America where it impacts blue mussel communities through predation (Lohrer and Whitlatch 2002). Examples of herbivorous crustacean invasions also exist: the porcelain crabs (e.g. *Petrolisthes armatus* and *Petrolisthes elongatus*) (Infraorder Anomura) are an aspect dominant species, achieving high population densities in benthic habitats with limited apparent impacts, and have been introduced to North America, South America, Bermuda, West Indies, the Caribbean, West Africa and Australia (Gore 1972; Hollebone and Hay 2007; Gribben et al. 2013). The use of aspect dominance is thought to be important in an invaded recipient ecosystem, as high densities achieved by introduced species can overcome native resistance (Hollebone and Hay 2007).

The success, or failure, of a species introduction is a result of multiple factors including, but not limited to, the native biotic resistance of the community the species is introduced to (i.e. competition, predation and parasitic infection), the traits of the invader which allows it to be successful, and propagule pressure (e.g. Johnston et al. 2009). Global crustacean invasions of species previously mentioned are a consequence of anthropogenic accidental transfers, however, not all introductions are successful and may be attributed to native biotic resistance (Bax et al. 2003; Hunt and Yamada 2003; deRivera et al. 2005). A study conducted in Oregon, United States revealed successful predation on the highly invasive *Carcinus maenas* by a native

predator, the native red rock crab *Cancer productus* which resulted in the limited distribution of *Carcinus maenas* along the coastal zone (Hunt and Yamada 2003). Additionally, deRivera et al (2005) also identified predation by a native crustacean (*Callinectes sapidus*) as a key factor in removing, or limiting the dispersal of an introduced species (*Carcinus maenas*). Parasites are recognised as being a factor in reducing the spread of introduced species; in some cases certain species of parasites may help control the spread of NIMS via castration which may reduce propagule pressure (Thresher et al. 2000; Mouritsen and Poulin 2002).

The traits of introduced species which can include high fecundity and densities (propagule pressure) and rapid maturation can aid in its successful establishment and regulation of populations in new environments (Johnston et al. 2009). The release of individuals, both mature and larvae, either as a single or multiple event (for example continued shipping into a port), can help in the establishment of an introduced species. Propagule pressure has been discussed as an important factor in identifying the mechanisms behind invasions, for example the porcelain crab *Petrolisthes armatus* was introduced into the United States and has successfully established populations over three states as a result of its overwhelming propagule pressure (Hollebone and Hay 2007). The rapid maturation of introduced species also aids in propagule pressure, with an ability to reproduce at an early life stage the contribution of larvae into the surrounding environment enhances the success rate of recently introduced populations (Johnston et al. 2009). However, it is important to note that not all introduced species successfully establish in recipient ecosystems.

Petrolisthes introductions

Two *Petrolisthes* species from separate native ranges (commonly known as porcelain crabs) have successfully invaded different 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). *Petrolisthes elongatus* (Milne-Edwards, 1837) is native to New Zealand and has been introduced into Tasmania (Australia).

Previous studies of invading *P. armatus* have commonly focused on distribution and abundance, effects on native biodiversity and possible negative impacts on bivalve fisheries (i.e. oysters) along the south-eastern seaboard of North America (Walton et al. 2002; Hollebone and Hay 2007). Due to an explosion of *P. armatus* abundance in oyster reef communities, it has been suggested that *P. armatus* exclude juvenile and mature native mud crabs (native predator) from their native ecosystem (Hollebone and Hay 2007). Furthermore, as a filter feeder, large numbers of *P. armatus* densely compacted (4,000 to 11,000 individuals m⁻²) can negatively affect nearby filter feeding communities including oyster populations (Hollebone and Hay 2007).

Previous studies on *P. elongatus* focused on the ecological factors that affect *P. elongatus* in its native range, such as intertidal zonation, desiccation and distribution limitations (Jones 1977; Jones and Greenwood 1982; Pellegrino 1984). However, unlike *P. armatus*, limited ecological research has been conducted on *P. elongatus* in its introduced range. The intertidal porcelain

crab, *P. elongatus*, was first introduced into Tasmania, Australia, from New Zealand approximately 100 years ago (King, 1997).

Petrolisthes elongatus was thought to have first been introduced into southern Tasmania in the late 19th century associated with dry ballast in relation to transport of Huon Pine timber, fruit (primarily apples) and the transfer of live Bluff oysters, *Tiostrea chilensis* (Philippi, 1845) from the South Island of New Zealand (Lodder 1902; McLay 1988; King 1997). It has since expanded its range up the eastern and the northern coasts of Tasmania (Aguenal 2002), with unconfirmed sightings on mainland Australia (Victoria) (<http://www.deh.gov.au/cgi-bin/species-bank/sbank-treatment.pl?id=78805>). This expansion is likely to have occurred through varying avenues such as human mediated movement including hitchhiking propagules or mature individuals within recreational fishing vessels (such as bycatch), biotic factors including propagule pressure and release, accidental catch and release by bird or fish species (Green and Figuerola, 2005; Darbyson et al. 2009), and abiotic factors such as currents. These can subsequently allow for the inoculation of new intertidal zones (Lockwood et al. 2005).

Petrolisthes elongatus is a small crustacean, growing to a maximum carapace length of 19mm, with a rounded carapace and a broadly round triangulate front. Significant features of the crab are its large flattened chelipeds and turquoise purple colour. This filter feeder commonly inhabits the lower intertidal zone under rocky substrate (Haig, 1960; Jones 1976; Jones and Greenwood 1982; Pellegrino 1984). Distribution and tolerance studies on *P. elongatus* in New Zealand show that this species prefers rocky substrate as suitable habitat for shelter and feeding (Jones 1976). Despite its observed ecological dominance in Tasmania, the lack of observed aggressiveness in

P. elongatus makes it difficult to determine the negative impacts on native biodiversity as those identified for *P. armatus* (see above; Hollebone and Hay 2007).

The invasion success and population dominance of *P. elongatus* around Tasmanian intertidal zones is significant based on personal observations and suggests that limited native resistance exists to this introduced crustacean, although few studies have been conducted to date. Currently, *Petrolisthes elongatus* is listed as a non-target invasive species within Tasmania (see Aquenal 2002; Whitehead 2008). Therefore, no direct managerial efforts have occurred for this introduced crab at State or Commonwealth levels even though the species is noted as a concern, has large populations, and may directly or indirectly impact native intertidal communities.

Conclusions and thesis aims

It is undisputed that introduced species alter ecosystems and in many instances impact environmental (Ruiz et al. 1997; Molnar et al. 2008), economic (Lovell et al. 2006; Pimentel et al. 2005), social (Hallegraeff 2003; Campbell and Hewitt 2013) and cultural values (Campbell 2008). Yet, in some instances, the impacts on these values are less apparent. The introduction of *P. elongatus* to Tasmania is a historical invasion that has resulted in the species becoming aspect dominant on a local scale, yet it displays little obvious detrimental behaviours to other native species and hence the question of true impact remains uncertain. The apparent lack of impact may be due to the species being a historical introduction, with no management associated with its introduction, or it could be a simple case of an understudied, cryptic invasion of a species that is

not commercially important or associated with a commercially important species in its introduced range.

Therefore, to investigate the direct or indirect effects of *Petrolisthes elongatus* on native Tasmanian intertidal communities this thesis will examine the biotic and abiotic factors that influence the distribution and densities of *P. elongatus* around Tasmania. Furthermore, morphology and demography differences between sites and coastlines were examined inter and intra annually to determine any potential seasonal differences. The following 10 hypotheses will be tested in the subsequent depths:

H₁: Biotic factors correlate with the current distribution and density of *P. elongatus*

H₂: Abiotic factors influence the current distribution and density of *P. elongatus*

H₃: There is no difference in carapace length of *P. elongatus* between Tasmanian sample sites and coastlines

H₄: *P. elongatus* shows no sexual dimorphism in relation to carapace size within Tasmanian sites

H₅: There is a 1:1 sex ratio of *P. elongatus* within all Tasmanian sample sites

H₆: There is no difference in the proportion of *P. elongatus* ovigerous females between Tasmanian sample sites;

H₇: There is no difference of carapace length (CL) between ovigerous females between sites; and non-ovigerous female *P. elongatus*

H₈: There is no intra-annual trend relating to *P. elongatus* densities of ovigerous females at Taylor's beach, Low Head, Tasmania

H₉: There is no intra-annual trend between *P. elongatus* sex ratios at Taylor's beach, Low Head, Tasmania

H₁₀: There is no intra-annual trend between *P. elongatus* CL at Taylor's beach, Low Head, Tasmania

Following this framework, this research aims to elucidate the historical and current invasion impacts of *Petrolisthes elongatus* on Tasmanian ecosystems. Chapter 2 examines hypotheses 1 and 2 by determining the biotic (presence of the native crabs *Paragrapsus quadridentatus* and *Paragrapsus laevis*) and abiotic (sediment grain size and exposure to wave energy) factors that have influenced the distribution and density of *P. elongatus*. These factors were selected because studies on *Petrolisthes* species in both the native and introduced ranges identified substrate and intertidal stressors as influencing factors on *Petrolisthes* distribution and intertidal zonation (Stillman and Somero 2000; Stillman 2002; Hollebone and Hay 2007; Miranda and Mantelatto 2009).

Chapter 3 examines hypotheses 3 through to 10 by examining carapace lengths and sex ratios of individuals and ovigerous females between Tasmania sites (north, east and south coast sites) to determine any biogeographical differences in morphology or population structure. Furthermore, a survey was conducted at Low Head (north Tasmania) from February 2012 to January 2013 to identify any annual seasonal changes in ovigerous females, morphology or sex ratios.

The final chapter (Chapter 4) synthesises the results from Chapters 2 and 3 to evaluate the overarching aim of the thesis and provide a conclusion. The outcome of this chapter provides

managers with valuable information about the historical and current invasions but also future directions that are relevant to *P. elongatus*.

Chapter 2

Preface

Chapter 2 was prepared as a stand-alone, peer reviewed publication, which was subsequently published in the international journal “Aquatic Invasions” (Gregory et al. 2012). I am the senior author on this paper and took primary responsibility for the development of research questions, research design and methods, analysis and writing this co-authored paper/chapter. The details of this publication and co-authorship are as follows:

- **Gregory LP**, Campbell ML, Primo C, Hewitt CL (2012). Biotic and abiotic factors affecting the Tasmanian distribution and density of the introduced New Zealand porcelain crab *Petrolisthes elongatus*. *Aquatic Invasions* 7 (4): 491-501

Development of this chapter stemmed from my initial thesis discussions with my primary supervisor Prof Chad Hewitt and the literature review that I had undertaken from my confirmation document. My primary supervisor, Prof Hewitt contributed to this chapter through the development of ideas, field methods and research questions. My co-supervisor, Prof M. Campbell helped to implement a structure and removed “interesting” questions that were beyond the scope of the topic, but had captured my attention (these “interesting” components became part of chapter 3). My other co-supervisor Dr C. Primo, provided field expertise and logistical support. All supervisors contributed to editing and comments on the manuscript. I collected all the data, carried out data analyses, and drafted the text for the paper. A version of this chapter is reprinted with permission from *REABIC*.

Chapter 2

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

Introduction

Non-indigenous species (NIS) are an increasing threat to biodiversity worldwide (e.g., Lubchenco et al. 1993) and 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 overpopulation 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 filter feeder commonly inhabits the lower intertidal zone 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 (Aguenau 2002); and mainland Australia (unconfirmed sighting) (<http://www.deh.gov.au/cgi-bin/species-bank/sbank-treatment.pl?id=78805>). 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 Aguénau 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 cinctipes* (Randall, 1840) and *Petrolisthes eriomerus* Stimpson, 1871 on the west coast of the United States indicated that competition and predation affected 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; Emparanza 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 native 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 Marrawah], 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). A total of 57 sites were visited during low tide between December 2010 and February 2011 (austral summer) where a search for the target species was conducted from the low tide to the high tide mark. A 30 minute timed search targeting the preferable habitat of these crabs (underneath 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 observed *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 the upper limit of observed *P. elongatus* population; and Q2 at half of the elevation difference between 0 m above sea level and the height measured at the upper limit of observed *P. elongatus*. 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 reduced the likelihood

of crabs escaping the quadrat area (Emparanza 2007). At Kettering (south coast), 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 (Permit #11145), 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* and the animals were released. Density was expressed as the total number of individuals per square metre. A Chi square test of independence was used to determine differences in *P. elongatus* densities between sites.

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 *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. Sediment was visually assessed at all sites and photographs were also taken for later assessment. 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 by others 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).

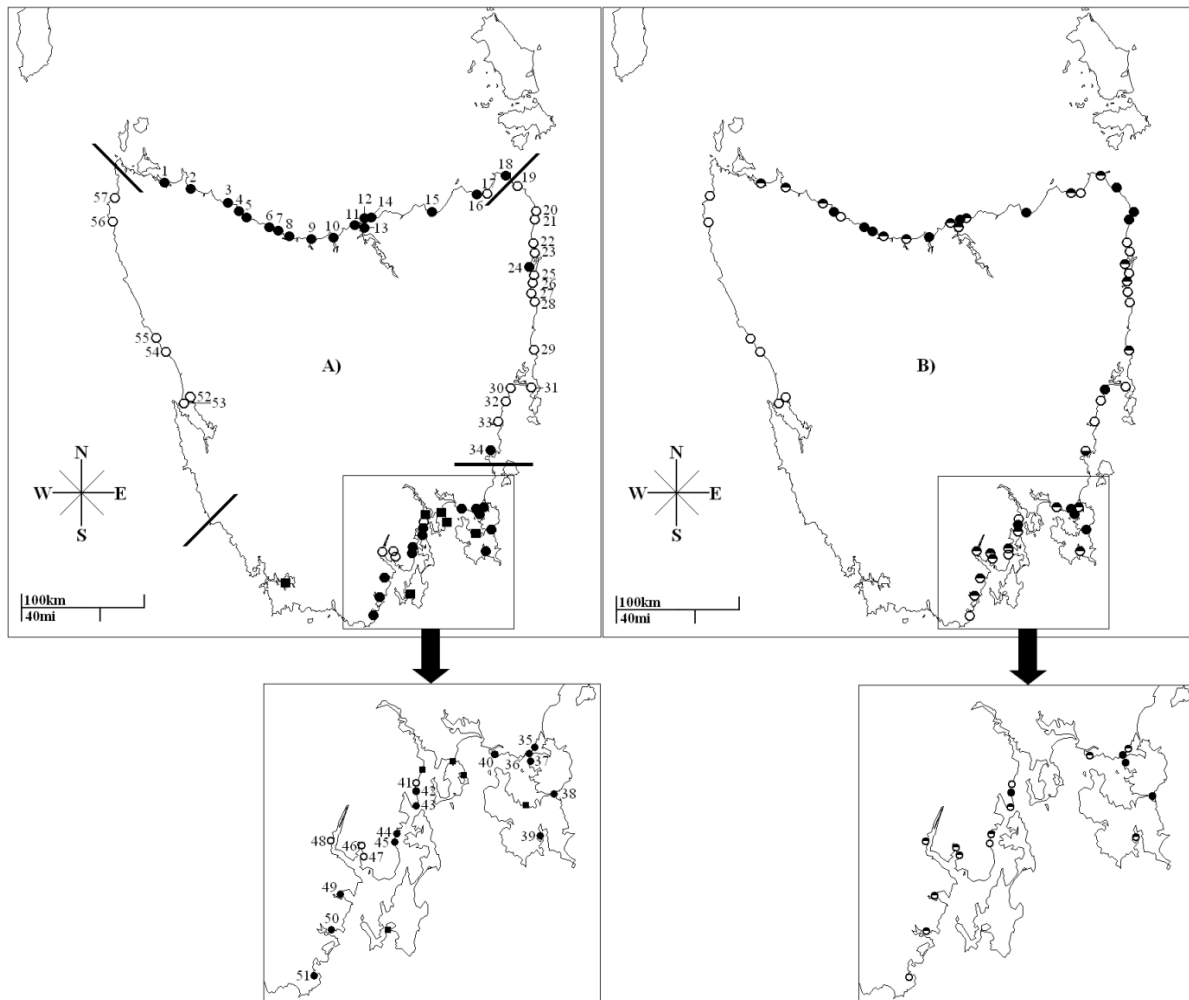


Figure 1: **A)** Tasmanian distribution of *Petrolisthes elongatus*. Filled circles represent presence; open circles represent absence; squares represent previous reports of *P. elongatus* presence. Black bars represent the separation of north, south, east and west. **B)** Tasmanian distribution of *Paragrapsus 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 Annex 1 for additional information.

Densities of *Petrolisthes elongatus* were significantly different between sites ($\chi^2_{[10]} = 18.307$; $P < 0.01$). Higher densities of *P. elongatus* are more prevalent along 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).

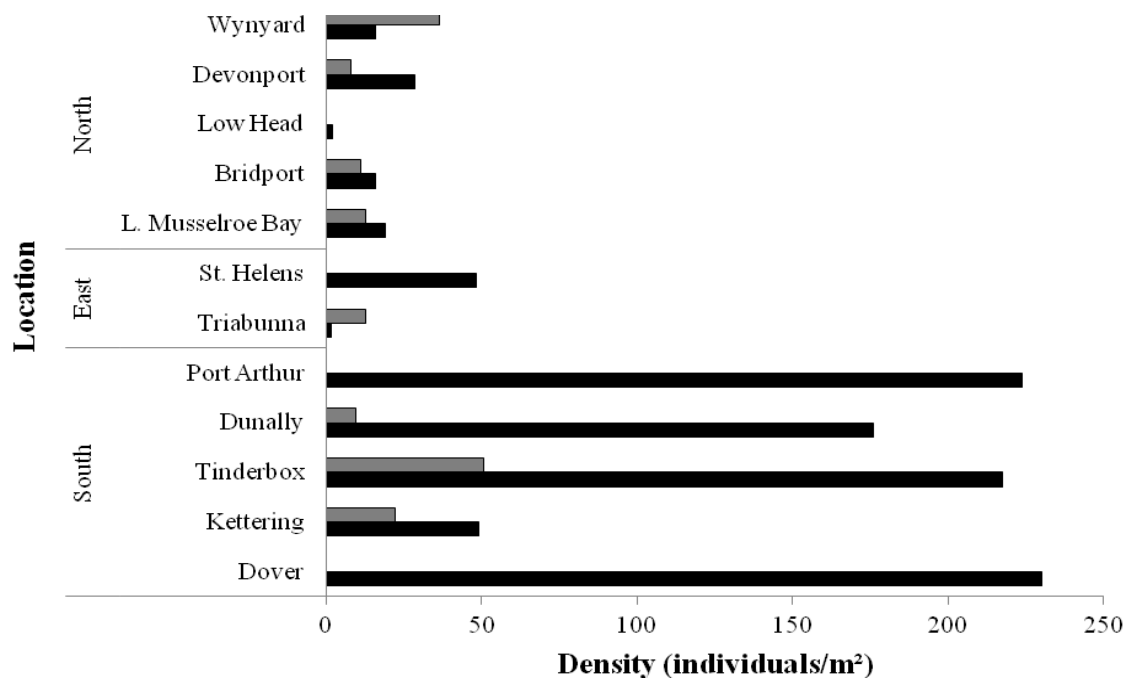


Figure 2: Density of *Petrolisthes elongatus* (black bars) and native grapsid crabs (grey bars) at Tasmanian sites. Data from the west coast omitted due to absence of all target crab species.

Biotic Factors

The presence of *P. elongatus* was found to be significantly associated with the presence of native grapsid crabs ($\chi^2_{[2]} = 9.488$; $P < 0.001$) (Figure 3). Almost 94% of sites visited around Tasmania with *P. elongatus* presence (n=32) also had grapsid crab populations (n=30).

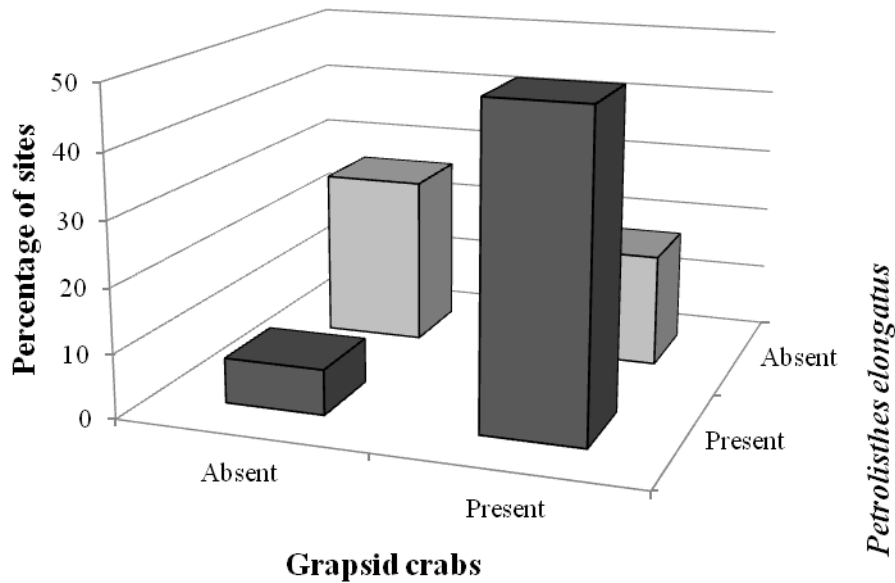


Figure 3: Percentage of Tasmanian sites (n = 57) illustrating the presence or absence of *Petrolisthes elongatus* and the native grapsid crabs *Paragrapsus quadridentatus* and *Paragrapsus laevis*.

Across sites, the density of *P. elongatus* was significantly higher than that of the native grapsids ($H_{[1]} = 7.593$; $P < 0.01$), (Figure 2). This result was largely driven by high densities of *P. elongatus* within southern sites (Figure 2). In contrast, there is no difference in densities of native grapsid crabs between sites in north Tasmania and south Tasmania, with density levels only spiking in Wynyard (north) and Tinderbox (south) (Figure 2). There was no correlation between densities of *Petrolisthes elongatus* and *Paragrapsus quadridentatus* and *Paragrapsus laevis* at either the site or quadrat scale (Figure 4).

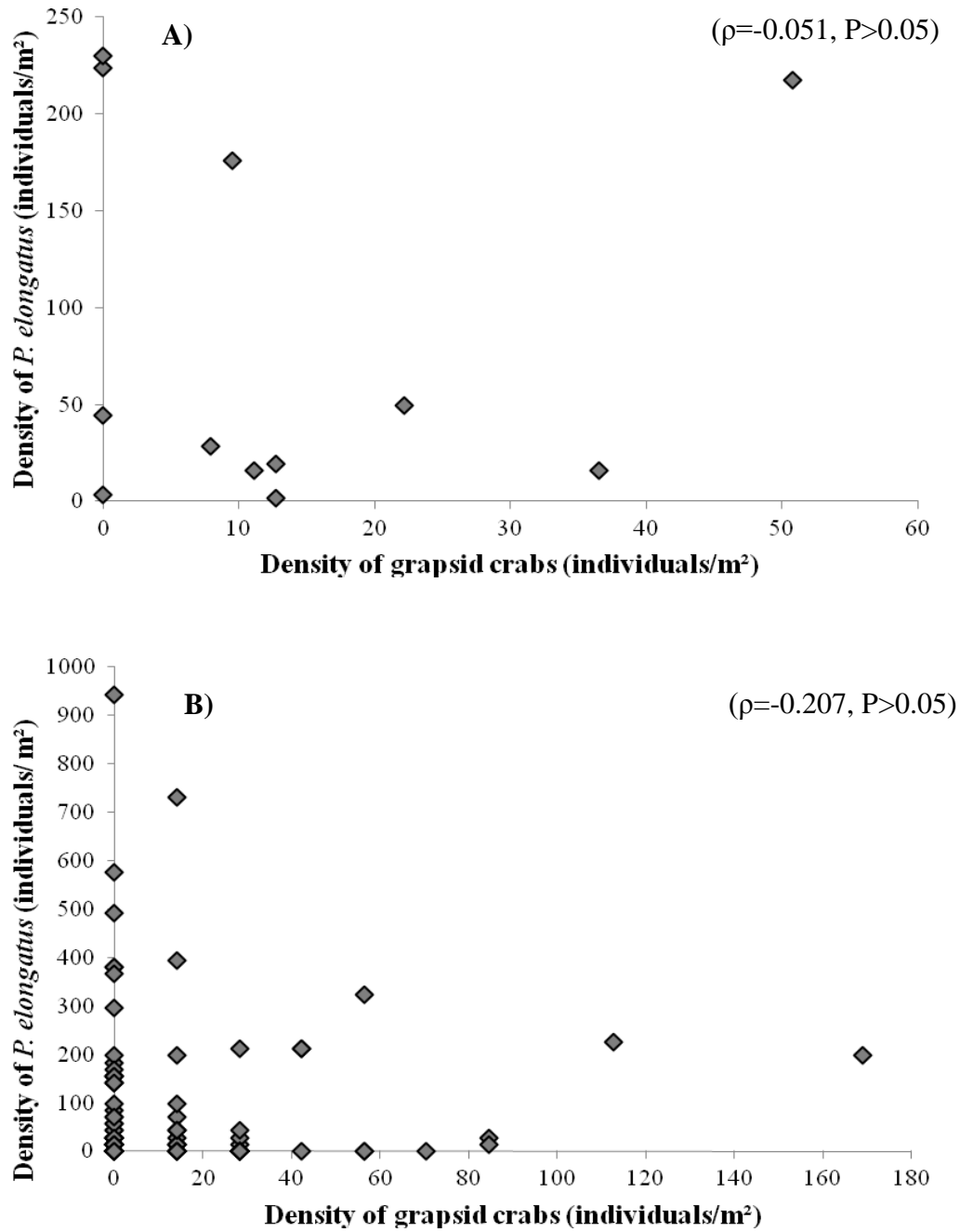


Figure 4: Density of *Petrolisthes elongatus* (y-axis) vs. density of grapsid crabs (x-axis) at **A)** site scale and **B)** at quadrat scale

Abiotic Factors

Presence of *P. elongatus* was positively correlated with 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 contained small rocks. Simultaneously, *P. elongatus* were present at 84% and 83% of sites containing rocky cobble and coarse sand respectively. In contrast, *P. elongatus* was absent in areas with fine sand ($\rho = -0.464$, $P < 0.05$) or large immovable rocks ($\rho = -0.447$, $P < 0.05$) (Figure 5).

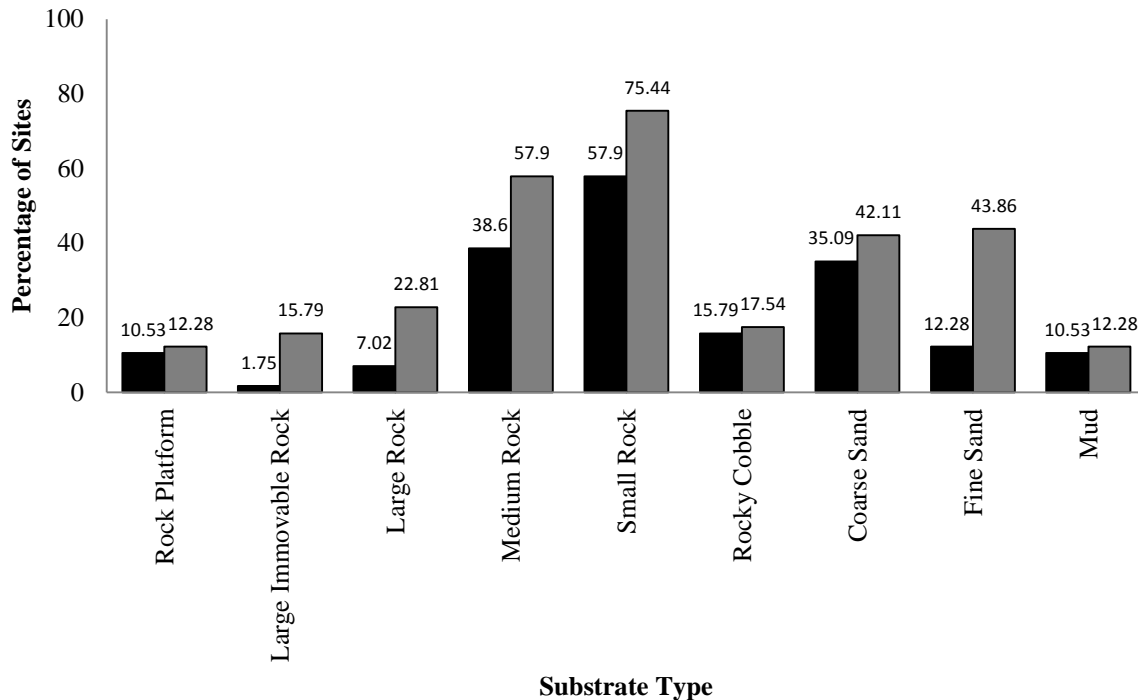


Figure 5: Presence of *Petrolisthes elongatus* in relation to substrate type. Grey bars represent the percentage of sites with certain substrate types while black bars represent the percentage of sites with *Petrolisthes elongatus* presence in relation to presence of substrate types;.

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).

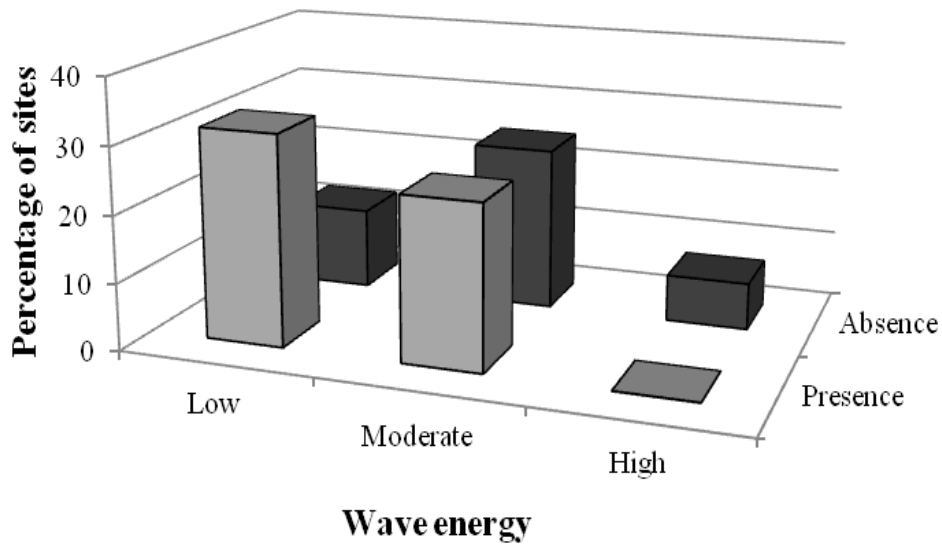


Figure 6: Percentage of sites with *Petrolisthes elongatus* presence and absence in relation to wave exposure levels.

Discussion

Our research explicitly focussed on the distribution and density of *Petrolisthes elongatus* around Tasmania with an assessment of biotic and abiotic factors that contribute to the current range of this introduced crab. *Petrolisthes elongatus* was found in 56% of studied sites (n = 57), furthermore, *Paragrapsus quadridentatus* and *Paragrapsus laevis* were found in 71% and 26% of sites studied. Densities of *P. elongatus* were higher in southern sample sites while presence of the introduced *P. elongatus* was significantly associated with presence of native grapsid crabs, however, no competitive or predatory correlation was found in this coinhabitation. *Petrolisthes elongatus* presence was correlated with substrate types including coarse sand, rocky cobble and small rocks and low to moderate wave energy coastal zones. The rarity of *P. elongatus* along the east coast, its absence along the west coast of Tasmania, and its putative initial inoculation site on the southern coast presents a conundrum: what mechanism(s) of dispersal inoculated such a large proportion of the northern coastline?

Two potential hitchhiker pathways are speculated to 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; and ii) dry-ballast of early trading vessels between Tasmania and New Zealand (King 1997). 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 *Patiriella 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).

The density of *P. elongatus* is greater along the southern coast 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 (higher fecundity and 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). There seems to be no significant competitive or predatory relationship existing 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 hypothesis 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*. 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 adult dispersal.

Along with other abiotic factors, weather exposure plays a role in the distribution of intertidal species and the inoculation success and population density of introduced organisms (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, as it 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 displace shelter and reduce filter feeding efficiency of *P. cinctipes* and *P. eriomerus* as fine sediments do not settle out of suspension (Jensen and Armstrong 1991; Osborne and Rooker 1999).

Furthermore, high concentrations of sediments in the water column have been shown to utilise more energy during filter feeding by *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 and reduced ability to filter feed; 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.

Our results rule out the natural dispersal of juvenile or adult *P. elongatus* along the Tasmanian coastlines, because of a lack of consistent suitable habitat. Larval dispersal around Tasmania may be explained by nearshore currents (Largier 2003). The currents that surround Tasmania show a south to north movement with the resulting flow into Bass Strait along the north coast. However, Ulloa and Palma (1998), in their study in Valparaíso 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 Valparaíso 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 as vessels moored between southern and northern ports in Tasmania (Campbell and Hewitt 1999). Similarly, multiple vectors may be operating (Floerl and Inglis 2005) or new inoculations could have occurred as planktonic larvae via ballast water transfer through direct shipping from New Zealand.

Introduced species have adapted to survive and expand in suitable new environments most of the time 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 on the north and south coasts of Tasmania. However, this study suggests that there are still uninvaded intertidal zones within Tasmania that consist of suitable substrate and exposure levels, namely on the east and west coasts. 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* along the Tasmanian coast 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.

Chapter 3

Morphometrics, sex ratio and annual reproductivity of the New Zealand porcelain crab

Petrolisthes elongatus

Introduction

Intertidal species have adapted to inhabit coastlines varying in abiotic conditions from emersion and desiccation to submersion and wave stress (Defur 1988; Somero 2002; Harley and Helmuth 2003). Adaptations include morphological, phenological, physiological, ecological and behavioural characteristics across and within populations. Morphological adaptations allow individuals to survive in stressful conditions and include, but are not limited to, adaptations in size, shape, colour, grooming appendages, feeding and defence organs (Wolcott 1973; Helmuth and Hofmann 2001; Somero 2002; Tomanek and Helmuth 2002). Differences in morphological characteristics are readily observed between the low, mid and high intertidal zones across multiple intertidal species across latitudes and longitudes (Wolcott 1973; Vermeij 1973; Helmuth and Hofmann 2001).

Several intertidal limpet species exhibit a variety of morphological differences that enable adaptation to different intertidal gradients of exposure, such as differing colours, shapes and sizes (Vermeij 1973; Wolcott 1973). Limpet species in the upper intertidal zone are usually lighter in colour with small ribbed shells to maximise both water retention and heat loss. Alternatively, limpets exposed to hydrodynamic forces (wave exposure in the low intertidal) have a smooth shell to decrease drag over the individual, which helps to avoid displacement (Wolcott 1973). Similarly, some crab species (e.g., European green crab *Carcinus maenas* (Linnaeus, 1758) and the Panamanian grapsid crab *Pachygrapsus transversus* (Gibbes, 1850)

utilise large cheliped size and body size for dominance in predation and interspecies and intraspecies competition (reproduction, habitat dominance, food resources); a morphological adaptation that aids to ensure the survival of an individual and longevity of a population (Christy 1987; Sneddon et al. 1997; Sneddon et al. 2000; Christofolletti et al. 2010).

Morphometrics (the quantitative analysis of morphological characteristics) can describe a population's size frequency distribution, growth rates between sexes and optimal reproduction size and give insight into a population's behaviour (Diaz and Conde 1989; Hines 1989; Hartnoll and Bryant 1990; Spivak et al. 1994). In relation to non-indigenous marine species (NIMS), morphometrics can reveal the success of an established population, and how they co-exist with native biota while also alluding to recruitment patterns through individual growth size of the population (Kaiser et al. 1990; Gribben et al. 2013). Species introduced to new environments have been observed to grow to larger sizes; empirical evidence suggests that one reason this occurs is because these species are released from natural enemies that provide them the opportunity to thrive without being impacted through predation, competition or parasitic infection (Torchin et al. 2001, 2002; Colautti et al. 2004). Predator release studies of *Carcinus maenas* have identified greater growth rates and higher biomass in recipient communities where native resistance (competition, predation and parasitism) was minimal (Grosholz and Ruiz 1996; Torchin et al. 2001, 2002, 2003). Furthermore, other factors influence the successful establishment of NIMS such as better abiotic conditions and increased food availability (Rahel and Olden 2008).

However, the morphology of new populations can alter due to environmental factors that may influence their growth positively or negatively (Grosholz and Ruiz 1996; Torchin et al. 2001, 2002, 2003; Kelley et al. 2011). Finding environmental factors that negatively affect growth rates can be fundamental in determining avenues to mitigate or eradicate introduced populations. As a component of this, understanding a species' size frequency distribution over a broad biogeographical range (both native and introduced) may influence recruitment patterns, mortality and behavioural differences (Diaz and Conde 1989; Hines 1989; Spivak et al. 1994; Mantelatto et al. 2010).

Sexual size dimorphism (i.e., the difference in morphology between male and female individuals within populations) (Shine 1989) may provide insights into potential characteristics that can be exploited in a population for eradication attempts or management. These differences are attributed to factors that aid in the survival and growth of species populations (Shine 1989). Differences in size morphology between sexes is typically explained as a direct result of sexual selection between mates, in which favouritism of certain body sizes and characteristics by one gender leads to the reproduction of young with these genetic attributes (Shine 1989). However, size selection between mates does not always favour the larger of the opposite sex (deRivera 2005). Sexual size dimorphism is evident in many intertidal crustaceans through differential chela and/or carapace sizes between sexes; males can have larger chela than females and grow to larger sizes to aid in competition for food resources and mating choice (Valiela et al. 1974; Elner 1980; Sneddon et al. 1997).

A dominant male with the ability to overpower conspecifics for mate choice will ultimately have a greater chance of reproducing; however social dominance can also have detrimental effects through energy expenditure and injury from intraspecific competition (Christy 1987; Sneddon et al. 2000; Sneddon et al. 2003). In some species, the female counterparts are smaller morphologically, which can be a factor that influences mate availability or the size at which female crustaceans mature and reproduce (Valiela et al. 1974; Caravello and Cameron 1987).

Species with high fecundity enables them to produce a lot of offspring and increase their propagule pressure with the expectation that only a very small number of those propagules will survive to reproduce themselves (Lockwood et al. 2005; Simberloff 2009). Females of certain species can also show sexual dimorphism of the abdominal flap, which, in the instance of the females, grows wider to accommodate large numbers of eggs that increases their reproductive output (Rhodes and Holdich 1984).

Intraspecific niche divergence also provides an explanation for sexual size dimorphism, which is thought to be determined by the ecological factors behind ecological processes within trophic structures (Selander 1972; Shine 1989; Fairbairn 2007). Sexual size dimorphism as a result of trophic level may be a factor of sexual specific ecological adaptations, where the males and females of the same species are adapted to utilise appendages in differing ways, hence why they have subtle or large differences in morphology (Shine 1989). Sexual dimorphism can be a factor of dietary choice, but the opposite can also occur where morphological adaptations (i.e., enlarged chela on male crabs from competition) can cause males to consume different food sources than females, ultimately causing a morphological shift between the sexes (Shine 1989). An example

of different morphology between sexes due to ecological adaptations occurs in fiddler crabs, for example, *Uca pugnax* (Smith, 1870) and *Uca panacea* Novak and Salmon, 1974, where the males have adapted a large chela for mating and competition, while females retain two small chela for feeding (Valiela et al. 1974; Crane 1975; Caravello and Cameron 1987).

Male and female densities within populations are broadly understood as being equal in order to have enough individuals to further the population (Fisher 1958; Hamilton 1967). According to Fisher's Principle (1958), populations reach male/female equilibrium when the parental total effort in developing young of both sexes is equal. Certain assumptions are made with Fisher's Principle that do not account for biological and ecological factors that can manipulate the outcome of sex ratios or the influence of biological differences between the adults themselves (Hamilton 1967). Biologically, sex ratios are determined through parental expenditure in which the amount of energy the mother expends to rear her young pre- and post-birth can determine the survival rate of select young individuals (Hamilton 1967).

This assumption is based on the equal chance of individuals being able to mate without the probability of conspecific mating competition and mortality (Hamilton 1967). Additionally, males and females of a species can mate more than once in a season with separate individuals to increase fertilisation, diversity and genetic compatibility. This trend renders the need for an equal sex ratio in a population as unnecessary (Hamilton 1967; Johnson and Brockmann 2010).

A number of both biotic and abiotic variables affect the outcome of sex ratios, including immigration and emigration from populations, latitude, temperature, competition and predation

(Jones and Simons 1983; Christy 1987; Abucay et al. 1999; Debuse et al. 1999). Again, these changes may occur due to reproductive efforts, food availability, or seasonal and climatic changes (Johnson 2003).

Examining biogeographical changes in ovigerous females over time can determine if a population's reproductive efforts and patterns are affected by environmental externalities such as temperature, food resource availability or photoperiods. This is especially true for a negatively phototactic genus such as *Petrolisthes* (Steele et al. 1977; Kruschwitz 1978; Lardies et al. 2004, 2010).

Reproduction is a costly process that requires energy input into rearing broods of eggs. As a result, certain species are seen to have seasonal fluctuations in reproduction, as certain times of the year may result in a more successful reproductive effort and output with less energy expenditure (Jones 1977; Lardies and Castilla 2001; Lardies et al. 2004; Gebauer et al. 2007). For example, herbivorous crustaceans in marine and intertidal environments rely largely upon algae as a food resource. Seasonal fluctuations in algal assemblages due to climate or trophic interactions can result in reduced reproductive output due to the reduction in resources (Kennish 1997). However, it is important to note that seasonal influences will also affect the densities of ovigerous females and output of propagules (see; Hollebone and Hay 2007; Johnston et al. 2009).

Aims and Hypotheses

This chapter aims to determine if there is sexual dimorphism and differences in morphological characteristics, sex ratios, and ovigerous female density between and within populations of *P. elongatus* at 12 coastal Tasmanian sites. This is achieved by identifying morphological differences in carapace length (CL) of *Petrolisthes elongatus* individuals for each sex, hence determining if there is a relationship between carapace size and sex type. Simultaneously, data on the number of ovigerous females will be used to isolate possible reproductive patterns over a one year period. Based on this, eight of the original thesis null hypotheses are tested:

Morphometrics

H₃: There is no difference in carapace length of *P. elongatus* between Tasmanian sample sites and coastlines

H₄: *P. elongatus* shows no sexual dimorphism in relation to carapace size within Tasmanian sites

Sex Ratio

H₅: There is a 1:1 sex ratio of *P. elongatus* within Tasmanian sample sites

Ovigerous Females

H₆: There is no difference in the proportion of *P. elongatus* ovigerous females to non-ovigerous females between Tasmanian sample sites;

H₇: There is no difference of CL between ovigerous females between sites; and non-ovigerous female *P. elongatus*

Annual Trends

H₈: There is no intra-annual trend relating to *P. elongatus* densities of ovigerous females at Taylor's beach, Low Head, Tasmania

H₉: There is no intra-annual trend between *P. elongatus* sex ratios at Taylor's beach, Low Head, Tasmania

H₁₀: There is no intra-annual trend between *P. elongatus* CL at Taylor's beach, Low Head, Tasmania

Materials and Methods

Petrolisthes elongatus individuals were collected from 12 sample sites from the north, east and south coasts of Tasmania during Austral summer (December 2010 – February 2011). The full details of these sites and how the crabs were collected are provided in the Chapter 2 section titled 'density patterns' sampling methods. Sampling did not occur on the west coast because preliminary research detected no *P. elongatus* populations (unpublished data).

Morphometrics

Measurements were conducted on 740 *P. elongatus* individuals across the 12 sample sites to identify size and recruitment differences between sites. Measurements were recorded utilising digital callipers with an accuracy of $\pm 0.01\text{mm}$. The measurements occurred along two points of the crabs carapace: i) CL was measured from between the eyestalks to the concave margin of the carapace (beginning of the abdominal flap) (Figure 7a); and ii) carapace width (CW) was measured between the third pereopods on either side of the carapace (Figure 7b).

A Pearson's correlation was used to determine whether CL is a suitable surrogate for CW as CL and CW growths are correlated with one another (see Pereyra 1965) (Figure 11). A Kruskal-Wallis non-parametric test was used (transformed data failed to meet normality) to determine

significant differences in crab morphology between coasts (north, east and south), in conjunction with a Mann-Whitney U Test for pairwise comparisons. A Bonferroni adjustment was used to reduce Type I errors. A Mann Whitney U Test was also used to identify the differences between male and female CLs where CL measurements for male and female *P. elongatus* were pooled separately.

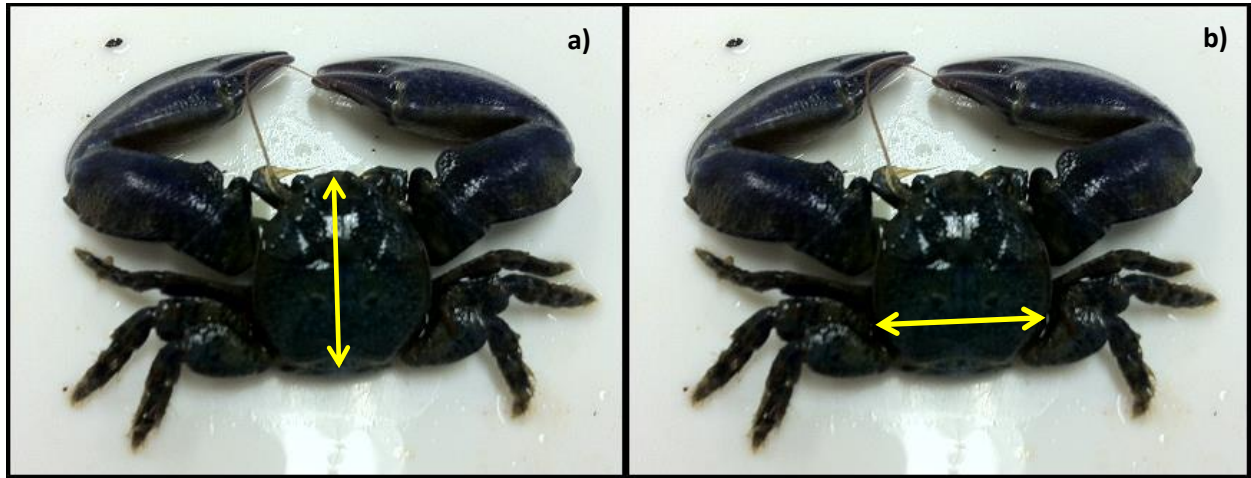


Figure 7: Morphometric characteristics measure for *P. elongatus*: a) CL measurement; and b) CW measurement

Sex Ratio

All 740 collected individuals were identified as being either male or female. Males were identified by two translucent penes located under the abdominal flap (Figure 8a). Females were identified by the gonopores located on the coxa of the third pereopods (Figure 8b). A G-test goodness of fit was conducted at each site to identify significant differences in sex ratios.

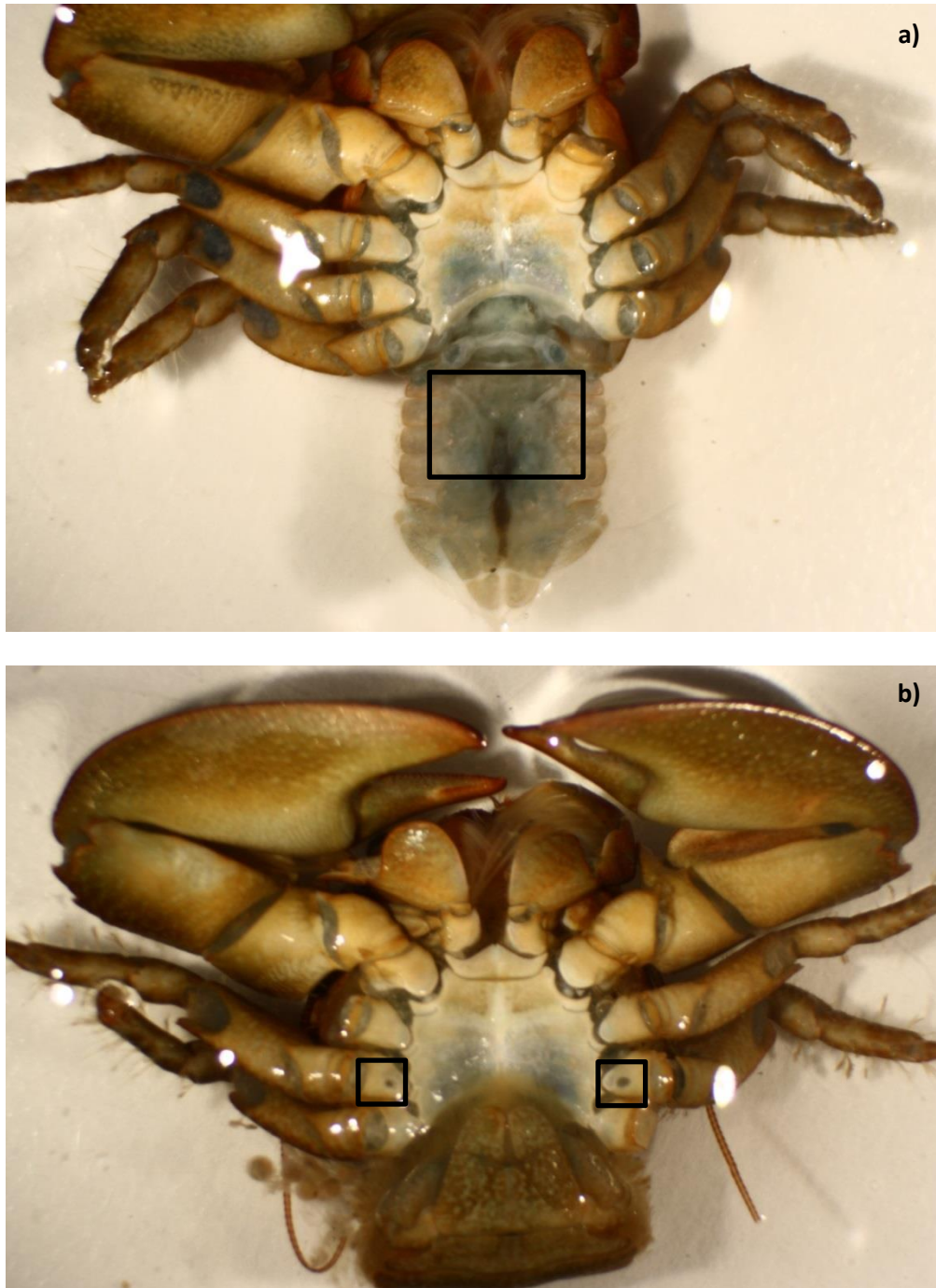


Figure 8: Characteristics used to identify the different sexes of *P. elongatus*: **a)** male reproductive organs; and **b)** female reproductive organs within black boxes.

Ovigerous Females

Ovigerous females were identified by the cluster of eggs under their abdominal flap (Figure 9). A test of the difference in densities of ovigerous females between sites was conducted using a chi square test of independence.

Female CL data was categorised by whether the female was ovigerous or non-ovigerous and Log10 transformed. An Analysis of Variance (ANOVA) used to determine if there was a significant difference between the CLs of ovigerous versus non-ovigerous female *P. elongatus*. All juvenile female crabs (<5mm carapace length) were removed prior to the analysis.



Figure 9: An ovigerous *P. elongatus* female

Annual Trends

Field research was conducted between February 2012 and January 2013 at one site (Taylor's Beach, Low Head; north Tasmania, 41° 5' 51.24" S -146° 48' 43.65" E) once a month (11 months) to identify variations of ovigerous *P. elongatus* females over a year. Unfortunately, the month of July was removed from the research due to external factors. *P. elongatus* individuals were hand collected using transects and quadrats along the intertidal at low tide. Three transects (50m long) 5m apart down the intertidal were established, each running parallel to the low tide mark.

Sampling occurred along each transect with a quadrat (bottomless bucket = 0.071m²) placed at 0m and every 2 metres thereafter for a total of 25 quadrats per transect line. This provided to total of 75 quadrats sampled, in total covering 5.625m². Each quadrat was searched for the presence of *P. elongatus*. Collected individuals were placed in quadrat specific zip lock bags, labelled and placed on ice until being ethically euthanised and preserved in 70% ethanol. Monthly collections were all conducted at the same location on Taylor's beach, Low Head within the intertidal zone consisting of suitable substrate. A total of 4,728 individuals were collected and used to measure CL and CW and to determine the number of ovigerous females and sex ratios.

This data was analysed using a one-way ANOVA to identify intra-annual fluctuations of ovigerous females. A G-Test goodness of fit was used to identify differences in male to female sex ratios during the sampled months. A one-way ANOVA with a post hoc Tukey's test was

used to determine if there was a difference in average CLs between months. IBM SPSS Statistics 21 was used to conduct all statistical analyses.

Results

Petrolisthes elongatus males, non-ovigerous females and ovigerous females found through our sampling methods along the north coast of Tasmania were evenly distributed in CL, showing no distinct growth separation between sex or ovigerous status (Figure 10). The CL of these populations was never lower than 6mm. Most females were ovigerous in their later growth stages (>8mm CL), although ovigerous females as small as 6mm CL were detected at the Devonport site (north coast) (Figure 10). Little Musselroe Bay (north coast) had the largest CL measurements from the north coast, with no individuals found under 9mm (Figure 10).

The St. Helens sample site (east coast) population had a relatively small CL, with females found in the juvenile growth stage (under 5mm, see Rivadeneira et al. 2010) and no individuals found above 11mm CL (Figure 10). Ovigerous females were bearing eggs at >8mm CL. At Triabunna (east coast) there was only one individual captured.

The size frequency of male, non-ovigerous females and ovigerous female individuals were found within all size classes beginning from 5mm CL, with males growing to the largest size (up to 18mm CL). Tinderbox (south coast) crabs showed a much smaller population with 19% of individuals still in their juvenile stage (<5mm) (Figure 10). Ovigerous females at Tinderbox had a smaller average CL compared to other sites (<8mm) (Figure 10). Ovigerous females at Dunalley (south coast) also had smaller CL; however the sexually mature females in this

population continued to reproduce late into their life cycle (~14mm) (Figure 10). Port Arthur and Dover (south coast) showed more of a northern coast trend, with ovigerous females found with a CL of ≥ 9 mm while females grew up to 14mm in CL (Figure 10).

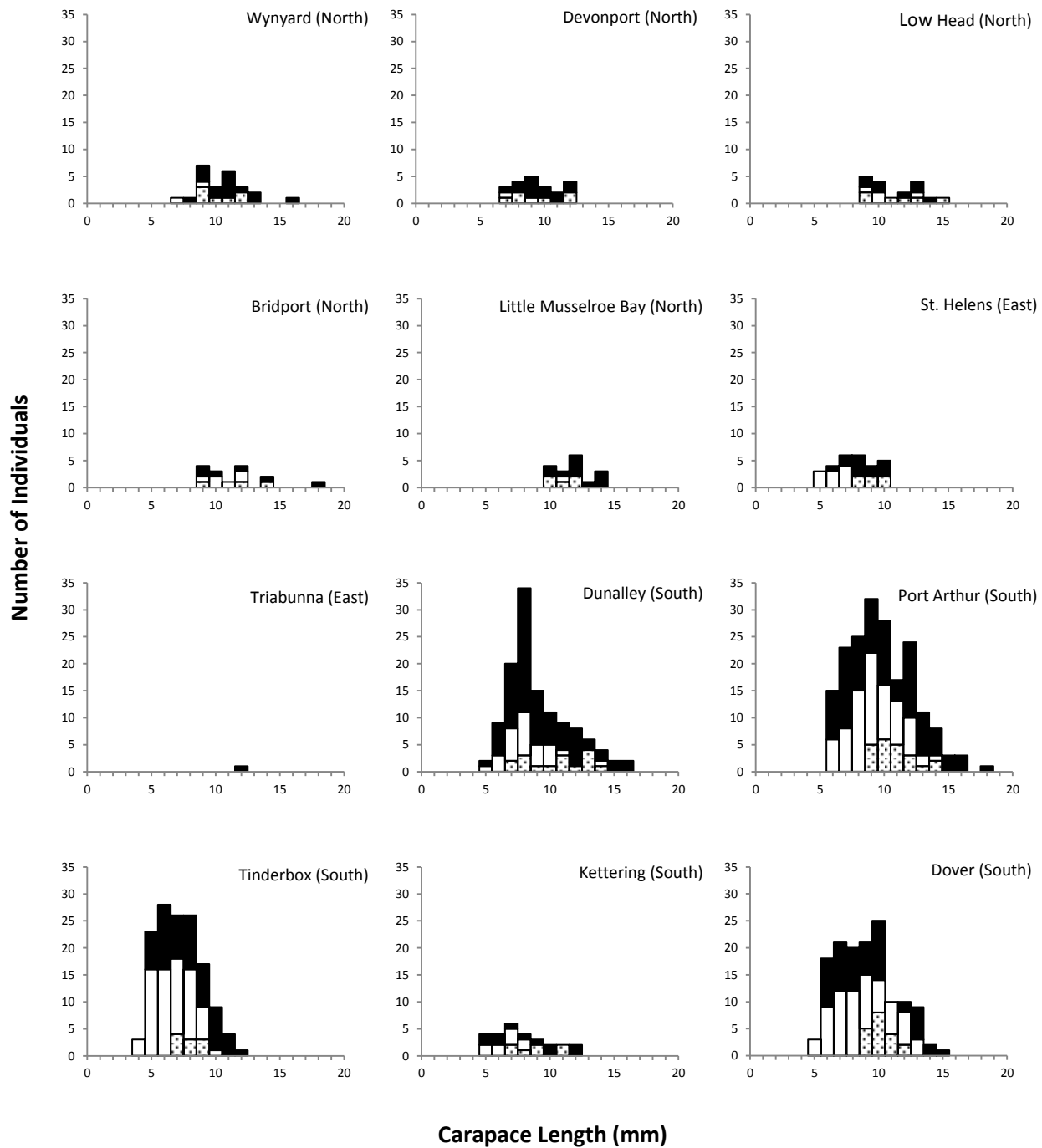


Figure 10: Size frequency histograms of *P. elongatus* individuals from Tasmanian sample sites.

Where black = males, white = females, and dotted columns = ovigerous females.

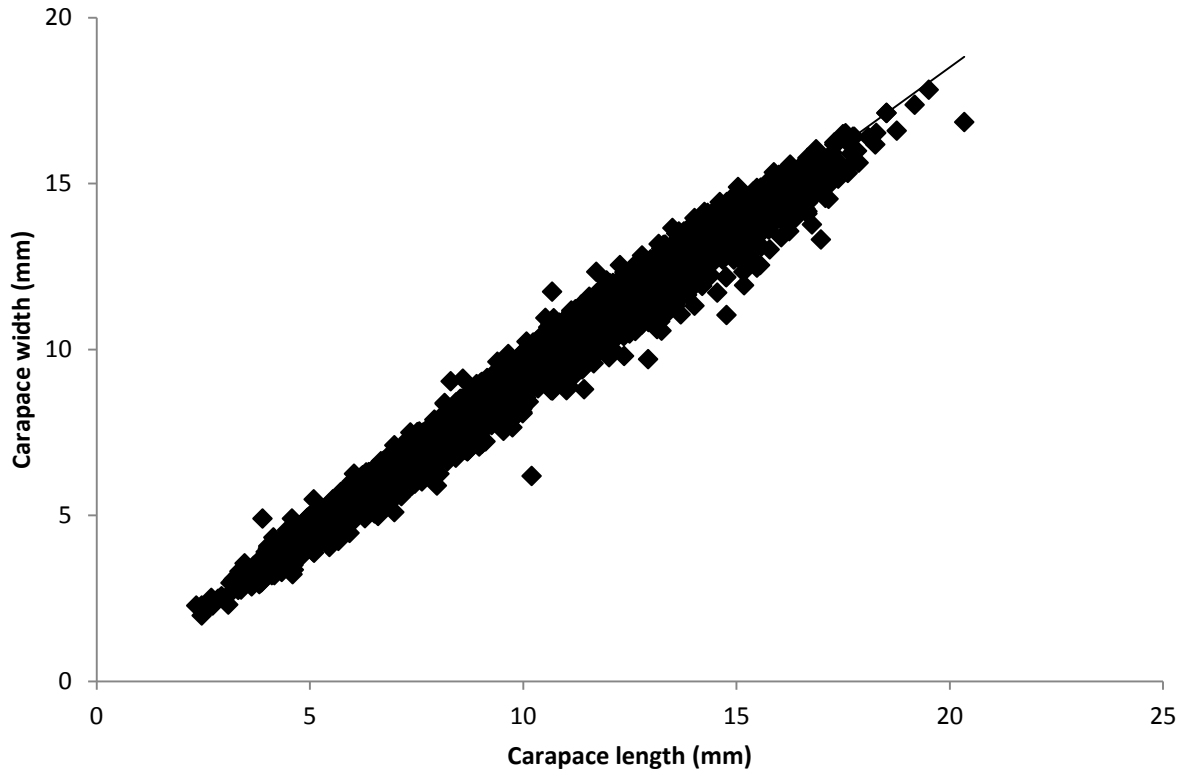


Figure 11: Carapace length vs carapace width of *P. elongatus* individuals collected from Taylor's Beach, Low Head, Tasmania over a one year time frame ($CW = 0.9306 * CL + 0.106$; $r^2 = 0.9802$; $p < 0.05$; $df = 1$).

Morphometrics

CL was statistically significantly different between Tasmanian coastlines (north, east and south) ($H_{[2]} = 66.41$, $p < 0.001$) (Figure 12). This was driven mostly by significantly larger carapace mean lengths between northern and southern coasts ($U_{[1]} = -7.57$, $p < 0.001$) (Figure 13).

Carapace mean length for the north coast ($\bar{x} = 10.35$) was larger compared to the south coast ($\bar{x} = 8.08$).

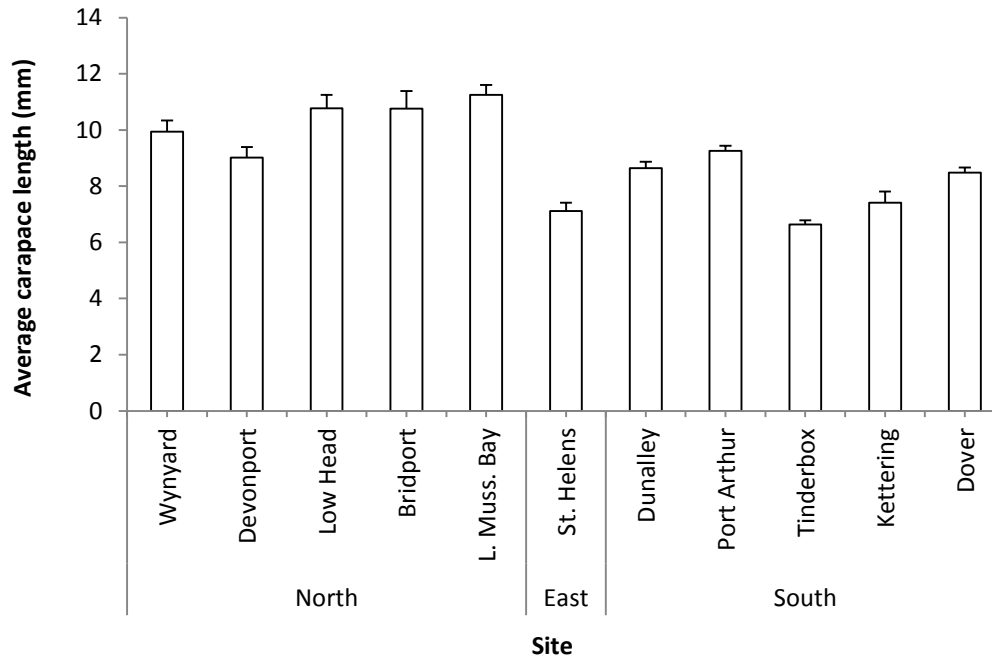


Figure 12: Average CL of *Petrolisthes elongatus* at the different Tasmanian sample sites (+ SE).

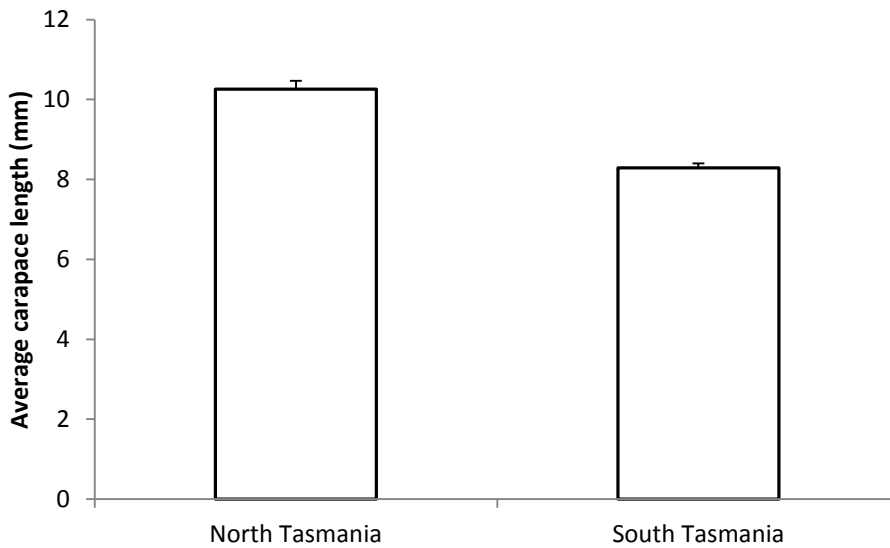


Figure 13: Average CLs of *Petrolisthes elongatus* between north and south Tasmania ($U_{[1]} = -7.57, p < 0.001$) (+SE)

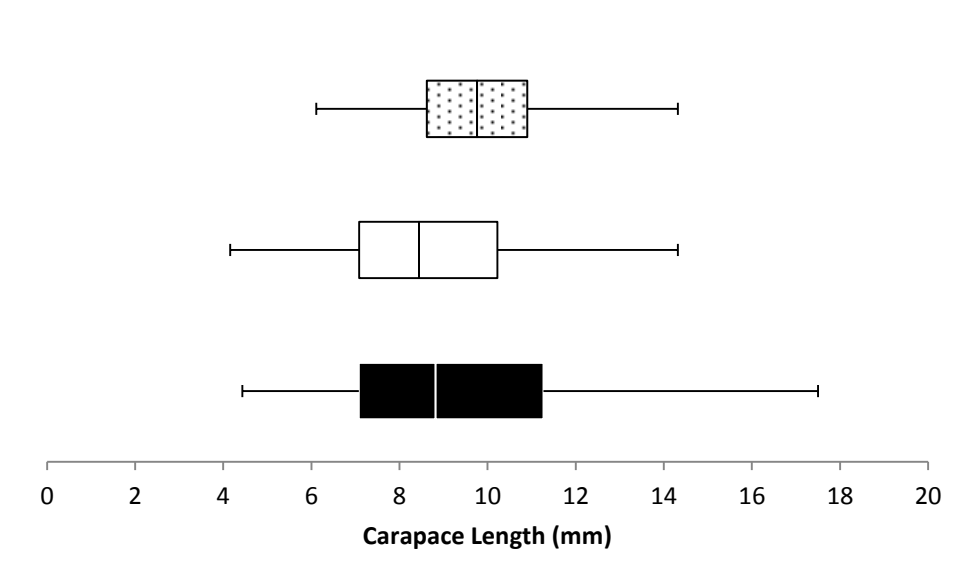


Figure 14: *Petrolisthes elongatus* CL of males (bottom), females (middle) and ovigerous females (top). Whiskers represent the smallest (left) and largest (right) CL found while the line in the middle of the box represents the average carapace length.

Average CLs between males and females were significantly different ($U_{[1]} = -8.722$; $p < 0.001$) (Figure 15). Figure 15 shows differences in male and female CL (mm) within sites excluding Low Head (north coast) and Dunalley (south coast) which refutes the hypothesis that there is no sexual dimorphism in relation to carapace size within Tasmanian sites.

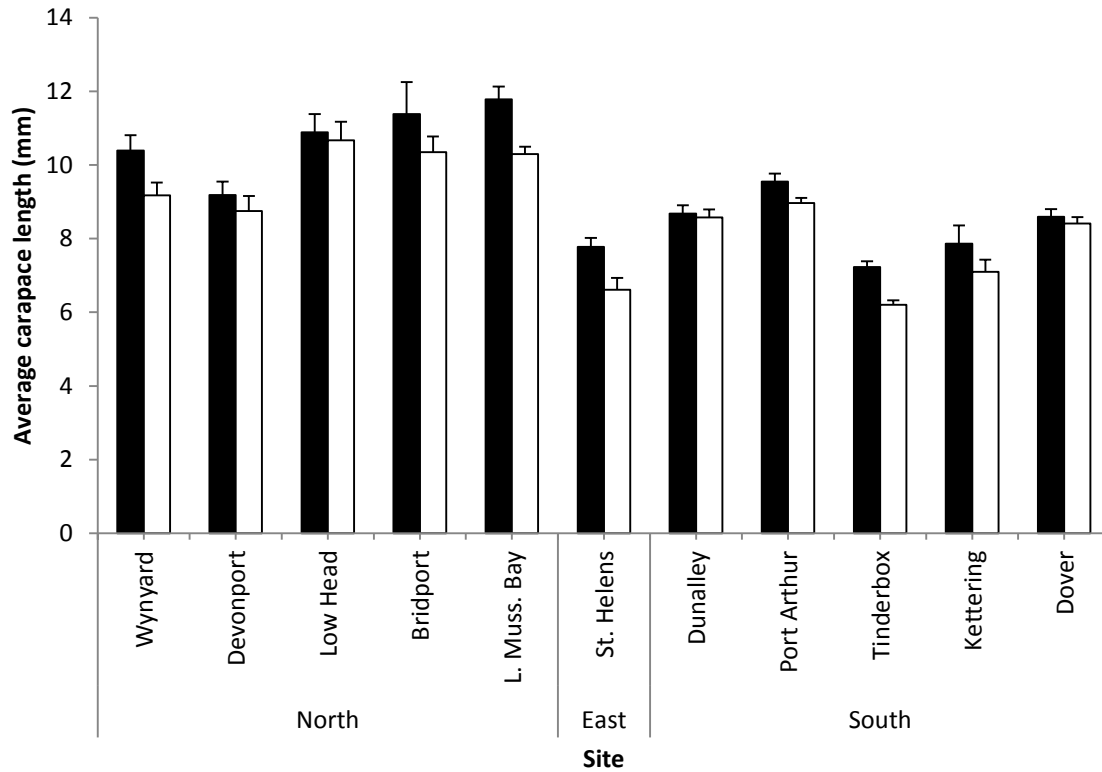


Figure 15: *Petrolisthes elongatus* average male and female CL at the different Tasmanian sample sites (+ SE) where male = black and female = white.

Sex ratio

Expected sex ratios of 1:1 were found at all sites except for Dunalley and Dover ($G_{[1]} = 9.6$; $p < 0.05$; $G_{[1]} = 7.4$; $p < 0.05$ respectively) on the south coast of Tasmania (Figure 16).

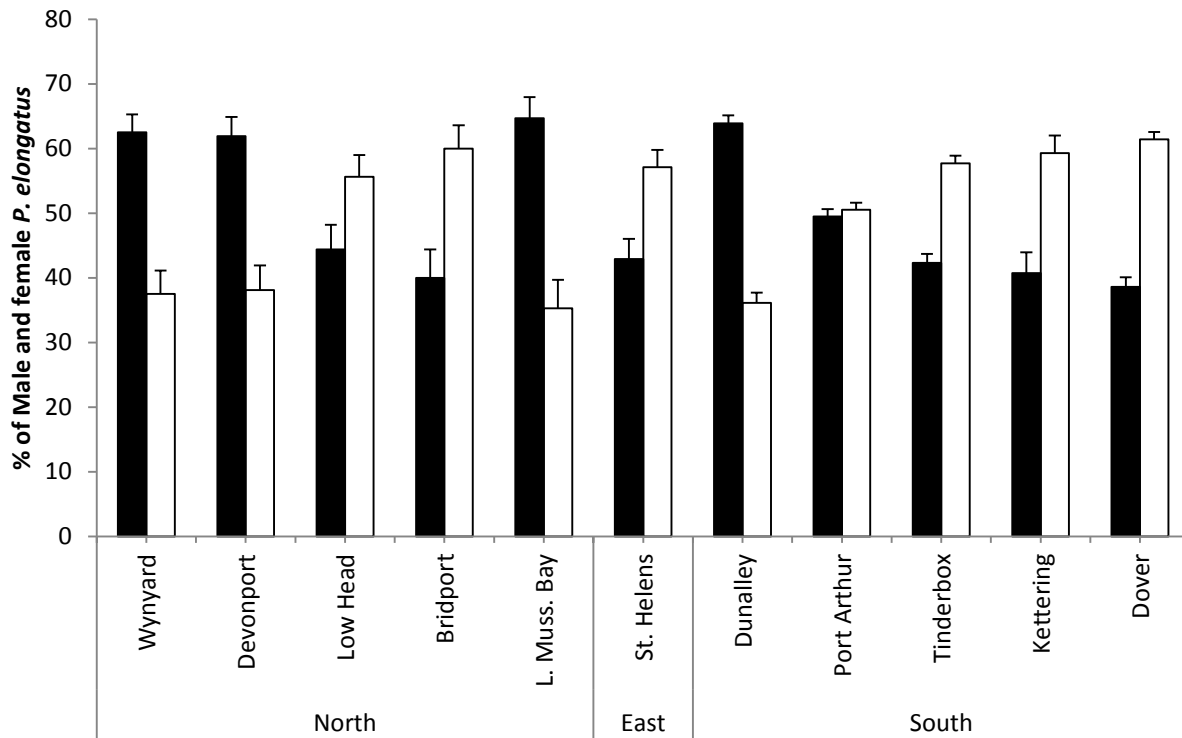


Figure 16: Percent of Male and female sex ratios at sites around Tasmania (+SE) where male = black and female = white.

Ovigerous females

The proportion (%) of ovigerous females differed significantly between Tasmanian sites ($\chi^2_{[10]} = 42.4$; $p < 0.001$) (Figure 17). Variances exist between northern, eastern and southern sites. In the northern coast, 80% of the sites have more than 50% of the female population bearing eggs, while the eastern and southern sites all had populations with less than 50% ovigerous females (Figure 17). The CL's of females between 8.42mm and 11.05mm were found to maintain the highest densities of ovigerous females.

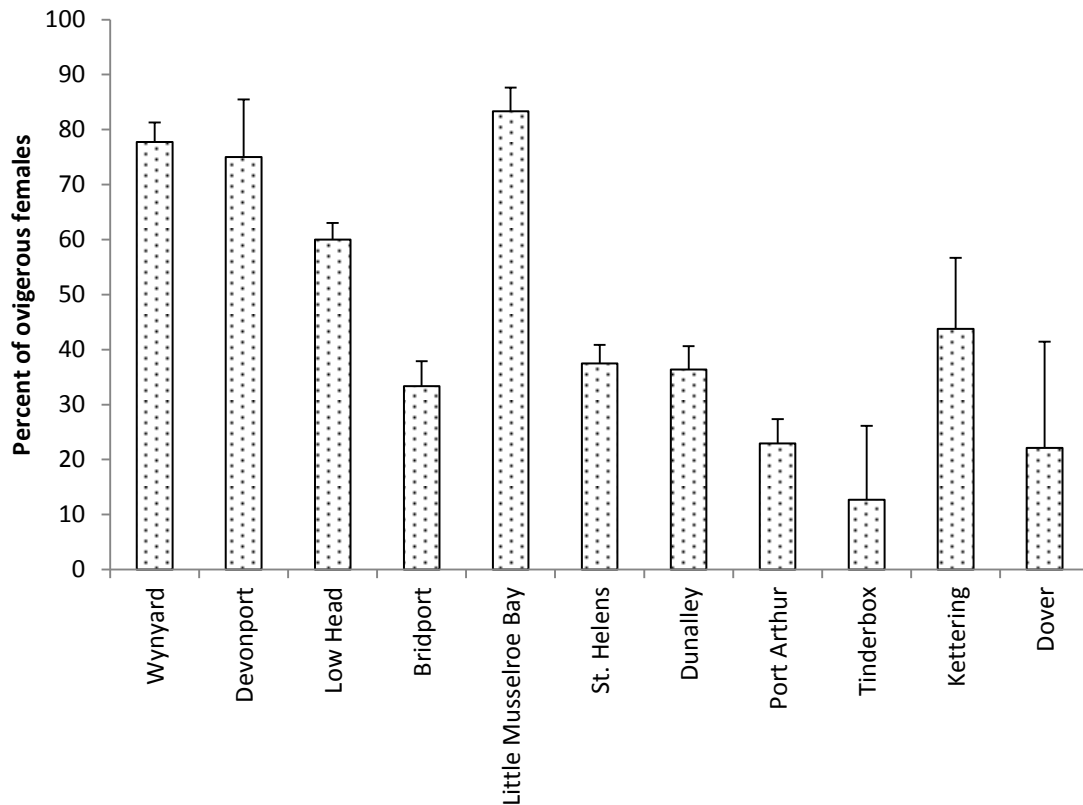


Figure 17: Percent of female *P. elongatus* that are ovigerous at the different sample sites during Austral summer (December 2010 – February 2011) (+SE).

There was a significant difference in CL between non-ovigerous females compared to ovigerous females ($F_{[1]} = 68.8$, $p > 0.001$). The average ovigerous female CL was 9.54mm, while non-ovigerous females were 7.59mm. Furthermore, no ovigerous females were less than 6mm in CL, while 23.8% of non-ovigerous females measured less than 6mm.

Annual trends

Of the 4,727 individuals collected over the course of the annual study (February 2012 – January 2013) at Taylor's Beach, Low Head 2,049 were male (43.3% of total population), 2,678 were

female (56.7% of total population) and 1,245 of the females were ovigerous (26.3% of total population and 46.5% of the female population). The proportion of ovigerous females varied significantly throughout the year ($F_{[1,70]}=9.224$, $p<0.01$) (Figure 18). Based on the presence of sexually mature individual females, *P. elongatus* could reproduce year round in Tasmania, with a rapid decline in reproduction during late autumn and winter months (<10% ovigerous female population). The densities of ovigerous females increased throughout spring (>40% ovigerous female population) and reached a peak in summer with ovigerous female densities reaching over 80% (Figure 18).

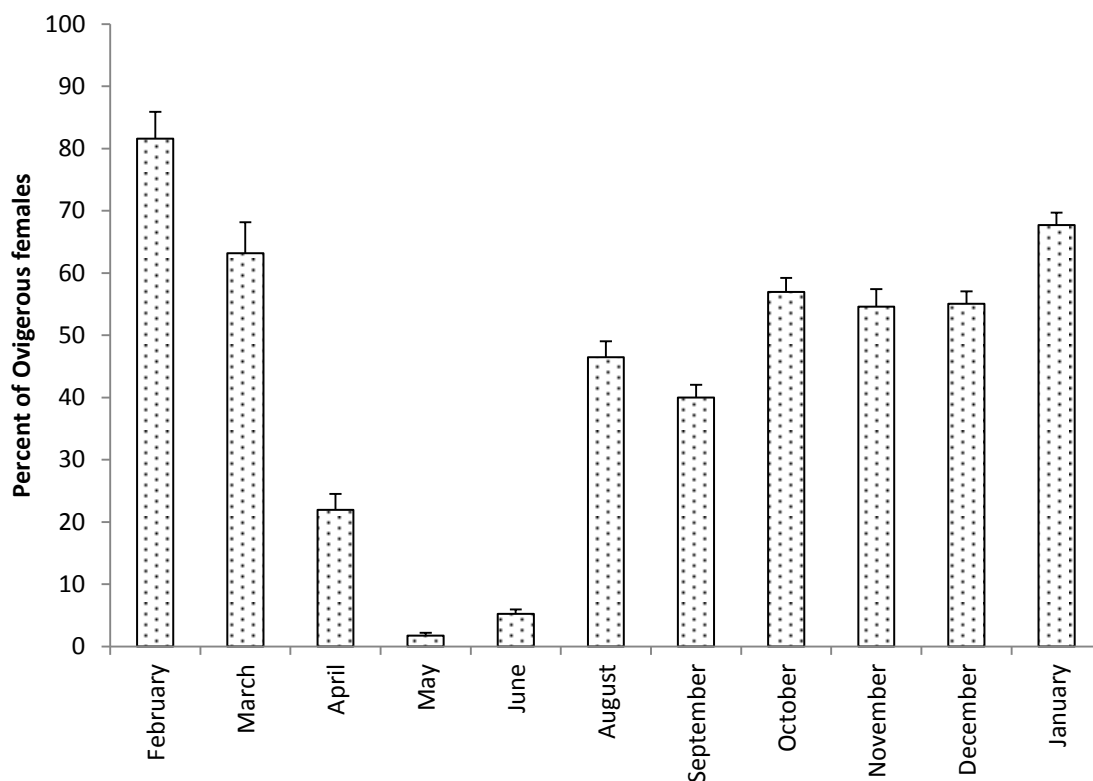


Figure 18: Percent of ovigerous *P. elongatus* females collected at the northern coast site of Taylor's beach, Low Head, Tasmania, between the months of February 2012 and January 2013 (+SE).

Female densities significantly exceeded male densities throughout the year with noticeable increases during the end of winter and into late spring at Taylor's beach (August: $G_{[1]} = 13.17$; $p = 0.001$, September: $G_{[1]} = 12.25$; $p = 0.001$, October: $G_{[1]} = 6.17$; $p < 0.05$ and November: $G_{[1]} = 4.66$; $p < 0.05$) (Figure 19). Sex ratios were almost 1:1 during early winter, with a 6-15% difference in male/female densities (Figure 19). During spring and summer, female densities, although not significant, became more common, with an increase in numbers of up to 20% (Figure 19).

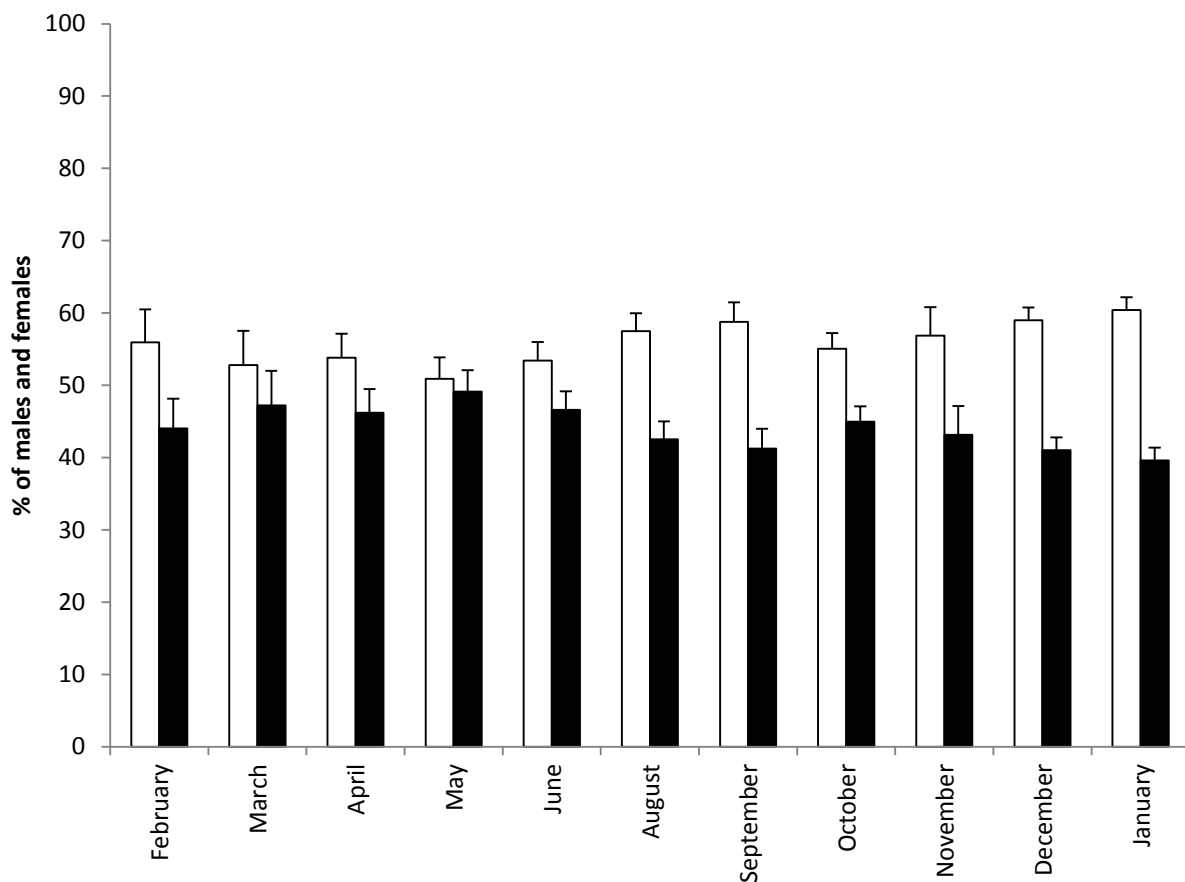


Figure 19: Male and female monthly sex ratios (+SE) of individuals collected at the northern coast site of Taylor's beach, Low Head, Tasmania where male = black and female = white.

There was a significant difference between the mean CLs of individuals throughout the study period (February 2012 – January 2013) ($F_{[1,10]} = 26.394$; $p < 0.001$) (Figure 20). A post hoc test showed larger average CLs during February, March and April ($> 11\text{mm CL}$) ($p < 0.05$), which coincides with the late Austral summer to autumn. From May to January there was a decrease in average CLs, ranging from 9.8mm CL in May to an average of 8.7mm CL in September (Figure 20).

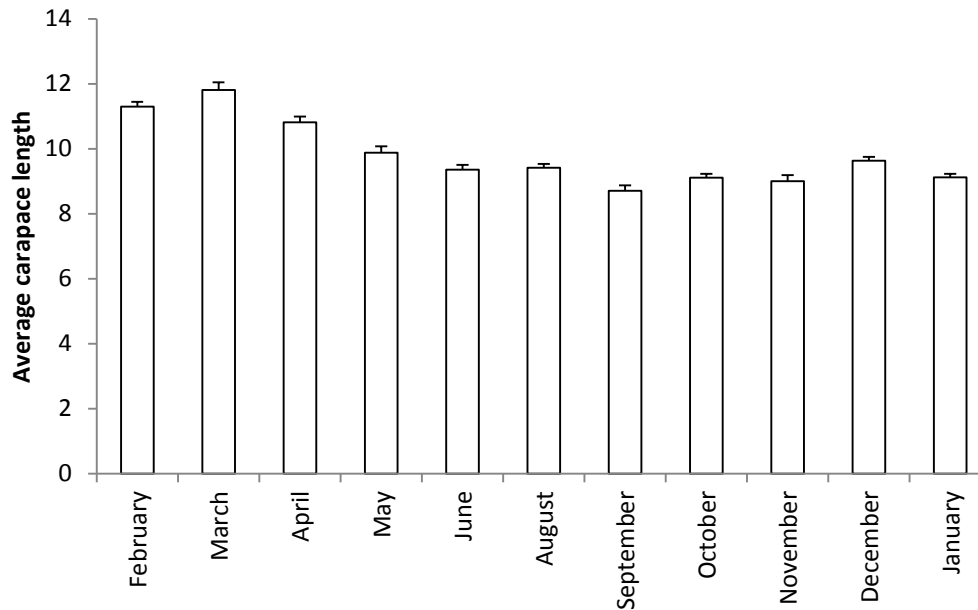


Figure 20: Average monthly *P. elongatus* CL's of individuals collected at the northern coast site of Taylor's beach, Low Head, Tasmania, during February 2012 to January 2013 (+SE).

Discussion

This chapter aimed to identify differences in CL (mm) of *P. elongatus* between sites and coastlines around Tasmania, with particular references to differences between sexes and ovigerous females. Sex ratios and ovigerous female densities within and between populations were also investigated. Furthermore, this chapter examined *P. elongatus* population structure over a one year time frame to determine any fluctuations in densities of ovigerous females, and sex ratios.

Morphometrics

The smaller average CL found in eastern and southern Tasmanian intertidal sites compared to northern sites reveals a difference between coastlines, thereby refuting the hypothesis that CL does not differ between sites and coastlines. This may be explained by factors ranging from environmental (temperature and desiccation), interspecific interactions (competition and predation) to intraspecific population variations (densities, sex ratios and ovigerous females) (Leffler 1972; Moksnes 2004). For example, Fisher (1999) noted that temperature influences the growth and early maturity in female blue crabs. Similarly, Ruscoe et al. (2004) identified increased mortality in colder waters compared to warmer waters in juvenile mud crabs.

It is unlikely that the morphometric trends seen were related to temperature differences, as the collection of *P. elongatus* used for the first morphometric analyses occurred over the Austral summer (December – February). However, sea surface temperatures do differ between coastlines. Northern Tasmania had ocean temperatures that were on average 2°C warmer than the

southern Tasmanian coastline (Australian Bureau of Meteorology 2012). Hence, a spatial water temperature influence may be the cause of the differences seen in this study.

The thermal phenotype of *Petrolisthes* enables this genus it to withstand temperature fluctuations and avoid desiccation (Stillman et al. 2006). *Petrolisthes* species in temperate climates can survive in an upper thermal tolerance limit, during emersion, of up to 27°C (Stillman 2002). *Petrolisthes eriomerus* and *Petrolisthes manimaculis* individuals in lower intertidal zones can acclimate to higher temperatures (up to 31°C before 50% mortality,) better than *Petrolisthes* species inhabiting the mid to upper intertidal zone with an acclimation limit of 1.9°C (*P. cinctipes*) (Stillman 2002).

Temperature is a contributing factor to growth and mortality in crustacean species (Jones and Greenwood 1982; Stillman and Somero 2000; Stillman 2002). Cooler climates produce smaller individuals of the same species that take longer to grow and mature, primarily due to the reduction in metabolic rates in colder water (Childress et al. 1990). Climates that are above optimal thermal limits can lead to desiccation (in the intertidal) and mortality of species, thereby reducing feeding abilities and lowering energy consumption resulting in smaller sized crustaceans (Rivadeneira et al 2010; Emparanza 2007; Stillman and Somero 2000; Stillman 2002).

Larger average CL's found in the north of Tasmania refute the hypothesis that there is no difference between average male and female CL, which may be explained by the percentage of

males in the *P. elongatus* populations studied. Males in this study had larger average CLs compared to females at all sites visited excluding Dunalley and Dover (south Tasmania) (Figure 12). Ahmed and Mustaquim (1974) also showed for *Petrolisthes boscii* and *Petrolisthes rufescens* similar morphological differences. This may be a result of energy allocation between different sexes, female crustaceans invest large amounts of energy during reproduction as found in the female blue crab *Callinectes sapidus* (Turner et al. 2003) while in certain cases male crabs invest less energy into reproduction, and more into growth for competitiveness and predation (Abrams 1988).

Sex Ratios

Sex ratios were found to not be significantly different from Fisher's Principle of 1:1 at all sites around Tasmania, excluding two sites along the south coast. Dunalley and Dover deviated from the 1:1 sex ratio, with Dunalley having a male dominated population (1.77 : 1) and Dover a female dominated population (1.59 : 1). This may be a result of the different environment at each of these sites. Dunalley is more exposed than Dover, and may have different abiotic conditions such as higher nutrients in the water, or food availability that can influence reproduction and sex ratios. Theory suggests that all sexually reproducing populations should not deviate from a 1:1 ratio, but exceptions do apply to this model. Exceptions can result because of factors such as size, foraging patterns, mortality after birth, parental energy expenditure during offspring rearing, different migration patterns, and seasonal changes (Darnell 1962; Leigh 1970; Wenner 1972).

Wenner (1972) determined that certain crustacean species rarely conform to the expected 1:1 sex ratio and further speculated that this lack of conformity may be across a broader species range. However, identifying sex ratios using the traditional method of male to female over a broad population may produce biased ratios based on the size of the individuals measured (Wenner 1972; Johnson 2003). Sex ratios have been shown to fluctuate based on the size ranges of individuals measured (Wenner 1972). For example, sex ratios show a 1:1 equilibrium as an overall population, but the common sand crab (*Emerita analoga*) males are dominant in the lower size classes (5mm – 10mm CL), with females dominating the upper ranges (10mm – 15mm CL) (Wenner 1972). Furthermore, mole crabs (*Hippa pacifica*) exhibit the same characteristics with sex ratios diverging across size classes (Wenner 1972).

If we apply these findings to the population and size of *P. elongatus* sampled in this study, there is no outstanding differentiation between sex and size class. Wenner's (1972) research on marine crustacea revealed a large separation between males and female ratios in relation to size.

Differential foraging patterns between the sexes can cause a large amount of collection bias and can contribute to deviations from the expected 1: sex ratios in crab populations (Johnson 2003).

A study on the fiddler crab, *Uca pugilator*, revealed the animal's behaviour can cause collection bias due to the more dominant nature of males in the open foraging areas of the intertidal while females were predominantly caught in burrows (Johnson 2003). In such situations, traditional methods of intertidal species collection (i.e., transect and quadrat, timed collection, trapping) will favour a male dominated collection, due to females remaining buried in the sediment. This bias can be discounted in this study, as the females continued to be the dominant sex throughout the annual study.

Ovigerous females

Ovigerous females had a significantly larger average CL compared to non-ovigerous females.

Ovigerous *P. elongatus* in this study were collected at early maturity (5mm CL) to late maturity (>12mm CL) (Figure 14), with the proportion of ovigerous female individuals collected dominating all collected females from 8mm – 12mm CL. Jones (1977), also found *P. elongatus* in Kaikoura, New Zealand (native range), with ovigerous females dominating the 8mm-10mm size class. As previously mentioned ovigerous females are not limited to this size range for reproduction, however; varying factors such as individual brood size and energy exertion can explain why *P. elongatus* females are most commonly ovigerous in this size class.

Mate choice in the environment is an integral role in the ongoing recruitment of offspring to populations (Christy 1987). In most cases, males utilise their strength and power or an array of morphological features, to win over a female mate (Sneddon et al. 2000, 2003; Coleman et al. 2004). This is most common in animals that have a low reproduction rate, slow growth and maturity, and live in small populations because they need to reproduce with the strongest or most colourful male to ensure that the energy they utilise to reproduce is for a genetically strong offspring (Kempnaers 2007).

In contrast, species that live in gregarious settlements (such as *P. elongatus*), with highly fecund females rearing young that reach maturity in the early stages of their growth cycle, may have a male choice preference based on the size of females (Reading and Backwell 2007) that enables a greater propagule production. Clutch size in *P. elongatus* is directly positively correlated to CL (Jones 1977). Hence, small mature females (5mm – 7mm CL), although fertile, have a smaller

egg rearing surface area compared to a larger fertile female (8mm-11mm CL) that has a higher carrying capacity. The large surface area difference for clutch size may explain why the average size class for ovigerous females lays between 8mm and 11mm CL, ensuring the maximum amount of young is reared from a female.

In contrast, females individuals than 11mm CL still have the potential to reproduce; however, these numbers were minimal. Females above 12mm CL have been through multiple summer brood cycles which consist of two egg rearing cycles (Scott 1958, Jones 1977), and the energy lost from reproduction may result in higher mortality rates. This would benefit the younger female population (8mm - 12mm CL) who continue to have double brood cycles through the summer season and smaller, younger females (early maturity between 4mm - 8mm CL) whom have singular cycles (Scott 1958; Jones 1977).

Annual trends

Little is known concerning the annual reproduction cycles of introduced populations of *P. elongatus* in Tasmania. Native and introduced *Petrolisthes* species worldwide have differing reproductive strategies ranging from increases in numbers of ovigerous females in winter (*Petrolisthes laevigatus* - southern Chile) (Lardies et al. 2004) or summer (*Petrolisthes armatus* – Georgia, USA) (Hollebone and Hay 2007). Some species only reproduce in certain seasons, while others reproduce year round (Booolootian et al. 1959; Antezana et al. 1965; Greenwood 1965; Baeza & Thiel 2000; Baeza et al. 2001; Lardies et al. 2010).

This study determined that introduced populations of *P. elongatus* in Tasmania may reproduce year round, with declines evident in winter and rapid increases in summer. This refutes the hypothesis that there is no seasonal trend in the densities of ovigerous *P. elongatus*. This enables the possibility of ongoing recruitment into the population throughout the year, which allows the invading species to fully utilise the habitat(s) over a longer temporal scale. In contrast, the study by Jones (1977) conducted at Kaikoura, New Zealand, identified that *P. elongatus* at this native site will only reproduce between the spring and summer months of October to March. During this period, densities reach their highest in January, with an absence in ovigerous females between April and September (Jones 1977). Insights based on the research by Jones (1977) could be applied in Tasmania, as this study detected dramatic decreases in the density of ovigerous females in cold weather (i.e., winter) (Figure 12). However the latitudes at Low Head, Tasmania, Australia, and the Kaikoura Peninsula, New Zealand, are not different enough to identify a climatic variable. Furthermore, the average monthly temperatures between Low Head and Kaikoura differ by only 1°C – 2°C (Australian Bureau of Meteorology, 2012; NIWA Weather 2012). Thus, the differences between densities of ovigerous *P. elongatus* females in the native and introduced populations might be explained by other environmental factors or availability of resources.

Species in their native range have evolved with surrounding biodiversity over centuries. This historic interaction between flora and fauna aids in determining population structure and reproduction, and as a result *P. elongatus* populations in New Zealand may not need to continually reproduce throughout the year as the recruitment during spring and summer is sufficient to ensure the population survives through the winter months. However, this decline of

ovigerous females in winter may also be a result of environmental cues such as burrowing or movement down the intertidal, or an increase in predation by native predators.

At one site (north coast) that was more intensively sample over a one year cycle, female individuals were the predominant sex for each month, thereby refuting Hypothesis 9 that there is no seasonal deviation from a 1:1 sex ratio (Figure 19). Sex ratios in *P. elongatus* populations are shown to have seasonal variation, with the 1:1 sex ratio apparent in winter months but female numbers increasing into spring and summer months. In other studies, the differentiation between male and female densities during spring and summer is attributed to increased temperature and chemical cues (Abucay et al. 1999; Lardies and Castilla 2001). Intertidal species utilise environmental cues to aid in foraging, mating and reproduction. These cues include temperature, pH and predatory, which can prevent mortality and aid in the timing and success of reproduction and population growth (Lardies and Castilla 2001). In this study, environmental cues such as increases in sea surface temperature increase may be the reason behind the increase in female individuals into spring and summer (warmer) months for greater reproductive output.

Petrolisthes species such as *P. armatus*, *P. laevigatus* and *P. cinctipes* are noted as having sex ratios that do not deviate from 1:1 (Hollebone and Hay 2007; Miranda and Mantelatto 2009). However, studies that have shown this trend were not conducted over different seasons (Hollebone and Hay 2007; Miranda and Mantelatto 2009). Conducting the current study over an annual platform, even though it was done at only one site, provides broader insight into how *P. elongatus* populations change throughout the course of the year. Yet, to be more robust, an

investigative study of this trend needs to occur over a longer time frame to enable inter and intra-annual patterns to be determined.

A potential variation was detected in relation to average CLs of *P. elongatus* between the sampled seasons, with larger individuals detected in the latter half of summer and into autumn (February to April). This refutes the Hypothesis 10 that there are no annual fluctuations in relation to CL. During this time, average CLs exceeded that of the other sampled months by up to 2mm.

Conclusions

Carapace length was found to differ between coastlines around Tasmania, with north coast populations of *Petrolisthes elongatus* having significantly larger carapace lengths than south coast populations. Male and female carapace lengths differed significantly within sites, excluding Low Head on the north coast and Dunalley on the south coast. Sex ratios were an expected 1:1 at all sites, excluding two sites on the south coast (Dunalley and Dover) which may be a result of differing abiotic conditions. Ovigerous females were found at higher proportions at sites along the north coast of Tasmania during the sample period (Dec 2010 – February 2011) compared to sites on the south coast, and average carapace length was significantly larger for ovigerous *P. elongatus*. The annual study conducted at Low Head, north Tasmania from February 2011 to January 2012 revealed an increase in ovigerous female abundance throughout the spring and a peak into summer months, while sex ratios were female dominated throughout the study. Average carapace lengths changed throughout the year, with increases in average size throughout summer and into autumn.

Chapter 4

Synthesis and Future Research

Discussion

The accidental and intentional human-mediated introduction of non-indigenous marine species (NIMS) is an ever increasing threat to native biodiversity, ecosystems and socio-economic systems, both locally and globally (Carlton and Geller 1993; Ricciardi et al. 1997; Parker et al. 1999; Hewitt 2003a, b; Bax et al. 2003; Campbell 2008; Molnar et al. 2008; Hewitt et al 2009a, b; Campbell and Hewitt 2013). The impacts associated with anthropogenic introductions can be minimal, but they can also modify and destroy native community assemblages, possibly resulting in the mortality of native species (Didham et al. 2005; Wallentinus and Nyberg 2007; Molnar et al. 2008). Understanding global invasions and identifying the mechanisms behind successful invasions, both biologically and ecologically, is continually increasing, thereby aiding the management, mitigation and removal of NIMS (e.g., Hewitt et al 2009a, b; Dahlstrom et al 2011, 2012). It is important to examine the spatial history of an invasion to understand invasion potential (how far individuals spread from the initial introduction zone). Investigating what factors determine why NIMS inoculate certain ecosystems can aid in mitigation methods.

To help broaden the available knowledge on introductions, this project has focussed on identifying the spread and density of *P. elongatus* in Tasmania. Morphometrics, sex ratios and the reproductive phenology females were also studied at 11 sites around Tasmania over an Austral summer (December 2010 – February 2011) and intensively over a one year period at one site (February 2012 – January 2012 – February 2013; reproductive phenology). This project allowed us to identify the spatial range of *P. elongatus* invasion and the locations of high density populations (south coast Tasmania) and low density populations (north coast Tasmania).

Furthermore, no apparent spatial relationship was found between *P. elongatus* and two native grapsid crabs, although abiotic conditions such as wind energy was found to influence the spatial detection of juvenile and adult *P. elongatus* populations. Temperature was also found to correlate with *P. elongatus* population structure with increases in female densities and ovigerous females throughout autumn and summer months.

As discussed in Chapter 1, *Petrolisthes elongatus* was introduced more than a century ago to Tasmania (Australia) and has since spread to cover a large spatial area of Tasmanian intertidal ecosystems. They are found in high densities in the rocky intertidal, ranging from the north-east coast to the southern coast of Tasmania. In Chapter 2, I examined the co-inhabitancy of this species with native grapsid crabs to identify any biotic interactions (competition and predation) which may determine the distribution and density of *P. elongatus* around Tasmania. This study detected no direct competition or negative interactions between the introduced and two native species (the species commonly found with *P. elongatus*). However this research focussed on grapsid crabs only and did not examine possible impacts and/or interactions with other benthic organisms.

In Chapter 2, I examined the correlation of abiotic conditions, such as coastal stressors, with established populations of *Petrolisthes elongatus*. Determining how certain abiotic factors changed over large spatial areas was undertaken to help identify potential future spread of *P. elongatus* around the Tasmanian coastline. *Petrolisthes elongatus* favours sheltered intertidal habitats, but its current disjunct geographic spread indicates that either multiple inoculations with

subsequent establishment have occurred or, different vectors of initial introduction or subsequent spread are occurring.

Chapter 3 determined that *Petrolisthes elongatus* in Tasmania have the potential for year-round reproductive output. This reproductive activity seems to be positively correlated with sea surface water temperature, with higher densities of ovigerous females found in warmer spring and summer months. Furthermore, the *P. elongatus* population at Low Head in the north of Tasmania is dominated by females year round, which may provide insight to sexual selection and propagule pressure in newly introduced populations. This is further supported by the larger average carapace length in the northern sites. This coincides with a recent *P. elongatus* study that examined the abundance and morphology between New Zealand and Tasmanian populations and found that the crabs had a larger body size in their introduced range (Gribben et al. 2013).

Decapod invasions

Decapod invasions have been occurring for centuries, associated with dry, semi-dry and water ballast on trading vessels (Carlton 1989; Hutchings 1992; King 1997; Hewitt et al 2004a; Hewitt and Campbell 2010). Certain decapod species have received wide attention within the scientific community due to the impacts they have had on native biodiversity and their global spread. Notable examples include the Chinese Mitten Crab *Eriocheir sinensis* Panner, 1938 (Cohen and Carlton 1997; Rudnick et al. 2003) and the European Green Crab *Carcinus maenas* (Grosholz and Ruiz 1995): these species are listed on the IUCN's "100 of the world's worst invasive alien species" (Lowe et al. 2000). For these two decapod crustaceans, the available literature encompasses multiple facets of the introductions and the species are largely seemingly

understood in relation to their invasion dynamics and success. Yet, other species have received relatively little attention, such as *P. elongatus*, but may still offer useful insights into various aspects of invasion ecology.

Anomuran invasions

Petrolisthes elongatus has received a limited amount of interest in relation to its distribution and possible effects on native biodiversity in Tasmania. This lack of interest may be a result of the unknown impacts associated with its introduction and the limited literature identifying the potential detrimental impacts this porcelain crab can achieve over time. It may also be a result of the age of introduction. *Petrolisthes elongatus* was introduced into Tasmania over a century ago, which is much longer as compared to other anomuran crabs such as *Paralithodes camtschatica* (Tilesius, 1815) (1960's – 1970's) and *Petrolisthes armatus* (1990's) (Hollebone and Hay 2007; Zelenina et al. 2008). This historic introduction may result in *P. elongatus* being identified as a “naturalised” species.

Anomuran crabs include species that have invaded intertidal and marine ecosystems globally (e.g., Orlov and Ivanov 1978; Hollebone and Hay 2007; Gribben et al. 2013). These include the intentionally introduced Kamchatka King Crab *Paralithodes camtschatica* and the accidental introductions of both *Petrolisthes armatus* and *Petrolisthes elongatus* (King 1997; Hollebone and Hay 2007; Zelenina et al. 2008; Gribben et al. 2013). The intentional introduction of *P. camtschatica* into the Barents Sea marine ecosystem in the 1960s has drawn much attention since, as a large carnivorous species, it can have vast detrimental impacts on native marine benthic ecosystems. However, the economic gain from introducing and harvesting this species

was concluded to far outweigh the environmental impacts (Jorgensen 2005; Zelenina et al. 2008). Since its introduction, observations and research have revealed a range expansion into Norwegian coastal waters, where deleterious effects on native benthic communities are possible (Jorgensen and Primicerio 2007). The slow growth and late maturation rates of these introduced king crabs were thought to make it an unlikely candidate for a successful accidental introduction; however stable propagule pressure into Barents Sea ensured the survival and growth of the population (Zelenina et al. 2008).

The accidental introduction of *Petrolisthes armatus* to the Atlantic coast of North America in the early 1990's has also received much attention due to the large densities that these porcelain crabs achieve on oyster reefs and the possible impacts (economic and environmental) associated with this habitat along the Georgia coastline (United States) (Hollebone and Hay 2007; Hollebone and Hay 2008). The large filter feeding populations of *P. armatus* (up to 11,000 individuals per m³) may reduce the amount of suspended food resources available for other native filter feeding organisms, thereby possibly impacting other benthic species utilising these reefs as shelter (Hollebone and Hay 2007; Hollebone and Hay 2008). Much like *P. elongatus*, *P. armatus* has been identified as a candidate for mitigation, possible eradication and subsequent monitoring (Harris et al. 2010). These policies include notes on *P. armatus* distribution, densities and possible impacts in the future, such as the destruction of important native benthic ecosystems. Despite these and other studies, *P. armatus* has not been targeted for removal.

Petrolisthes elongatus invasion

The characteristics associated with the successful invasion of both *Petrolisthes armatus* and *Petrolisthes elongatus* are aspect dominance and the associated propagule pressures within populations that overpower the founder effects of native resistance (Hollebone and Hay 2007; Lockwood et al. 2005; Colautti et al. 2006; Johnston et al. 2009; Simberloff 2009). These attributes can also be seen in exemplar invasions such as the introduced green crab *Carcinus maenas*, the northern Pacific seastar *Asterias amurensis* and the introduced kelp *Undaria pinnatifida* (Clayton 1990; Valentine and Johnson 2003; Roman and Palumbi 2004; Hewitt et al. 2005; Ling et al. 2012).

Current observations of introduced *P. elongatus* populations reveal aspect dominance in native ecosystems (Chapter 2), however no other direct or indirect impacts on native species were detected in this study. The impacts of *P. elongatus* in Tasmania are still not completely understood, but could include habitat modification, trophic structure alteration, or mortality of displaced intertidal species and filter feeding benthic species. Introduced species have the ability to alter and modify native ecosystems (Carlton and Geller 1993; Ricciardi et al. 1997; Parker et al. 1999), and *P. elongatus* as a highly fecund introduced species has the potential to modify and damage their invaded ecosystem in Tasmania.

Although this species is not visibly aggressive (Chapter 2), the high biomass detected in populations (Chapter 2) suggests that there will be (or may already have been) ecosystem shift(s). Similar predictions have also been made with the high density populations of the

introduced *Petrolisthes armatus* (Hollebone and Hay 2007). However, historical records are too patchy to note environmental impacts that may have occurred since their invasion.

Habitat modification can lead to the indirect modification of fragile trophic structures (Townsend et al. 1997; Didham et al. 2007). As climate change related range shifts increase (Sorte et al 2010; Poloczanska et al 2011, 2013; Przeslawski et al 2012) the native community in Tasmania will represent a fundamentally different community and may exhibit increased resistance to climate-related invasions from *P. elongatus*. If *P. elongatus* populations become more dominant, a local shift towards filter-feeding communities will also likely place increasing stress on native Tasmanian species that are already present, potentially resulting in indirect competitive stresses.

The prediction of impacts associated with the introduction of *P. elongatus* can only be truly determined through future research efforts. Understanding why an invasion is successful is an important link to determining the strengths and weaknesses of an introduced species. The current lack of literature and knowledge on *P. elongatus* makes it difficult to pinpoint the true impacts of this introduced species. In the past, there has been a focus on *P. elongatus* throughout the concerning larval development, breeding, seasonal changes in native populations, genetics and morphology between native and invaded populations (see; Greenwood 1965; Jones 1977; King 1997; Gribben et al. 2013), yet research identifying invasion characteristics, impacts and invasion pathways has only been touched upon in comparison with other invasive crustacean species.

Future work

Petrolisthes elongatus has successfully established populations around Tasmania and has the potential to spread to other suitable intertidal ecosystems around Tasmania. However, there are a number of important research questions that remain unanswered for this species. Future work could build upon the work by King (1997) who undertook a study to determine the source populations in New Zealand from which Tasmanian populations were derived (King 1997); however her study was limited to southern Tasmania. The need to determine the origins of Tasmanian introduced populations is important in identifying the acceptable abiotic and biotic range limits of *P. elongatus*. At the moment it is known that identical haplotypes are found between North Island New Zealand populations and introduced populations in the south of Tasmania (King 1997). Simultaneously, it is also important to identify the possibility of multiple secondary introductions and anthropogenic hitchhiking mechanisms between Tasmanian intertidal sites. Hence, a more comparative and in depth study identifying origins of introduction between introduced Tasmanian populations and native New Zealand populations of *P. elongatus* is important.

To address this, a comparative annual study between north, east and southern Tasmanian populations will help distinguish local changes in sex ratios and the proportion of ovigerous females. In Chapter 3, some information on this aspect was investigated but this was limited to one site in northern Tasmania and was temporally limited. This study should be expanded to other sites and over multiple years to determine seasonal trends. Identifying differences in populations may reveal biotic and abiotic factors that play a role in controlling or influencing *P. elongatus* populations.

Other future work in correlating introduced population success, biomass and population characteristics to environmental conditions such as temperature and ocean salinity would also be useful. These variables have been noted as influencing size, fecundity and propagule release in intertidal species (Bas and Spivak 2000; Roman 2006). Understanding the effects of environmental factors on introduced *P. elongatus* may lead to identifying a tolerance ranges that could ultimately determine future invasion potentials.

Petrolisthes elongatus has been sighted in Victoria, Australia; although, unconfirmed (Species Bank 2007). The potential for *P. elongatus* to be transferred into Victorian waters, most likely to Port Phillip Bay or Western Port Bay, is presumably high due to the increasing marine traffic between the two states of Tasmania and Victoria. However, as an intertidal benthic species, and dry and semi-dry ballast no longer in use, this greatly reduces the chance of accidental uptake of mature individuals. Species could be transferred via fishing nets and traps as has occurred for other introduced species, such as the jump dispersal movements of *Undaria pinnatifida* in Tasmania via commercial urchin fishers movements.

The possibility also exists for uptake and transfer of larvae and juveniles in the water column. An important step in determining dispersal capability would be to determine whether *P. elongatus* has successfully inoculated Victorian intertidal ecosystems, or if it was a single observation that has since become locally extinct rather than establishing. If established populations are found, it would open up the opportunity to undertake comparative studies between Victoria and Tasmania examining the variables that may be influencing both populations.

Eradication

Eradication efforts on marine and intertidal based introductions are difficult, especially over a large spatial scale, and eradication efforts rarely successful (Culver and Kuris 2000). Response time is important when attempting to eradicate an introduced species (Willan et al. 2000), with the motility of an introduced species potentially influencing eradication success. For example, invasive benthic sessile organisms (i.e., mussels *Dreissena polymorpha* (Pallas, 1771) and *Mytilopsis* spp.) can be removed directly from substrates, while much more effort is required to completely eradicate a highly mobile invasive species like *C. maenas*.

Successful eradications do occur when appropriate actions are taken quickly and efficiently. For example, the introduction of *Mytilopsis* spp. in a marina at Darwin Harbour only took six months to develop a biomass over 20,000 individuals per m² (Willan et al. 2000). However, quick response to this introduction and efforts led by the government and other agencies led to its successful eradication and prevented further spread (Willan et al. 2000; Bax et al. 2003). The impacts associated with this introduced mussel would have affected local infrastructure and aquaculture that provides a substantial input into the local and national economy (Willan et al. 2000; Bax et al. 2003). The eradication in this instance killed all species in the infected marinas and hence left open niches that could have been recolonised by more introduced species. The Northern Territory Government has been vigilant and pro-active in the monitoring the recovery of this system and further invasion (Willan et al. 2000).

Eradication efforts are not always solely focussed on the introduced species itself. In many instances, introduced species hitchhike on native host organisms and can only be successfully

removed if the host is also removed (Culver and Kuris 2000). The eradication of the introduced polychaete *Terebrasabella heterouncinata* in California (accidentally introduced with aquaculture stock enhancement) was conducted via the removal of the preferred native host (Black Turban Snail *Tegula funebris* (Adams, 1854)): over a million host individuals were removed along with other preferred substrate (Culver and Kuris 2000). The eradication effort was successful and led to new proactive methods to remove introduced species (Culver and Kuris 2000). Yet, the impact upon the native ecosystem from the removal of hundreds of thousands of intertidal benthic snails is of concern, as it may impact upon trophic structures.

Conclusions

This research has given insight to several aspects of the population demography of *Petrolisthes elongatus* (distribution, densities, size, reproduction, sex ratios) at the local and coastal scale related to biotic and abiotic factors along the Tasmanian coastlines. The ultimate question is: should efforts be made to mitigate this introduced crab? In the short term, with the limited knowledge available, mitigation would not be feasible. Therefore, the more appropriate path to take would be to investigate the invasion characteristics and impact potential of *P. elongatus*. Through extensive research in both native and introduced ranges, the potential future invasion pathways and more robust information on factors influencing spread can be achieved and can inform the development of future predictions on the impacts of *P. elongatus* in Tasmania. This in turn, can improve the management of a non-indigenous marine species in Tasmania.

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Appendix 1: Geo-referenced species record information around Tasmania (December 2010 – January 2011), where X denotes presence at a locality.

Site No.	Location	<i>Petrolisthes</i>	<i>Paragrapsus</i>	<i>Paragrapsus laevis</i>	Record Coordinates	
		<i>elongatus</i>	<i>quadridentatus</i>		latitude	longitude
1	Smithton	X	X		40° 48' 5.95"S	145° 6' 39.26"E
2	Black River	X	X		40° 50' 33.46"S	145° 18' 44.64"E
3	Boat Harbour	X	X		40° 55' 40.94"S	145° 37' 6.01"E
4	Wynyard	X	X	X	40° 59' 21.91"S	145° 44' 33.95"E
5	Somerset	X			41° 2' 6.18"S	145° 49' 36.36"E
6	Burnie	X	X	X	41° 3' 41.13"S	145° 54' 52.38"E
7	Sulphur Creek	X	X	X	41° 5' 27.14"S	146° 1' 5.76"E
8	Penguin	X	X		41° 6' 46.63"S	146° 4' 23.85"E
9	Ulverstone	X	X		41° 9' 7.23"S	146° 10' 9.37"E
10	Devonport	X	X	X	41° 9' 41.89"S	146° 20' 57.04"E
11	Greens Beach	X	X		41° 5' 0.65"S	146° 44' 35.15"E
12	Low Head	X	X	X	41° 5' 0.53"S	146° 48' 35.71"E
13	George Town	X	X		41° 6' 27.29"S	146° 49' 32.26"E
14	Bell Buoy Bay	X	X		41° 3' 22.06"S	146° 48' 59.67"E
15	Bridport	X	X	X	40° 59' 58.46"S	147° 23' 34.87"E
16	Tomohawk	X	X		40° 52' 11.64"S	147° 45' 59.22"E
17	Boobyalla				40° 52' 42.41"S	147° 52' 43.34"E
18	Little Musselroe Bay	X	X		40° 45' 36.50"S	148° 2' 13.01"E
19	Musselroe Bay		X	X	40° 49' 41.90"S	148° 10' 29.44"E
20	Eddystone Point		X	X	40° 59' 28.54"S	148° 20' 50.52"E
21	Ansons Bay		X	X	41° 2' 15.41"S	148° 16' 15.00"E
22	The Gardens				41° 10' 43.08"S	148° 16' 24.71"E
23	Binalong Bay				41° 14' 53.50"S	148° 18' 38.85"E
24	St. Helens	X	X		41° 19' 47.81"S	148° 14' 59.74"E
25	Beaumaris				41° 24' 55.54"S	148° 16' 46.09"E
26	Scamander		X		41° 27' 45.18"S	148° 15' 52.64"E
27	Falmouth				41° 30' 34.54"S	148° 16' 32.15"E
28	Four Mile Creek				41° 33' 25.61"S	148° 17' 29.57"E
29	Bicheno		X		41° 52' 17.85"S	148° 18' 10.80"E

Appendix 1: Continued

Site	Location	<i>Petrolisthes</i>	<i>Paragrapsus</i>	<i>Paragrapsus laevis</i>	Record Coordinates	
No.		<i>elongatus</i>	<i>quadridentatus</i>		latitude	longitude
30	Swansea		X	X	42° 7' 24.56"S	148° 4' 41.61"E
31	Coles Bay				42° 7' 21.49"S	148° 16' 57.83"E
32	Shelly Point				42° 12' 23.51"S	148° 2' 42.97"E
33	Pontypool				42° 20' 41.96"S	147° 55' 54.40"E
34	Triabunna	X		X	42° 31' 16.85"S	147° 53' 55.38"E
35	Blackman Bay	X	X		42° 50' 51.27"S	147° 50' 32.91"E
36	Dunalley	X	X	X	42° 53' 37.13"S	147° 48' 10.71"E
37	Sunset Beach	X	X	X	42° 54' 31.27"S	147° 49' 18.52"E
38	Eaglehawk Neck	X	X	X	43° 1' 1.24"S	147° 55' 30.93"E
39	Port Arthur	X	X		43° 8' 7.34"S	147° 51' 19.32"E
40	Primrose Sands	X	X		42° 53' 37.51"S	147° 41' 16.67"E
41	Kingston				42° 58' 55.37"S	147° 19' 30.29"E
42	Blackmans Bay	X	X	X	43° 0' 12.95"S	147° 19' 28.95"E
43	Tinderbox	X	X		43° 2' 21.43"S	147° 20' 17.51"E
44	Kettering	X	X		43° 7' 59.75"S	147° 15' 6.78"E
45	Woodbridge	X			43° 9' 29.19"S	147° 14' 28.03"E
46	Gardners Bay		X		43° 11' 1.51"S	147° 5' 49.28"E
47	Deep Bay		X		43° 12' 22.79"S	147° 6' 33.45"E
48	Port Huon		X		43° 9' 36.63"S	146° 57' 23.17"E
49	Dover	X	X		43° 18' 58.80"S	147° 0' 59.90"E
50	Southport	X	X		43° 26' 3.31"S	146° 58' 41.92"E
51	Recherche Bay	X			43° 31' 37.71"S	146° 53' 47.39"E
52	Strahan				42° 9' 17.30"S	145° 19' 36.76"E
53	Long Bay				42° 11' 20.81"S	145° 16' 59.16"E
54	Trial Harbour				41° 55' 49.21"S	145° 10' 29.04"E
55	Granville Harbour				41° 50' 10.39"S	145° 4' 1.84"E
56	Arthur River				41° 3' 22.87"S	144° 39' 27.25"E
57	Marrawah				40° 55' 4.54"S	144° 38' 59.28"E

Appendix 2: Published manuscript

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

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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 (Aqueal 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 Aqueal 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 cinctipes* (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 Marrawah], 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

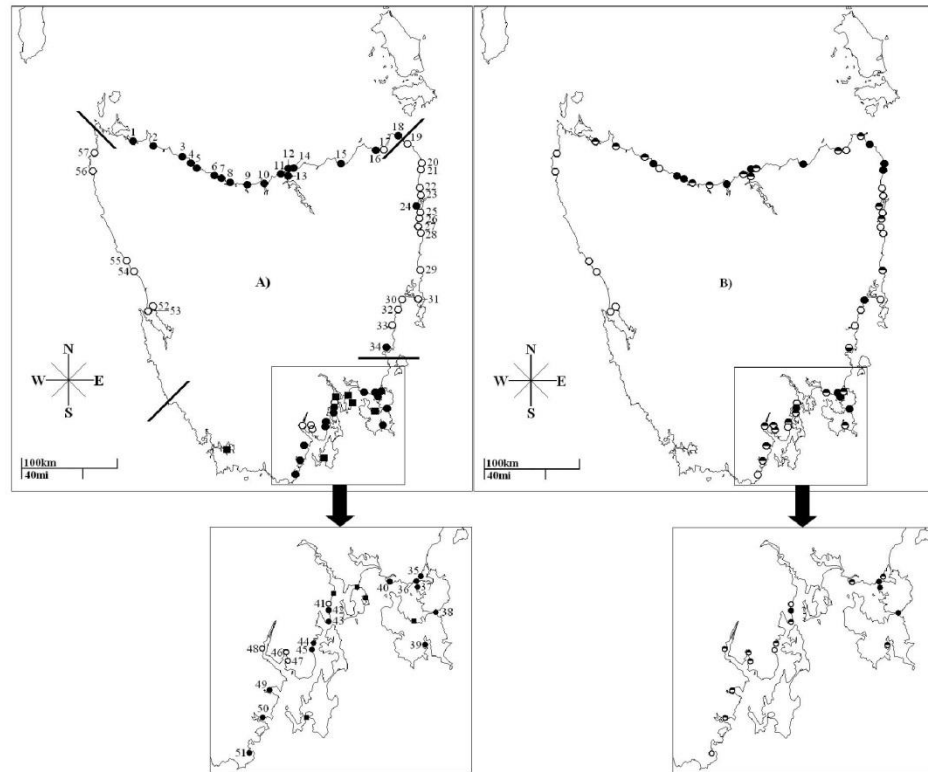


Figure 1. A) Tasmanian distribution of *Petrolisthes elongatus* (introduced species). Filled shapes represent presence; open circles represent absence; squares represent sites found through literature with *P. elongatus* presence. Black bars represent the separation of north, south, east and west. B) 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), Taroona, 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.

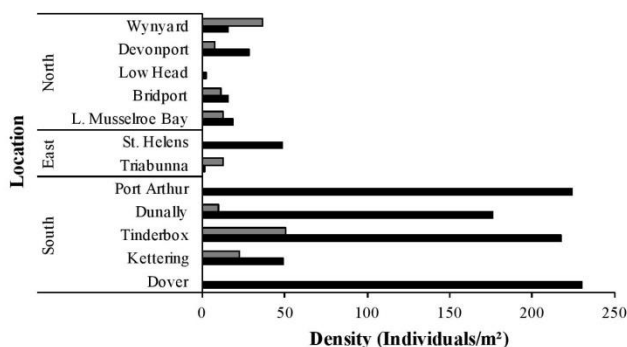
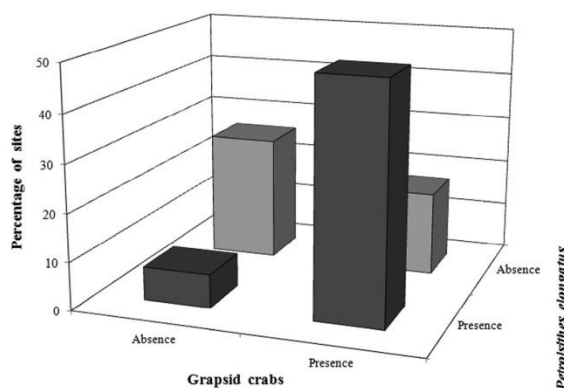


Figure 3. Percentage of Tasmanian sites (n = 57) illustrating the presence or absence of *Petrolisthes elongatus* and the native grapsid crabs *Paragrapsus quadridentatus* and *Paragrapsus laevis*.



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;

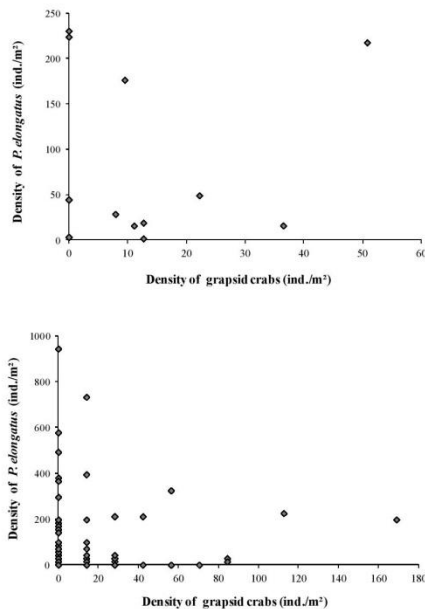


Figure 4. Density of *Petrolisthes elongatus* (y-axis) vs. density of grapsid crabs (x-axis) at site scale (upper chart) and at quadrat scale (lower chart).

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 *Patiriella 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 Valparaíso 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 Valparaíso 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.

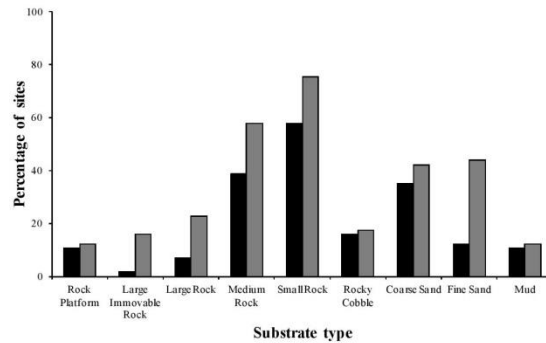
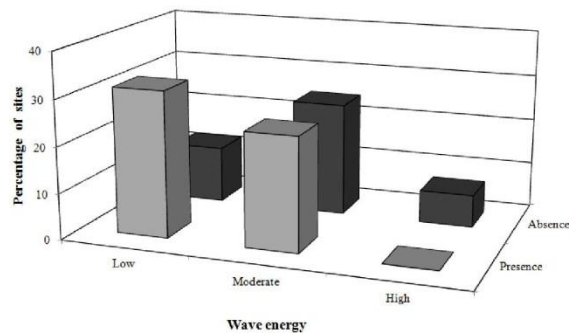


Figure 6. Percentage of sites with *Petrolisthes elongatus* presence and absence in relation to wave exposure levels.



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.

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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_et_al_Supplement.pdf