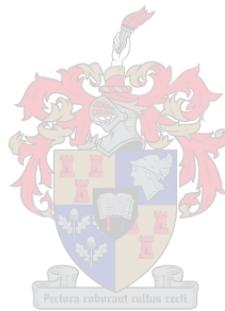


An assessment of invasive predatory marine crabs and the threat they pose along the South African coastline

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Declaration

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Abstract

Invasions by marine alien species are occurring at an unprecedented rate and are known to negatively impact upon society and biodiversity. Due to the weak regulatory forces exerted by native predators, South African intertidal systems could be considered vulnerable to the invasion by predatory crabs. As this group has been suggested as one of the most successful marine invasive taxa and can have negative ecological impacts in recipient regions, mitigating their potential establishment is important. As such the main aim of this study was to review global invasions by predatory crabs, assess their ecological impacts and finally create a watch-list of species that could establish along the South African coastline under both current and predicted future temperature regimes.

As part of the review, a list was developed of all predatory crab species reported as alien. Additionally, their global occurrence, vectors and potential traits associated with their successful establishment were documented. In total, 56 alien crab species were recorded with more than half these being documented in the last two decades. The majority of species originated from the North West Pacific, while the Mediterranean received more alien crabs (33 species) than any other bioregion. Shipping, specifically ballast water, has been responsible for the majority of introductions. Unexpectedly, no biological or ecological traits could be identified as good predictors of establishment success in crabs. While this work identified the most important vectors and most invasive crab families, it emphasises the need for more studies considering the basic biology of these crabs so as to improve our understanding of the traits governing their invasion.

The Environmental Impact Classification for Alien Taxa (EICAT) was used to assess the impacts of the species identified in the review. It was found that impacts had been quantified for only 9% of the 56 alien crab species. Thus, only five species could be allocated EICAT ratings due to the data deficiency of the remaining 51 species. The Japanese shore crab *Hemigrapsus sanguineus* was rated as having Major impacts, while impacts of the remaining four species, the Chinese mitten crab *Eriocheir sinensis*, European shore crab *Carcinus maenas*, Indo-Pacific swimming crab *Charybdis hellerii* and brush-clawed shore crab *Hemigrapsus takanoi* were rated as Moderate.

To create an ordered watch-list for South Africa, species that could be expected to reach the region, on account of the pathways they are associated with, were identified. Their realised temperature ranges were compared to that of each of the four South African marine ecoregions and finally they were ranked based on their EICAT rating. In total, 28 alien crab species had pathways to reach South Africa, with shipping highlighted as the most important pathway. At least 26 species could survive along the South African coast under both present and predicted future temperatures, with warm water species being excluded from the cool west coast and temperate species excluded from the warm east coast. Three species, *H. sanguineus*, *E. sinensis* and *H. takanoi* were placed on the top of the

watch-list due to their negative ecological impacts identified by the EICAT scheme. This study provides the first South African horizon scanning assessment to identify and prioritise potential marine alien species. This watch-list can be used to support at-border management enabling the fast response to new arrivals, ultimately minimising chances of establishment of these alien crabs along South African shores.

This thesis has provided a detailed global review of predatory marine crab invasions. It has highlighted that despite few studies quantifying impacts of these invaders, it is clear that they can have notable ecological impacts in recipient regions. Nonetheless, there is a dire need for more research into their impacts so as to support evidence based management. Until such evidence becomes available it is suggested that a precautionary approach be applied when managing alien crabs.

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Introduction

Following the trend of terrestrial (Richardson et al. 2000), freshwater (Sala et al. 2000) and estuarine systems (Ruiz et al. 1999), marine biological invasions have received increasing attention in the scientific literature over the last 30 years (Lodge 1993; Ruiz et al. 2000; Mead et al. 2011a, b; Katsanevakis et al. 2014a). This reflects the rise in the number and rate of invasions around the globe (Wonham and Carlton 2005; Simberloff et al. 2013; Seebens et al. 2017) and the scale of their ecological, economic and social impacts (Pyšek and Richardson 2010; Katsanevakis et al. 2014b). The increasing number of species introduced to areas outside of their native range can be attributed to an increase in suitable pathways and associated vectors, global connectedness and intensification of global trade (Whinam et al. 2005; Wilson et al. 2009; Ruiz et al. 2011), which are a result of the escalating needs of our growing and changing population (Bax et al. 2003). Although some species are introduced intentionally for the purpose of aquaculture and mariculture (Ruesink et al. 2005; Mead et al. 2011b), a portion of successful invasions occur as a result of accidental introductions (Lonhart 2009).

Confusion between terms and ambiguities among definitions in the field of biological invasions are well recognised (Colautti and MacIsaac 2004; Falk-Petersen et al. 2006). This study defines alien or non-indigenous species as those whose presence in a region is attributable to human actions that enabled them to overcome fundamental biogeographical barriers (i.e. human-mediated extra-range dispersal (Robinson et al. 2016). In contrast, invasive species are considered to be those alien species that have self-replacing populations over several generations and have spread from their point of introduction (Robinson et al. 2016). This definition of invasive species excludes the requirement of impact (as applied by the Convention on Biological Diversity (CBD 2013)). This is because recent developments in the field have acknowledged that by their very presence, alien species have impact and thus a more appropriate measure of invasiveness is actually spread. Following work by Blackburn et al. (2011), before a species can be considered invasive, it must pass through the four stages of the invasion process i.e. transport, introduction, establishment and natural range expansion. These stages are separated by numerous biotic and abiotic barriers that must be overcome to move to the next stage (Fig. i). These barriers include geographic and environmental barriers, as well as barriers to captivity, survival, reproduction and dispersal (Blackburn et al. 2011). Together, alien and invasive species constitute one of the largest threats to biodiversity and ecosystem functioning (Crooks 2002; Grosholz 2002; Vilà et al. 2011). Invasive species can also severely impact the ecology of the invaded

ranges as well as socio-economic values and human health (Pimentel et al. 2001; Binimelis et al. 2008; Simberloff et al. 2013; Hulme 2014). The severity of these impacts has led to an urgency to identify these species, the drivers behind their invasive ability and their resulting impacts (Ruiz et al. 1997; Grosholz 2002; Jeschke et al. 2014).

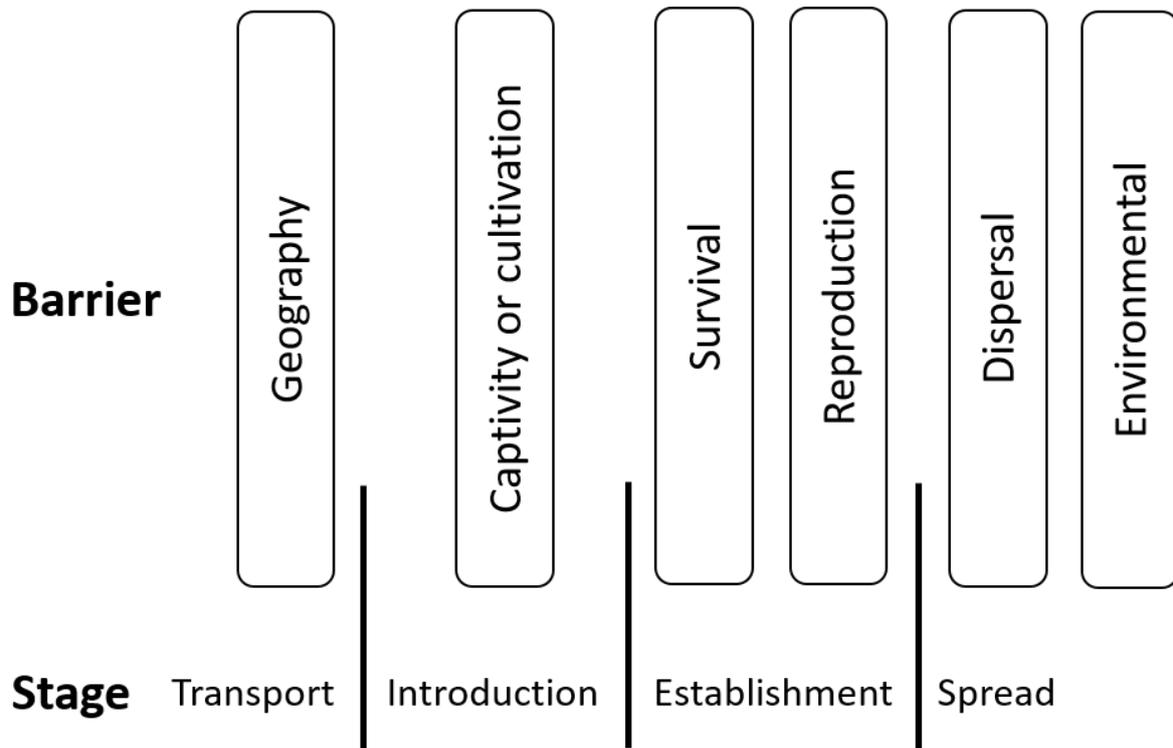


Figure 1 A schematic diagram representing the Blackburn et al. (2011) framework for biological invasions showing how the invasion process can be divided into four stages, each separated by biotic and abiotic barriers that must be overcome for a species to advance to the next stage.

Factors contributing to invasion success

Invasion history currently offers one of the best basis for predicting future invasion success (Hayes and Barry 2008; Richardson and Rejmánek 2011; Hulme 2012; Zaiko et al. 2014). This is thought to be due to species with an invasion history possessing traits that contribute to their successful invasion (Ehrlich 1989) and secondly their established association with vectors (Hayes and Sliwa 2003) increasing their chances of invading again. There is, however, a concern that this approach does not account for species with no invasion history, despite them possessing the potential to invade (Hayes and Sliwa 2003; Ricciardi 2003). Despite this concern, invasion history is still used as it offers a good model in the absence of other predictive models (Kolar and Lodge 2002; Hayes and Barry 2008;

Faulkner et al. 2014; Novoa et al. 2015). In addition, several exogenous and endogenous factors are often correlated with successful invasions. The interaction of these factors, in combination with optimal timing, determines invasion success (Crawley 1989; Ehrlich 1989).

Exogenous factors

Vector strength

Pathways and vectors play a pivotal role in successful introductions (Ruiz et al. 2000; Padilla and Williams 2004; Hulme et al. 2008). Pathways are recognised as the route by which species are transported and introduced whereas the associated vectors are the physical means of transport. Over the last few centuries, there has been a global increase in suitable pathways and associated vectors (Wilson et al. 2009) to meet the needs of the growing and changing population. This has enabled the faster transportation of more species to more habitats (Grosholz 2002), providing much potential for future introductions of marine alien species (Wonham et al. 2000; Mead et al. 2011a). Important pathways include shipping, man-made ocean canals such as the Suez-Canal (Galil et al. 2015), mariculture operations (Grosholz et al. 2015), the aquarium and pet trade (Padilla and Williams 2004) and live seafood (Ruiz et al. 2011). Shipping is well recognised as the primary pathway for the introduction of species to coastal systems (Carlton 1985; Griffiths et al. 2009; Hewitt et al. 2009; Mead et al. 2011a). Hull fouling is recognised as the main shipping related vector (Hewitt et al. 2009; Mead et al. 2011b) and has recently increased in importance. This is mainly due to the banning of Tributyltin (TBT)-based anti-fouling paints, which were previously used as an effective method for preventing hull fouling of small and commercial vessels (Smith et al. 2008). The banning of this substance was pursued due to its toxicity and negative impacts on coastal systems (IMO 2001), but has concurrently resulted in an increased prevalence of fouling. Ballast water is another important shipping vector and is responsible for transferring species present in the water column or associated sediments (Wonham et al. 2001; Hewitt et al. 2009; Albert et al. 2013). Mariculture is one of the fastest growing food production sectors (De Silva 2012). It is based, to a large extent, on the farming of non-native species including fish, molluscs, crustaceans and aquatic plants (Naylor et al. 2001; De Silva 2012). It has, therefore, been responsible for the intentional introduction of these taxa as well as the unintentional introduction of numerous associated species, pathogens and parasites inadvertently transferred with the target species (Naylor et al. 2001; Grosholz et al. 2015). Likewise, the ornamental pet and aquarium trade is a growing multi-billion dollar industry and includes the trade in thousands of foreign species. Many of these species are introduced and can become established in natural waters when they are released by the owners (Padilla and Williams 2004; Cohen et al. 2007; Gertzen et al. 2008;

Williams et al. 2012). The importance of the live seafood trade as a vector is increasing (Weigle et al. 2005; Wang et al. 2006; Minchin 2007) due to the increasing demands for the importation of these species by the different consumer markets (Ng 1998). Species are imported from around the globe after which they can be released or escape into the wild (Dittel and Epifanio 2009).

Native range size

Large native ranges can play an important role in the successful introduction of species to new areas (Hayes and Barry 2008; Novoa et al. 2015). A few explanations have been proposed as to why this is. Firstly, larger native ranges can attribute to a higher transport frequency and introductions of more individuals (Wonham et al. 2000; Jeschke and Strayer 2006). Secondly, increased introductions are thought to result in populations that are more genetically diverse (Genton et al. 2005), which is an important characteristic that enhances chances of successful establishment and invasion (Sakai et al. 2001). Thirdly, species from larger native ranges may be generalists when it comes to resource acquisition and habitat use, allowing them to more easily adapt to new environments (Brown 1995). Lastly, it has been suggested that these species are also more likely to have broad tolerance ranges to environmental conditions and therefore more climatically suited to a wider range of environmental conditions and habitats (Pyšek and Richardson 2008).

Propagule pressure

Propagule pressure refers to the number of individuals introduced and the number of introduction events of an alien species into a recipient area (Lockwood et al. 2005). High propagule pressure increases the genetic diversity of the alien species in the recipient habitat (Ahlroth et al. 2003; Lawson Handley et al. 2011), as well as the probability of such species encountering favourable environmental conditions when arriving (Lockwood et al. 2005). It is therefore an important determinant of successful establishment and invasion of alien species (Colautti et al. 2006; Simberloff 2009).

Climate change

Global climate is changing at an unprecedented rate and is predicted to alter thermal regimes and climatic conditions in the future (Occhipinti-Ambrogi 2007; Rouault et al. 2010; IPCC 2014). In the marine realm, climate change is expected to result in a variety of physical changes in the ocean environment including changes in water temperatures, salinity, ice cover and elevated CO₂ levels (Gibson and Najjar 2000; Occhipinti-Ambrogi 2007; Rahel and Olden 2008). It has been suggested that altered thermal regimes could ultimately contribute to increased invasion success of alien species (Walther et al. 2009; Sorte et al. 2010). This could occur via numerous mechanisms. Firstly, such changes are anticipated to enable species presently restricted in their distribution due to narrow

tolerance ranges to extend their range and establish in areas previously unsuitable for their survival (Stachowicz et al. 2002a; Whitney and Gabler 2008; Sorte et al. 2010; Zerebecki and Sorte 2011). Warmer water for example, will lead to an increase in suitable habitat for warm water species, allowing them to extend their range to previously inaccessible colder areas (Rahel and Olden 2008). Secondly, it might lead to increased growth, reproduction (Sorte et al. 2010), competitive dominance and native prey consumption, all of which could ultimately increase the survival of alien species (Rahel and Olden 2008). Lastly, changes in thermal regimes could alter native species diversity and community composition which could facilitate the establishment of alien species (Helmuth et al. 2002; Lord 2017).

Nature of the recipient habitat

The physical characteristics (Airoldi et al. 2015) and climatic conditions of the recipient habitat (Faulkner et al. 2014) are very important in determining whether an introduced species will be able to establish and invade an area. Furthermore, the climatic similarity of the recipient habitats and the native ranges of the invading species have been proposed as an important predictor of invasion success (Richardson et al. 2011; Seebens et al. 2013; Novoa et al. 2015) as species are usually limited by their physiological tolerance ranges (Ashton et al. 2007).

Human altered systems (Mascaro et al. 2013) disturbed and polluted habitats (Clark and Johnston 2011; Crooks et al. 2011) and man-made structures including seawalls, marinas, ports and harbours in particular, support high numbers of alien and invasive marine species (Bulleri and Airoldi 2005; Glasby et al. 2007). This pattern can be driven by numerous factors. Firstly, native diversity is often depressed in these disturbed habitats (Ordóñez et al. 2013; Airoldi et al. 2015). Secondly, artificial habitats provide not only novel habitat types for intertidal and subtidal species (Arenas et al. 2006; Bulleri and Chapman 2010), but can also provide shelter from harsh environmental conditions (Bulleri and Chapman 2004). Lastly, artificial habitats commonly occur in areas with frequent shipping and aquaculture activities, contributing to increased propagule pressure of alien species (Wasson et al. 2005; Bulleri and Chapman 2010).

Status of native communities

The status of the recipient community is important in determining the persistence, abundance, range expansion and ultimately invasion success of newly arriving species (Grosholz 2002; Miller et al. 2002). The combination of native predators, competitors, pathogens, parasites, previously introduced species (Vermeij 1996; Simberloff and Von Holle 1999; Keane and Crawley 2002), biotic interactions

(Robinson et al. 2015) and availability of resources (Davis 2003) plays an important role in the environment's invasibility.

Numerous hypotheses have been developed to explain these complex interactions between invasive species and their recipient communities in an attempt to explain their role in invasion success. The oldest of these hypotheses is that of biotic resistance (Elton 1958). The diversity driven biotic resistance hypothesis suggests that communities with high species diversity are more resistant to invasions. The underlying mechanism is thought to be increased competition for resources, which leaves fewer resources available for invaders (Elton 1958; Stachowicz et al. 2002b). Disturbed environments where extinction and overexploitation are high, are therefore commonly invaded because of decreased diversity and reduced biotic resistance (Vermeij 1991; Simberloff and Von Holle 1999). This initial hypothesis has since been extended to include predation-driven biotic resistance where predation by native predators is thought to resist invasions (Reusch 1998; Shinen et al. 2009).

In contrast to predator-driven biotic resistance, the enemy release hypothesis suggests that introduced species will be free from the pressures of natural enemies in their introduced range. This hypothesis makes the following three assumptions: 1) specialist enemies of the alien species are absent in the introduced region; 2) native enemies will not affect alien species; and 3) generalist enemies will have a bigger impact on the native competitors than on the alien competitor (Keane and Crawley 2002). If these assumptions hold, then alien prey species will be able to rapidly increase their abundance and distribution. In addition, in the absence of natural enemies, alien species can invest fewer resources towards predator defence, allowing more resources to be allocated towards growth and reproduction (Keane and Crawley 2002).

The absence of natural enemies has been proposed as one of the mechanism contributing to increased competitive ability of alien species. This is encapsulated in the evolution of increased competitive ability hypothesis (Blossey and Nötzold 1995). The development of novel weapons hypothesis has been proposed as an alternative mechanism for increased competitive ability. It suggests that some invaders have a competitive advantage over native species as they possess new biochemicals and microbes, or novel weapons, that native species have never encountered before nor had the chance to adapt to (Callaway and Ridenour 2004). These function as allelopathic agents and negatively affect the growth, reproduction and survival of native species, supplying alien species with a distinct advantage (Callaway and Ridenour 2004).

The notion that frequently invaded systems with a high numbers of alien species are more susceptible to future invasions than non-invaded systems is one that has been proposed numerous times in the

invasion biology literature (Ehrlich 1989; Ruiz et al. 1997; Bax et al. 2003). It was Simberloff and Von Holle (1999) that explored this phenomenon experimentally and termed it the invasional meltdown theory. This hypothesis suggests that as the cumulative number of introductions and invaders increase, a threshold of invasion pressure is reached, causing the structure of the community to collapse, making the community more susceptible to future invasions. The combined impact of these species is often more severe than that of their individual impacts and leads to an increased magnitude of impacts on native ecosystems (Simberloff and Von Holle 1999)

Another factor fundamental to the invasion success of species, is that of niche opportunities (Shea and Chesson 2002). Ecological niches can be described as the functional role of an organism within the ecosystem or trophic web (Elton 1927) or the interaction with its environment (Chesson 2000; Pulliam 2000; Schoener 2009). Empty niches within communities are very common (Walker and Valentine 1984; Chown et al. 1998; Whinam et al. 2005) and may be as a result of a specific role that has not been filled or species that are absent as they have never arrived or evolved in situ (Walker and Valentine 1984; Schoener 2009; Lloyd-Smith 2013). Empty niches can be filled (Lekevičius 2009) if the species possess the appropriate characteristics to fill the niche (Pulliam 2000; Schoener 2009), when there are sufficient resources available in the ecosystem (Armstrong and McGehee 1980) and if the invaded and native habitat of the alien species are climatically similar (Novoa et al. 2015). According to the empty niche hypothesis, ecosystems with empty niches are more vulnerable to invasion by alien species (Shea and Chesson 2002), firstly as invasive species may possess traits which enhance their ability to take advantage of these open niches (Airoldi and Bulleri 2011) and secondly as a result of decreased biotic resistance, limited resource opportunities for natives, decreased competition and low abundance of natural enemies in empty niches (Udvardy 1969; Preisler et al. 2009).

Endogenous traits of invasive species

Traits are the measurable characteristics of the organism which are usually allocated at species level (McGill et al. 2006). Certain traits can predispose species to become successful invaders in new ranges and identifying these traits associated with invasiveness can be useful for managing future introductions and invasions (Pyšek and Richardson 2007; Blackburn et al. 2011; Novoa et al. 2015). In addition, comparing traits between invasive and alien species have been proposed as important to determine characteristics that makes a species a successful invader (Radford and Cousens 2000; Kolar and Lodge 2001; Dick et al. 2014). Some of the ecologically important traits that can affect the success of alien marine species include those that maximise survival, growth and reproduction (Table i).

Table i Traits that have been identified as being beneficial to invaders in each stage of the invasion process.

Colonisation	Establishment	Range expansion
<ul style="list-style-type: none"> • R-selected life history strategy (Sakai et al. 2001) <ul style="list-style-type: none"> ○ Short generation time ○ Rapid growth rate ○ Rapid sexual maturation ○ High Fecundity • Generalist <ul style="list-style-type: none"> ○ Broad environmental tolerances (Marvier et al. 2004) ○ Diverse diet (Snyder and Evans 2006) • High genetic diversity (Roman and Darling 2007) and phenotypic plasticity (Troost 2010) 	<ul style="list-style-type: none"> • Ecosystem engineer (Cuddington and Hastings 2004) • Heightened competitive ability (Callaway and Ridenour 2004) • Adult longevity (Kolar and Lodge 2001) • Multiple reproductive strategies (sexual and asexual (Sakai et al. 2001)) • High genetic diversity (Roman and Darling 2007) and phenotypic plasticity (Troost 2010) • Gregarious behaviour (Lodge 1993) 	<ul style="list-style-type: none"> • High dispersal ability (Viard et al. 2006)

Crabs as invasive predators

Crabs are considered to be amongst one of the most successful marine invasive taxa (Grosholz and Ruiz 2003; Kraemer et al. 2007; Hänfling et al. 2011; Brousseau and McSweeney 2016) with predatory, intertidal crabs comprising the majority of these invaders (Brockerhoff and McLay 2011). It should be noted that crabs are in most cases generalist opportunistic predators that switch between feeding modes (Wieczorek and Hooper 1995; Jiang et al. 1998; Rudnick and Resh 2005). As such, crabs are considered “predators” when they, in addition to other food sources, also prey upon animals. As a group, crabs occupy a variety of marine, estuarine, freshwater and terrestrial habitats, with some species occurring in a combination of these (Ng et al. 2008). Their successfulness is thought to be facilitated by their generalist behaviour in terms of food (Rudnick and Resh 2005; Brockerhoff and McLay 2011), habitat (Veilleux and de Lafontaine 2007) and salinity tolerance (Dittel and Epifanio 2009; Hänfling et al. 2011) coupled with a competitive and aggressive nature (Grosholz et al. 2000; Weis 2010; Epifanio 2013). The success of certain species have been attributed to traits such as migratory behaviour, high larval dispersal potential, elevated fecundity, early sexual maturation, long larval development (Paula and Hartnoll 1989; Weis 2010; Hänfling et al. 2011; Brousseau and

McSweeney 2016) and potential for range changes following climate change (Roman 2006; de Rivera et al. 2007a; Katsanevakis et al. 2011). Another factor that has been found to play a role in the success of certain populations of alien crabs is the enemy release hypothesis. Alien population of the European shore crab, *Carcinus maenas* for example, has been found to be less infected by parasites which normally suppress the performance of native populations in Europe. This release from parasites are believed to be the reason for the crab's better performance and its success as an invader in its introduced ranges (Torchin et al. 2001).

Crabs are globally associated with significant ecological (Kraemer et al. 2007; Rudnick et al. 2005a; Dauvin et al. 2009; Garbary et al. 2014), socio-economic (Lafferty and Kuris 1996; Normant et al. 2002) and health impacts in both their native and invaded ranges (Chakraborty et al. 2002). Some common socio-economic impacts associated with crabs include destroying natural and man-made bank structure through burrowing (Panning 1939; Rudnick et al. 2000; Rudnick et al. 2005b), infiltrating drinking water plants during migrations (Foss and Veldhuizen 2001), damaging fishing nets (Normant et al. 2002; Beqiraj and Kashta 2010) and significantly impacting commercial fisheries by predation on commercially important species (Boulding and Hay 1984; Rudnick and Resh 2002). The Chinese mitten crab *Eriocheir sinensis* has also been reported to be a health hazard in its native range through its role as an intermediate host to the human lung fluke (Ingle 1986). Through their role as aggressive predators (Clark et al. 1999; Grosholz et al. 2000) and competitors (Normant et al. 2002) and through their strong top-down predator control (Grosholz et al. 2000), alien crabs have been found to significantly affect the abundance and structure of native communities (Ross et al. 2004; Brousseau et al. 2014), alter food webs (Grosholz et al. 2000; Kimbro et al. 2009), biotic interactions (Forsström et al. 2015) and ecosystem functioning (Grosholz and Ruiz 1995).

The South African context

Intertidal and shallow nearshore habitats along the South African coastline are well studied. While much research focused on describing the biodiversity in intertidal systems along the coastline (Stephenson 1948; Day 1974; Blamey and Branch 2009), a large amount of work also focused on identifying the abiotic (McQuaid and Branch 1984; McQuaid and Dower 1990; Field and Griffiths 1991) and biotic drivers and interactions structuring these biotic communities (Branch 1985; Branch et al. 1987; Bosman and Hockey 1988; Van Zyl and Robertson 1991). From this work, it is evident that predators are not strong regulators of community structure along this coastline (Bustamante and Branch 1996) and thus this region is considered depauperate of dominant marine intertidal predators that are typical of such systems elsewhere (for example see Connell 1970 and Menge 1976).

Based on the empty niche hypothesis (Shea and Chesson 2002), it is predicted that systems that have few species in a specific functional group would be vulnerable to invasion by that functional group. As such, systems like those in South Africa that are depauperate of the dominant benthic predators that typify such systems elsewhere (Bustamante and Branch 1996), could be predicted to be vulnerable to invasions by such predators. Considering that the introduction of alien species has been identified as a significant factor influencing community structure within intertidal systems (Branch et al. 2008) and that predators that have been introduced into marine systems have had notable impacts on native communities (Dick and Platvoet 2000; Normant et al. 2002; Ross et al. 2004), their introduction into the South African intertidal system would be of great concern.

To date, two crabs have invaded the South African coast, i.e. the European shore crab *Carcinus maenas* (Le Roux et al. 1990) and the Mediterranean shore crab *C. aestuarii* (Geller et al. 1997). Despite *C. maenas* globally having a wide-spread alien range (Carlton and Cohen 2003) and the fact that it has become one of the most damaging predators in nearshore communities in North America (Grosholz et al. 2002), in South Africa it is currently confined to two harbours along the Cape Peninsula (Mabin et al. in press). The reasons behind its restricted range are not well-understood, but are thought to result from an inability to survive on this wave-exposed coast (Hampton and Griffiths 2007) in combination with predation by native fish (Mabin et al. in press). In contrast, *C. aestuarii* is believed to no longer occur in the region and has not been detected here since 1997 (Robinson et al. 2005).

Rationale behind this study

Despite the prediction that the South African intertidal and nearshore is vulnerable to invasions by benthic predators, there has to date been no invasions of dominant predators (besides *C. maenas*) along this coastline. This provides an opportunity for managing authorities to institute pre-emptive monitoring and management plans that could help to reduce the threat of an invasion and the associated negative impacts.

In light of this, the present study aimed to 1) compile a review of invasions by marine predatory brachyuran crabs, so as to gain an understanding of their invasion patterns and vectors as well as traits associated with their successful establishment; 2) undertake a global assessment of the ecological impacts of these crabs; and 3) develop a watch-list of marine predatory crabs that could pose a threat along the South African coast.

Chapter 1: Patterns, vectors and traits associated with alien predatory crabs

Predatory crabs are considered amongst the most successful marine invasive groups and reflecting this, have received much attention in the literature. However, the majority of studies have been descriptive in nature or biased towards specific species or regions, while seldom considering traits or factors associated with invasiveness. As such, this study aimed to review invasions by this group. A total of 56 alien marine predatory crab species belonging to 15 families were identified as having spread outside their native ranges. The family Portunidae supported the highest number of alien crabs. The majority of crabs had their origin in the North West Pacific whereas the Mediterranean Sea was the most invaded bioregion. Although a series of pathways have played a role in the introduction of alien crabs, shipping and specifically ballast water has been responsible for the majority of these introductions. The rate of discovery of alien crab species has increased exponentially over the past two centuries, with more than half of known alien species being discovered in last two decades. Although this pattern might have been influenced by an increase in search efforts, an increase in crab introductions cannot be disregarded. Biological trait analysis could only be undertaken for 28 of the 56 species due to a lack of information for the remaining species. Unexpectedly, no suites of traits associated with the successful establishment of crabs could be identified, but this finding might have been as a result of the paucity of data. While this study revealed that invasions by crabs and the drivers behind their success remain largely unpredictable, it also highlighted the most invasive crab families, the important vectors and the most common donating and receiving regions. Such information can be important in directing management strategies aimed at minimising the risk of introduction of alien crabs.

Introduction

Studies reviewing the distribution and vectors of marine alien species are numerous and include those that focus at the global scale (Carlton 1996; Bax et al. 2003; Ruiz et al. 2011) as well as region specific studies (e.g. America (Ruiz et al. 2000); Australia (Hewitt et al. 2004a); Europe (Galil et al. 2014); Mediterranean (Zenetos et al. 2010); South Africa (Mead et al. 2011a, b)). However, these studies are often descriptive in nature, providing first insights into the marine invasions in a region. Recently there has been a move to advance this approach by identifying recipient regions and vectors associated with alien taxa as well as applying biological trait analysis to identify taxa that are likely to become invaders. The use of these analyses add statistical power to the conclusions drawn about the factors that may

play a role in the spread and establishment of alien species (Cardeccia et al. in press). An additional approach to understanding patterns of invasions comes in the form of taxon specific reviews (Çinar 2013; Nawrot et al. 2015; Zhan et al. 2015; Marchini and Cardeccia 2017). Such reviews can be insightful as they focus on highly invasive taxa from well-studied groups, enabling detailed analyses of factors driving their invasion success (Kolar and Lodge 2002; Hänfling et al. 2011).

Crabs are a taxon that has become a globally successful invasive group (Brockerhoff and McLay 2011; Jormalainen et al. 2016), associated with significant ecological (Kraemer et al. 2007; Garbary et al. 2014) and socio-economic impacts (White et al. 2000; Chakraborty et al. 2002). These impacts likely reflect that crabs are a highly diverse group, known from a variety of marine habitats (Ng et al. 2008) with an ability to adapt to a range of salinity and temperature conditions (Dittel and Epifanio 2009). This group is further described as possessing good dispersal abilities (Gust and Inglis 2006) and high reproductive potential (Brousseau and McSweeney 2016).

In light of the large invasive ranges and notable impacts associated with some crab species (e.g. *Hemigrapsus sanguineus* (Kraemer et al. 2007); *Charybdis hellerii* (Felder et al. 2009) and *Carcinus maenas* (de Rivera et al. 2011)), crab invasions have received considerable attention in the literature. However, studies considering these crab invasions have been mostly region specific (e.g. America (Rathbun 1925); Laccadive Archipelago (Sankarankutty 1961); Mediterranean (García Muñoz et al. 2008)) or species specific (e.g. *Callinectes sapidus* (Millikin and Williams 1984); *Eriocheir sinensis* (Veilleux and de Lafontaine 2007)). Some species specific studies have considered traits, generally applying one of two approaches: comparing the traits of alien crab species in both their native and invaded ranges (Grosholz and Ruiz 2003) or comparing traits between an established alien crab and native crabs in a particular region (Brousseau and McSweeney 2016). However, these studies were species specific, biased towards commonly known crab invaders and considered only a few selected traits, thus not revealing general patterns about the invasiveness of crabs as a group. While there has been one review of crab invasions (Brockerhoff and McLay 2011), this study was broad in its taxonomic focus (i.e. considered brachyuran crabs as well as two families from the crab-like anomuran decapods (i.e. Lithodidae and Porcellanidae)), considered invasions in shallow water and offshore environments and has become outdated. While this work did consider the role of one trait (i.e. egg size) in invasion success, it used a limited number of species to do so. This limited sample size and the use of only a single trait prohibited broadly applicable conclusions. A multi-species, multi-trait approach to investigate crabs as a group, with the specific aim to identify traits profiles specifically associated with the successful invasion of predatory crabs is thus lacking.

Thus in an effort to gain insight into predatory crab invasions, that may ultimately affect the South African coast, this chapter reviewed all reported invasions within this taxonomic group. The specific aims of this study were to 1) compile a list of predatory crabs that have an invasion history (i.e. they have been recorded outside their native range); 2) document the donor and receiving bioregions of these alien species; 3) identify vectors associated with the transfer of these predators; 4) determine rate of discovery of crab invasions; and 5) consider traits that may be associated with their successful establishment. Based on the literature (Crawley 1989; Ehrlich 1989; Weis 2010; Hänfling et al. 2011) it was hypothesised that traits that predispose species to being able to survive under a variety of conditions would typify crab species that have been reported as having established alien populations. In contrast, traits that facilitate transfer by humans (e.g. adult longevity and long larval development) would be shared by both established alien species and those that are represented by only single records outside of their native ranges. A broad global review of this group will provide a baseline of their global occurrence and provide the first assessment of the complex drivers of the invasion processes associated with this group. These outcomes are important tools for developing management strategies aimed at minimising the risk of introduction (Faulkner et al. 2014; Zaiko et al. 2014).

Methods

Species and variables reviewed

To compile a list of predatory crabs with an invasion history, this chapter reviewed the literature reporting on marine crab invasions across the globe. Species were classified to family level following the World Registry of Marine Species (WoRMS). Information regarding each species in both their native and alien ranges was recorded (Table 1.1). Species were included if they were fully marine or catadromous. Species placed on the list included predatory crabs classified as alien as per the definition of Robinson et al. (2016). As crabs switch between feeding modes depending on food availability, crab species were classified as “predators” if the species has been recorded to actively prey upon animals at some stage. The species that were included were thus not always specialised predators, but also opportunistic or generalist predators. Species recorded in the literature as being herbivorous or detritivorous, with no reference to preying upon animals, were, however, excluded. Species were also excluded from the list when it could not be established from the literature if they are predators or not. Species were also excluded when no information was available on their native range. These exclusion criteria resulted in the exclusion of 42 species.

Information was sourced from a variety of well-known online databases. The most often used were WRIMS: World Register of Introduced Marine Species (www.marinespecies.org/introduced/), CABI: Centre for Agriculture and Biosciences International (www.cabi.org/), GISD: Global Invasive Species Database (<http://www.iucngisd.org/gisd/>), CIESM: The Mediterranean Science Commission Atlas of exotic crustaceans in the Mediterranean (<http://www.ciesm.org/atlas/index.html>). Smaller regional databases were used when appropriate. Additional sources of information used included peer-reviewed articles, published books, technical reports and online theses, all sourced using the browser Google Scholar® (see Appendix 1.1 for a complete list of all sources). Compilation of the species list was done between September and November 2015, while the extraction of relevant information was done between November 2015 and February 2016.

Table 1.1 Information that was recorded for each predatory crab in their native and alien ranges.

Variables	Data recorded
Invasion status	Species reported only from a single record or established populations
Distribution range	Using reports in the literature species ranges were defined in terms of provinces (as defined by Spalding et al. (2007)). If a species had been reported from a location within a province, its distribution was taken to include that whole province
Donating and receiving regions	These regions were defined following the IUCN bioregions defined by Kelleher et al. (1995a, b, c, d)
Vectors	This was based on the literature and included ship fouling, ballast water, solid ballast, yacht fouling, Suez Canal, freshwater canals, aquarium trade, live seafood, aquaculture products, intentional release and unknown if vector was not known
Date of first discovery	Extracted from the literature
Biological traits	Size, adult longevity, adult mobility, fecundity, migratory behaviour, larval development time, generation time (See Table 1.2 for details)
Ecological traits	Range size, substratum type (See Table 1.2 for details)

It has been suggested that the most appropriate method for characterising traits of invasive species is to compare invaders with those of the same taxonomic group that have not spread outside their native ranges (Nawrot et al. 2015; Novoa et al. 2015). While the strengths of this approach are clear, it was not viable to do so for crabs. This was because this group is large (containing 1271 genera and an

estimated 6793 described species (Ng et al. 2008)) and widely distributed, occurring on all continents. In addition, trait information simply is not available for most species. While this approach was pursued using species from a well-studied region (i.e. China using the Chinese Registry of Marine Species ChaRMS), trait information was available for less than 3% of crab species, resulting in the abandonment of this methodology. As a result, to get a better understanding of the patterns of crab invasions and which traits may play a role in the successful invasion of these crabs, I compared those alien species that have been documented as supporting established populations with those species for which no evidence exists for their successful establishment. Single record species were defined as those with single or sporadic recordings of one or a few individuals with no evidence of self-sustaining populations. In contrast, established species were defined as those with self-sustaining populations. To assess if the number of established species is related to the number of alien species known from a family, a Spearman's rank correlation was undertaken between the number of alien species and established species known from each family. All univariate analyses were done in Statistica 13.

Distribution ranges

Native and invaded range sizes were determined for each species. Range size was defined as the number of provinces (as defined by Spalding et al. 2007) in which a species occurred. The relationship between native and invaded range was investigated using a Spearman's rank correlation.

Donating and recipient regions

In this study donating and receiving regions were defined in terms of the 18 IUCN bioregions (Kelleher et al. 1995 a, b, c, d; Fig. 1.1). Information was extracted from the literature and if the donating region was not noted for a particular species, this was identified based on the most likely shipping routes, as suggested by Seebens et al. (2013). The package *circlize* in R version 3.3.2 was used to visualise the relationships between the various regions through the use of a chord diagram.

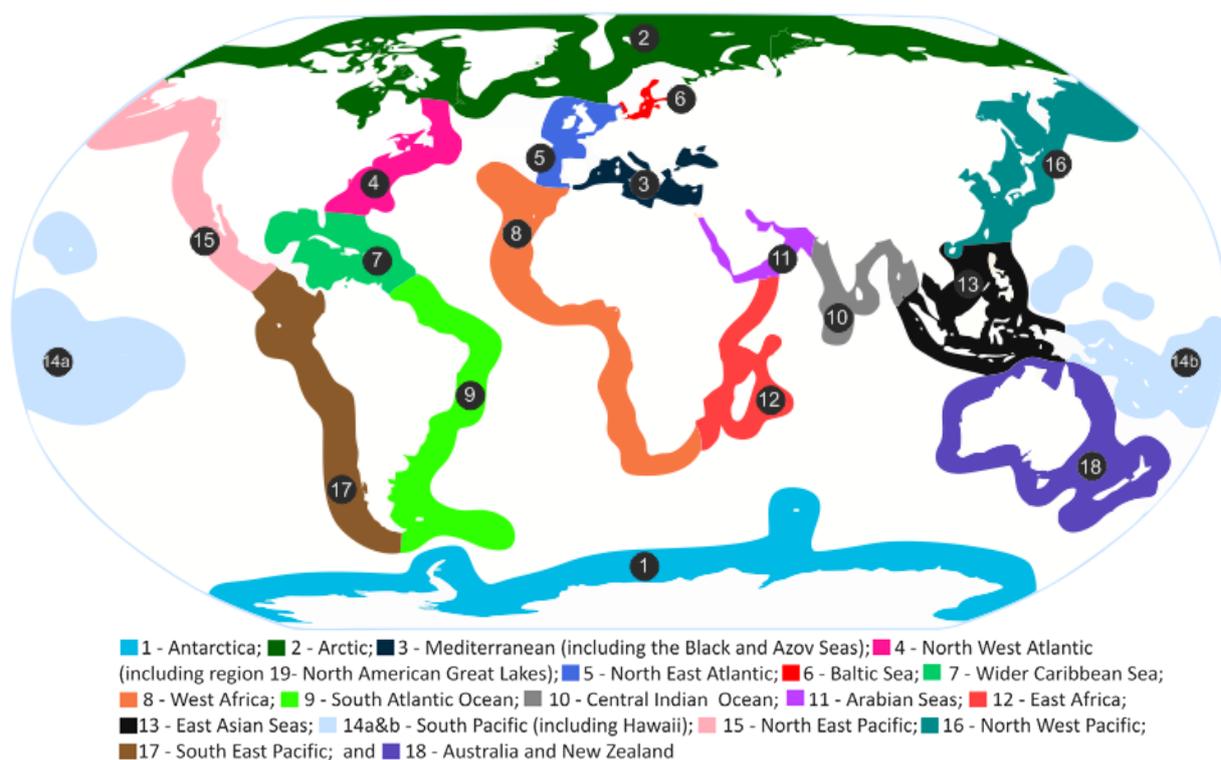


Figure 1.1 The 18 IUCN bioregions used for identifying the donating and receiving regions of crab invasions. Bioregions defined by Kelleher et al. (1995a, b, c, d). Figure modified from Hewitt et al. (2011).

Vectors and dates of discovery

To identify dominant vectors and to establish if vectors varied at the family level, the number of species in the various families were compared across vectors using a two-way Chi-squared test. Where a vector was reported simply as shipping and could have been either ballast water or hull-fouling, it was classified as unspecified shipping. When mode of introduction was unclear, it was classified as unknown. Dates of discovery were used as a proxy for dates of introduction as this information is not always known. Cumulative number of species was regressed against date of first introduction using an exponential relationship to determine rate of discovery.

Analysis of traits

Detailed information regarding the biological and ecological traits of alien species (hereafter referred to as traits) were recorded and categorised for each trait. Each trait had a minimum of two and maximum of four categories (Table 1.2). Following Bremner et al. (2006) who suggest that biological trait analysis should include as many possible traits for which data is available, nine of the traits suggested to be important in contributing to invasion success were included (Crawley 1989; Ehrlich

1989; Weis 2010; Hänfling et al. 2011; Table 1.2). While it would have been preferable to include salinity and temperature tolerance and growth rate as traits, these had to be excluded due to a lack of information in the literature. Definition of traits and categories were adapted from Bremner et al. (2006), MarLIN (2006) and Cardeccia et al. (in press).

Table 1.2 Trait information that was recorded for each alien species.

Traits	Information recorded	Categories
Size	Carapace width (cm)	Small (≤ 5), Medium (5.1-10), Large (10.1-15), X-large (≥ 15.1)
Longevity	Years	Short (≤ 2), Medium (3-5), Long (6-8), Very long (≥ 9)
Adult mobility	Mode of movement and behaviour	Walking, Swimming, Burrowing, Drifting
Migratory behaviour	Migratory or not	Seasonal migration, Non-migratory
Larval development time	Development time (days)	Short (≤ 20), Long (21-40), Protracted (≥ 41)
Fecundity	Number of eggs/year	Low (≤ 0.25 million), Medium (0.25-0.5 million), High (0.5-2 million), Very High (≥ 2 million)
Generation time	Average time between two consecutive generations (months)	Short (≤ 12), Medium (13-23), Long (≥ 24)
Range size	Number of provinces (Spalding et al. 2007)	Small (1), Medium (2-5), Large (6-10), Very Large (≥ 11)
Substratum type	Types of substratum in which species are present	Sandy (sandy/muddy/ saltmarsh/ seagrass/ eelgrass/ clay), Rocky (rocky/oyster beds/ algae/ seaweed), Artificial, Biogenic reefs (syllid tubes/ coral)

For this study, the affinity of each species to the trait categories was captured by allocating a score from 0-4 to each category of every trait where 0 reflects no affinity and 4 a high affinity. As the “fuzzy coding” approach (Chevenet et al. 1994) was applied, a species could receive several scores for any trait thus incorporating variation in the affinity of a species to trait categories. For every trait, the sum of the scores for the various categories added up to 4. This allowed the transformation of trait data into quantitative affinity values that could be used in multivariate analysis. To attribute affinities consistently across traits, set criteria were applied. When a species showed an affinity for multiple categories, the category most frequently displayed received the highest score while if two categories were equally represented, an affinity of 2 was allocated for both categories. When the literature was contradictory, scores were assigned based on expert judgement. Information was obtained at species

level, but in the event that information was not available at this level, a search was conducted at the genus level. Following Fleddum et al. (2013), if information was still unavailable, a zero was allocated to all categories within that trait. When information was not available for three or more traits, the species was excluded from the analysis. Traits were thus analysed for 28 of the 56 species. To identify if certain suites of traits predispose species to successfully establishing alien populations, the traits of single record species were compared to those of established species.

A combination of multivariate methods were used during the analysis of traits. This allowed the identification of patterns in the trait profiles of a cluster of species (Bremner et al. 2006). A hierarchical cluster analysis was performed on the matrix of species by trait categories and used to identify clusters of species sharing similar suites of traits, ecological equivalents (i.e. species sharing exactly the same traits) and outliers (i.e. species displaying a unique combination of traits). This analysis allowed the measurement of the level of similarity of the trait profiles amongst the alien crab species and the consideration of differences between established and single record species (Cardeccia et al. in press). Analysis was performed in the PRIMER software package (Plymouth Marine Laboratory, Plymouth, UK) and applied to fourth-root transformed non-standardised data, based on Bray-Curtis similarities.

As cluster analysis is unable to identify the traits responsible for the variation observed within the data Fuzzy Correspondence Analysis (FCA) was performed on the data matrix to explore this feature. This multivariate analysis is adapted to analyse fuzzy coded data and applies Euclidean distances that are calculated from the frequencies of each trait category to ordinate the species (Chevenet et al. 1994; Bremner et al. 2006). The plot generated by the FCA was used to identify patterns in the trait profiles of species and identify the traits responsible for the variation in the data. The traits of a species determines its distribution across the plot with species sharing similar traits located close to each other on the plot. Species in the FCA plots were labelled according to their invasion status (i.e. single record or established species), family, donating bioregion and vector. This enabled consideration of status, family, donating bioregion and vectors in relation to species that share similar traits. Analyses were conducted in R using the library ade4. Traits were also considered separately to identify those traits that varied most amongst species. The correlation ratio between each trait and the FCA axes was calculated. The higher the correlation ratio, the more that trait is responsible for the variation with the data.

Results

A total of 56 alien predatory brachyuran crab species from 15 families were identified as having spread outside of their native ranges (Table 1.3). The family Portunidae supported the highest number of alien species (22), followed by Varunidae (6), Cancridae (5), Pilumnidae (5), Grapsidae (4), Hymenosomatidae (3), Matutidae (2), Xanthidae (2) and Calappidae, Carpiliidae, Dairidae, Menippidae, Raninidae, Oregoniidae and Panopeidae (1 species each). Of these 56 alien species, 36 species (64%) have been reported as supporting established populations (Fig. 1.2). The largest number of established species was from the family Portunidae (i.e. the swimming and shore crabs) and included species such as the European shore crab, *Carcinus maenas*. The families supporting the next most established alien species were the Varunidae (i.e. mitten crabs), Cancridae (i.e. rock crabs), Pilumnidae (i.e. hairy crabs) and Grapsidae (i.e. marsh crabs), highlighting a positive correlation between the number of alien species known from a family and the number of established species in that family (Spearman's rank correlation; $r = 0.79$, $p < 0.001$). Notably no such relationship was found between the number of established species and the total number of species known from the various families (Spearman's rank correlation; $r = 0.50$; $p = 0.057$).

Table 1.3 List of 56 crab species within 15 families that have been recorded outside their native ranges. Labels apply to Figure 1.7. (*) denotes single record species. (#) indicates the 28 species that were included in the trait analysis.

Taxa	Labels	Taxa	Labels
Calappidae		Portunidae	
<i>Calappa hepatica</i>	CalH	<i>Callinectes bocourti</i>	CalB
		<i>Callinectes danae</i> *#	CalD
Cancridae		<i>Callinectes exasperatus</i> *#	CalE
<i>Cancer irroratus</i> #	CanI	<i>Callinectes sapidus</i> #	CalS
<i>Glebocarcinus amphioetus</i> #	GleA	<i>Carcinus aestuarii</i> #	CarA
<i>Metacarcinus magister</i> *#	MetM	<i>Carcinus maenas</i> #	CarM
<i>Metacarcinus novaezelandiae</i> #	MetN	<i>Carupa tenuipes</i>	CarT
<i>Romaleon gibbosulum</i>	RomG	<i>Charybdis feriata</i> *#	ChaF
		<i>Charybdis hellerii</i> #	ChaH
Carpiliidae		<i>Charybdis japonica</i> #	ChaJ
<i>Dyspanopeus sayi</i> #	DysS	<i>Charybdis longicollis</i>	ChaLo
		<i>Charybdis lucifera</i> *	ChaL
Dairidae		<i>Charybdis variegata</i> *	ChaV
<i>Daira perlata</i> *	DaiP	<i>Gonioinfradens paucidentatus</i>	GonP
		<i>Liocarcinus navigator</i> *#	LioN
Grapsidae		<i>Necora puber</i> #	NecP
<i>Metopograpsus oceanicus</i>	MetO	<i>Portunus pelagicus</i> #	PorP
<i>Pachygrapsus marmoratus</i> #	PacM	<i>Portunus segnis</i> #	PorS
<i>Pachygrapsus transversus</i> #	PacT	<i>Scylla serrata</i> #	ScyS
<i>Percnon gibbesi</i> #	PerG	<i>Thalamita gloriensis</i>	ThaG
		<i>Thalamita indistincta</i>	ThaI
Hymenosomatidae		<i>Thalamita poissonii</i>	ThaP
<i>Elamena mathoei</i> *	ElaM		
<i>Halicarcinus innominatus</i>	Hall	Raninidae	
<i>Halicarcinus planatus</i> *#	HalP	<i>Notopus dorsipes</i> *	NotD
Matutidae		Varunidae	
<i>Ashtoret lunaris</i> *	AshL	<i>Brachynotus sexdentatus</i> *	BraS
<i>Matuta victor</i> *	MatV	<i>Eriocheir hepuensis</i> #	EriH
		<i>Eriocheir japonica</i> *#	EriJ
Menippidae		<i>Eriocheir sinensis</i> #	EriS
<i>Sphaerozius nitidus</i> *	SphN	<i>Hemigrapsus sanguineus</i> #	HemS
		<i>Hemigrapsus takanoi</i> #	HemT
Oregoniidae			
<i>Chionoecetes opilio</i> #	ChiO	Xanthidae	
		<i>Atergatis roseus</i>	AteR
Panopeidae		<i>Xanthias lamarckii</i> *	XanL
<i>Panopeus lacustris</i>	PanL		
Pilumnidae			
<i>Actumnus globulus</i> *	ActG		
<i>Eurycarcinus integrifrons</i>	EurI		
<i>Pilumnopeus vauquelini</i>	PilV		
<i>Pilumnus minutus</i> *	PilM		
<i>Pilumnus spinifer</i> *	PilS		

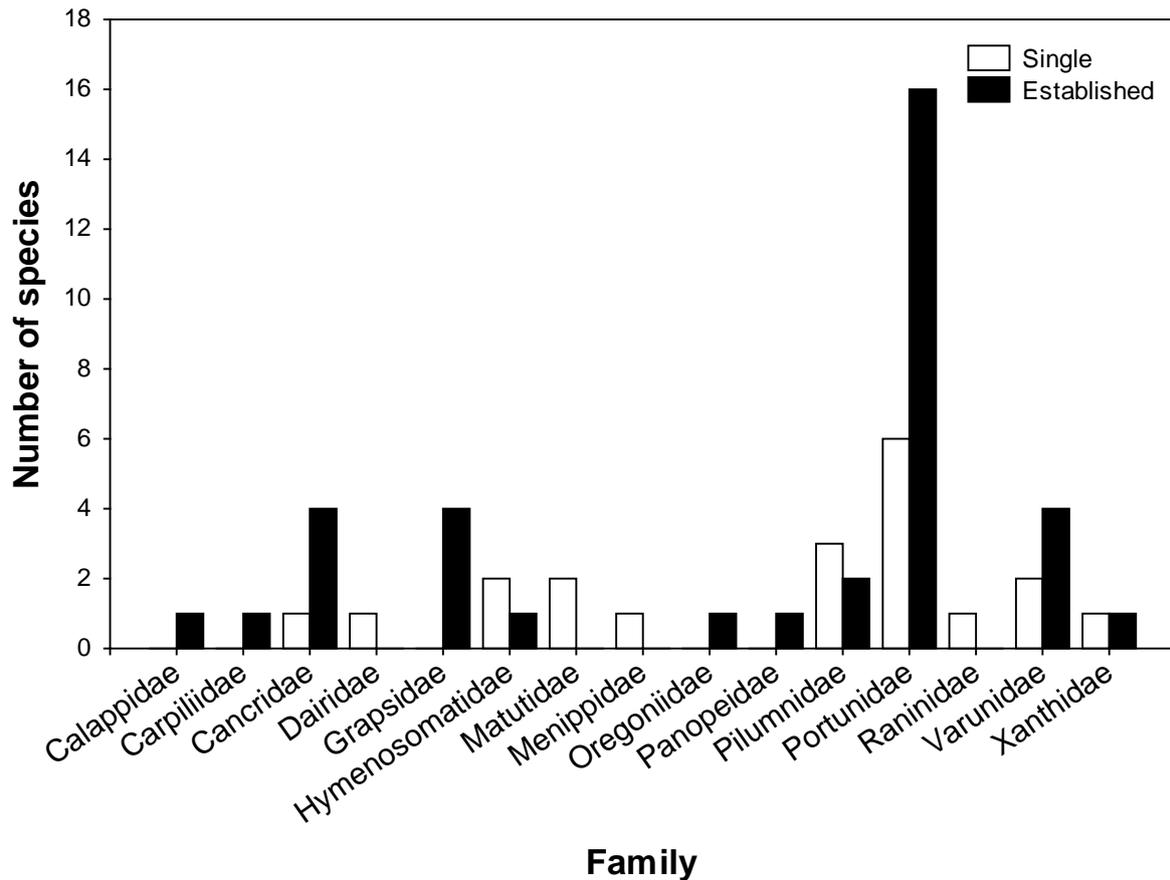


Figure 1.2 Number of established and single record predatory alien crab species recorded in each family.

The literature revealed that most alien crabs are not specialised predators, but rather generalist opportunistic predators that switch between scavenging, omnivory and predation (Wieczorek and Hooper 1995; Jiang et al. 1998; Rudnick and Resh 2005; Brockerhoff and McLay 2011). As a group these crabs eat a wide variety of prey items with most recorded to prey on benthic invertebrates such as bivalves, gastropods, polychaetes, amphipods, echinoderms (Williams 1982; Cresswell and Marsden 1990; Sant'Anna et al. 2015; Stasolla et al. 2015) and juvenile crabs (Prasad and Tampi 1953; Sant'Anna et al. 2015). Some species (e.g. Chinese mitten crab *Eriocheir sinensis*) also eat fish eggs (Rainbow et al. 2003). When these items are not available these crabs eat anything from detritus (Rudnick and Resh 2005) to plant material (Ledesma and O'Connor 2001). Many of the larger crabs (e.g. the blue crab *Callinectes sapidus* (Gómez Luna et al. 2009), the Asian paddle crab *Charybdis japonica* (Jiang et al. 1998) and the giant mud crab *Scylla serrata* (Lemaitre et al. 2013)) also feed on fish. Crabs were reported from a variety of coastal marine habitats types including rocky, sandy, muddy, salt marsh, estuaries, reefs (oyster and biogenic) and artificial habitats (Apel and Spiridonov 1998; Asakura and Watanabe 2005; Dauvin et al. 2009; Dittel and Epifanio 2009). A greater percentage

of established species were present in artificial habitats (28%) than single record species (15%) and fewer of these established species were restricted to a single substratum type (22% in contrast to 40% of single record species).

Distribution ranges

Only 15 species had very large native ranges (≥ 11 provinces) although the invaded ranges of these crabs were amongst the smallest (≤ 3 provinces) with the exception of one species, the Indo-Pacific swimming crab *Charybdis hellerii* which had an invaded range size of eight provinces (Fig. 1.3). Notably no correlation was found between native and invaded range sizes of alien crabs (Spearman's rank correlation; $r = -0.08$, $p = 0.57$).

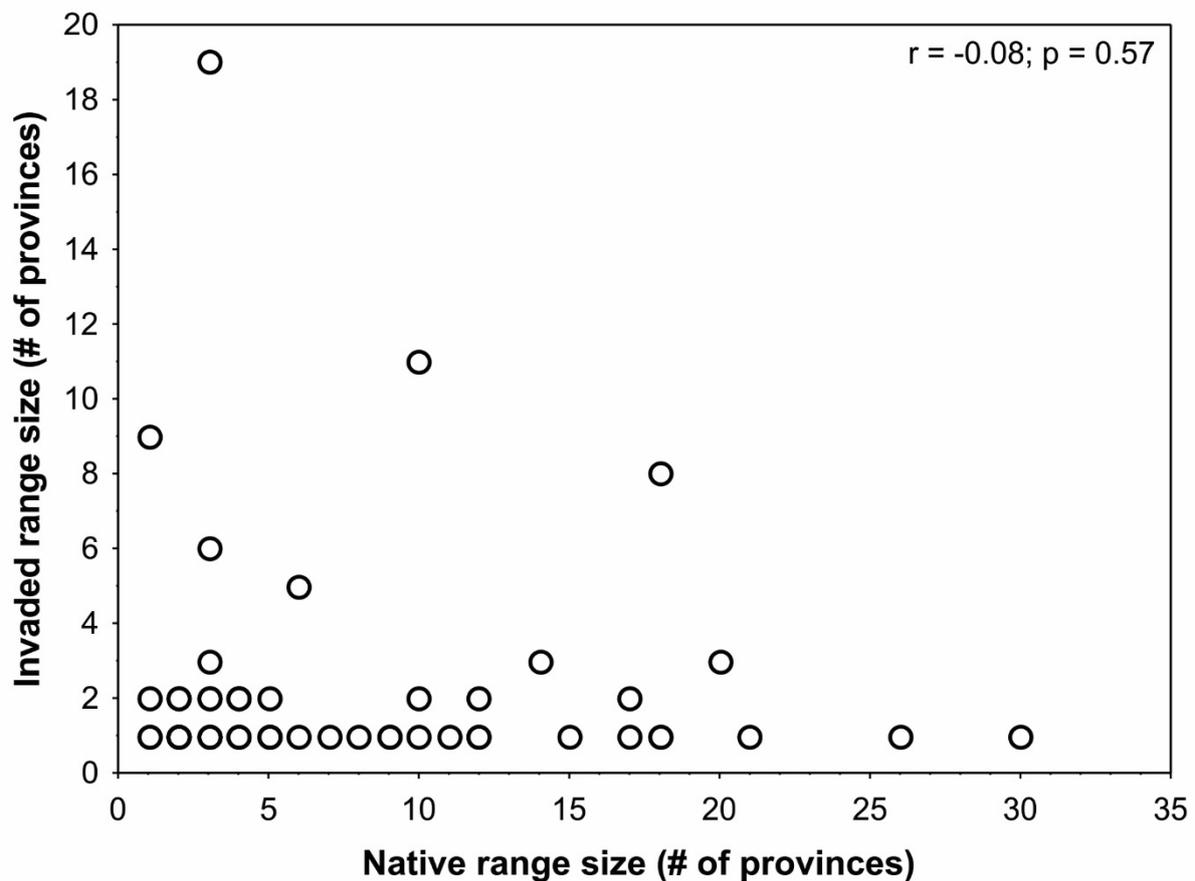


Figure 1.3 Invaded range size of alien crab species in relation to their native range size. Range size reflects the number of provinces in which a species has been recorded. Provinces as defined by Spalding et al. (2007).

Donating and recipient regions

Of the 18 IUCN bioregions, 15 were found to donate alien crab species, while 17 bioregions received these crabs (Fig. 1.4). It was notable that some species were donated by more than one bioregion (e.g. *C. sapidus* was donated from the North West Atlantic, Wider Caribbean Sea and the South Atlantic), while other species were received by multiple bioregions (e.g. *E. sinensis* has been introduced to the North East Atlantic, North West Atlantic, North East Pacific and the Arabian Seas). The majority of alien crabs (27 species) were donated from the North West Pacific. Although the Arabian Seas were also responsible for donating many crab species (21 species) it was notable that this region only donated to the Mediterranean Sea. The Mediterranean Sea was the most invaded bioregion, receiving the most species overall (33 species). The South Pacific received species from the most bioregions (7 bioregions) while the North East Atlantic donated to the most bioregions (14 bioregions). East Africa and the South Pacific only received species, while no alien crabs were donated or received by Antarctica.

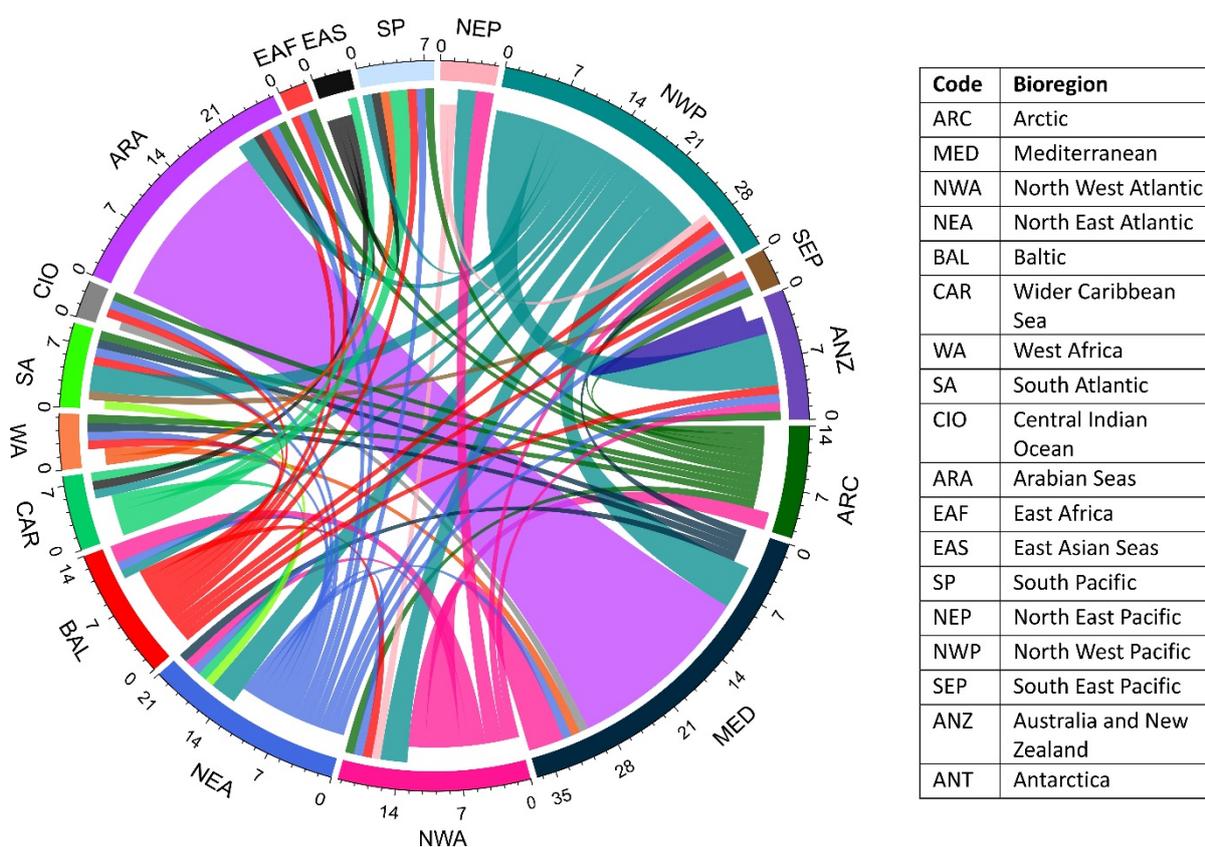


Figure 1.4 Bioregions that donate and receive alien crab species. Bioregions are represented by the different coloured segments. Lines that are the same colour as the segments represent species donated from that bioregion. Lines radiate to the bioregions to which species were donated. The numbers around the diagram represent the numbers of species.

Vectors and dates of discovery

Twelve modes of introduction were identified as being involved in the transport of alien crabs (Fig. 1.5), with the number of alien crab species differing significantly among families and vectors (Two-way Chi-squared; $X^2= 106.18$, $df = 9$, $p < 0.001$). Ballast water was responsible for the majority of introductions, introducing species from seven crab families. The Suez Canal was the second most important vector in the transport of alien crabs and although fewer species have been introduced via this vector, it has resulted in the transport of more alien crab families (eight families) than ballast water. All of the species from the families Calappidae, Dairidae, Matutidae, Menippidae and Raninidae were solely introduced by the Suez Canal. The impact of shipping as a pathway can be seen in the high number of introductions associated with the vectors within this pathway. The transfer of species with aquaculture products and the live seafood trade have been responsible for the introduction of seven and six species respectively. Only four species are believed to have been intentionally released and include *C. sapidus*, *E. sinensis*, *Necora puber* and *S. serrata*, although not all have been successful in establishing fisheries. Two species from the family Varunidae, *E. sinensis* and *E. hepuensis*, were the only species introduced via freshwater canals. Lastly, only two species were introduced via the aquarium trade (i.e. *Percnon gibbesi* and *Callinectes sapidus*), while the vectors responsible for the introduction of *Xanthias lamarckii* and *Gonioinfradens paucidentatus* remain unknown. While the Portunidae accounted for the most alien crab species, this family has also been introduced by the largest number of vectors, with species from this family being introduced by 10 of the 12 vectors (Fig. 1.5). Other families that have been introduced by a variety of vectors include the Varunidae (eight vectors), Cancridae (five vectors) and Grapsidae (five vectors).

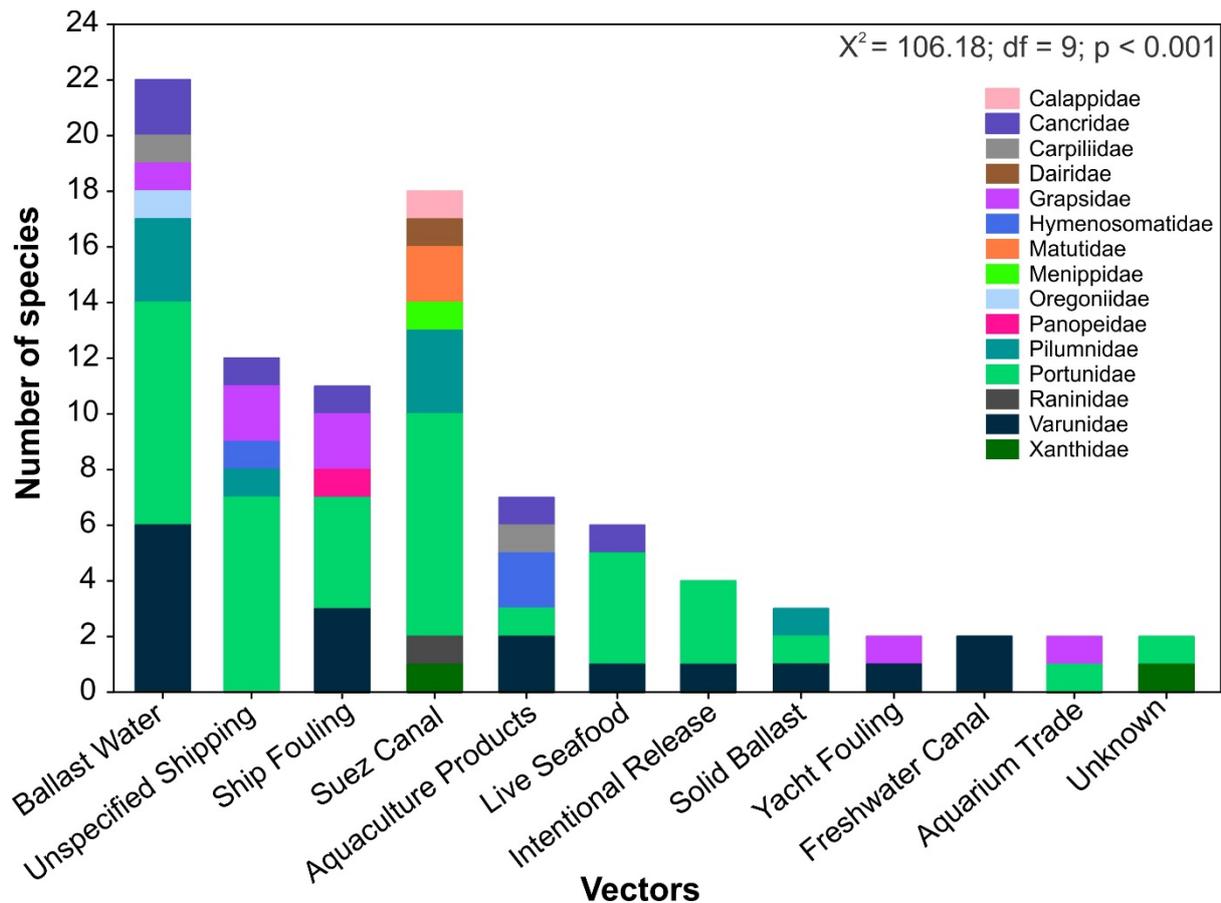


Figure 1.5 Likely vectors responsible for the introduction of alien crabs presented per family (Note: some species have been introduced by more than one vector and therefore sum of the number of species transported via the various vectors does not depict total number of alien crab species identified in this study).

The rate of discovery of alien crabs was calculated using data for 55 of the 56 species recorded as no available information on the date of first collection was available for *Halicarcinus planatus*. The first species to be recorded was *C. maenas* in 1817 (Say 1817) and the most recent record was of *X. lamarckii*, discovered in 2013 (Corsini-Foka et al. 2013). The rate of discovery of alien predatory crabs has increased exponentially through time (non-linear estimation; $R^2 = 0.98$, $p < 0.001$, Equation: Number of species = $1.0354 \times 10^{-18} e^{0.0225 \times \text{Time}}$; Fig. 1.6). From 1817 to 1900 the discovery rate of marine alien crabs was relatively low (0.72 species per decade). It increased slightly to 1.8 species per decade during the first half of the 1900's while the second half of the century saw an increase to 3.75 species per decade. Since the turn of the century there was a rapid increase in the rate of discovery with 10.87 species being noted per decade. More than half of the species in this study were discovered in the last 23 years.

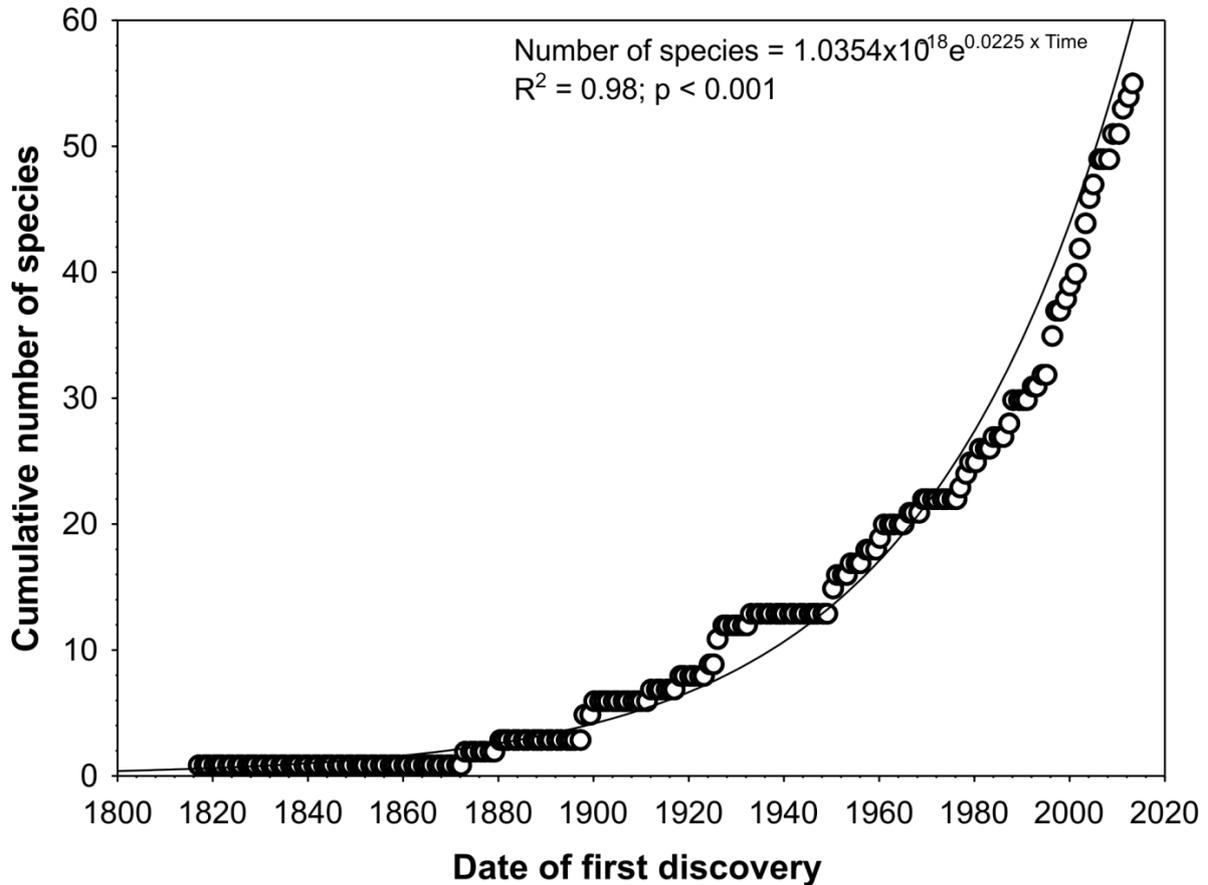


Figure 1.6 Rate of discovery of predatory alien brachyuran crabs.

Analysis of traits

When exploring traits through the use of a cluster analysis, no species were found to be ecological equivalents (i.e. none demonstrated 100% similarity in trait structure) and no outliers were identified (Fig. 1.7). All the species grouped at 37% similarity, after which two main groups could be identified. At the 50% similarity threshold, 6 groups of species (G1- G6) were identified. Single record and established species did not group together, but were distributed amongst the groupings, suggesting that they don't have separate suites of traits. Although one group contained only species from the family Portunidae, overall no pattern related to family was evident.

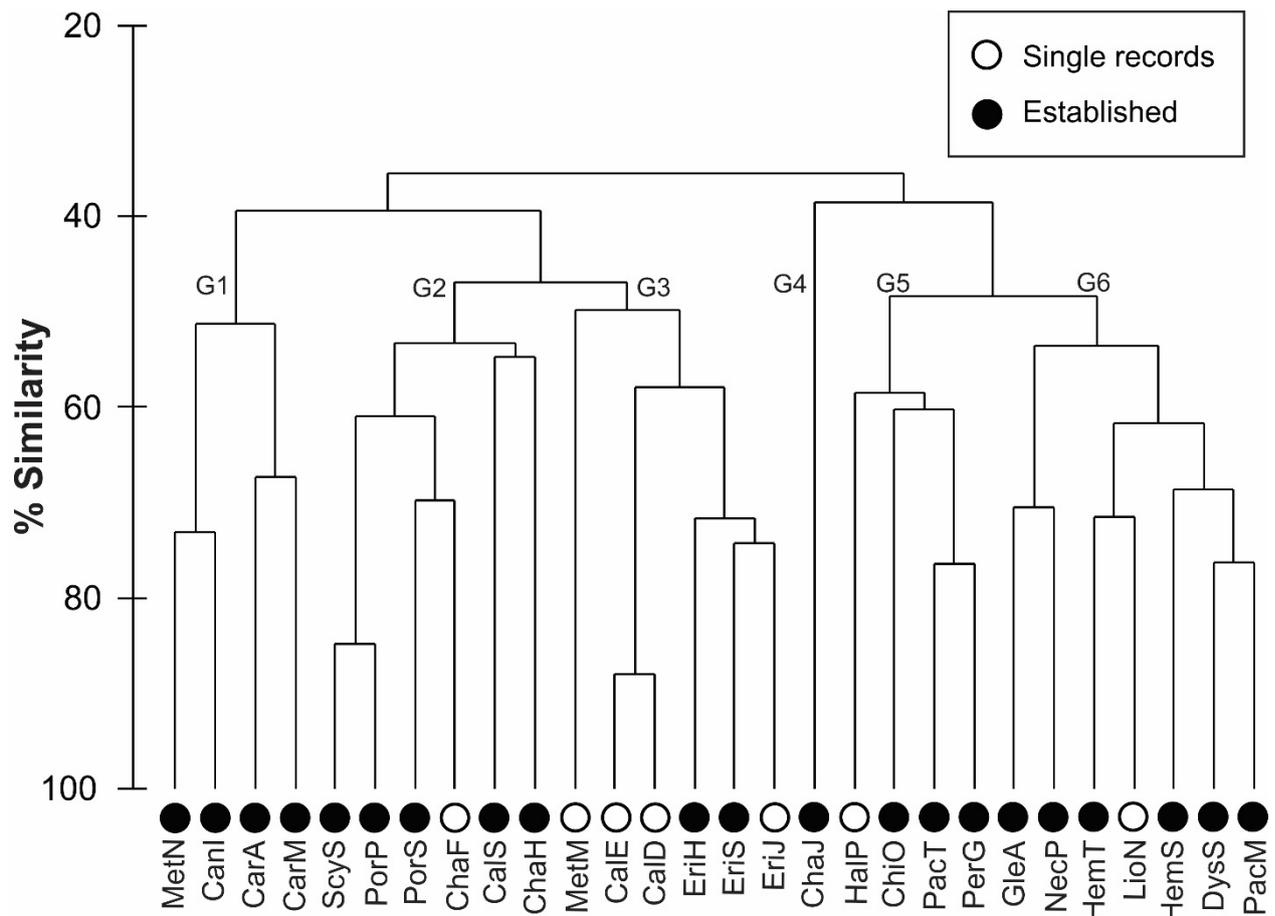


Figure 1.7 Dendrogram based on Bray-Curtis measures of similarity for single record and established species. The 6 groups of species identified at the 50% similarity threshold are indicated by G1-G6. See Table 1.3 for species labels.

Fuzzy Correspondence Analysis (FCA) allowed the identification of those traits most responsible for the variation seen within the data. In this plot the traits associated with each species determine where it is located on the plot. The two FCA axes explain the variability within the dataset, with the first axis explaining the most variability. For this dataset, very little of the total variability is explained by the two axes (Axis 1 + Axis 2: 31%; Fig. 1.8). To investigate if any patterns in the traits displayed by the crabs were related to their invasion status, family, donating bioregion or vectors, these variables were overlaid in Figure 1.8. Unexpectedly, species did not form separate groups based on these variables, rather they were interspersed across the plot indicating that separate suites of traits are not associated with the different levels of these variables. To fully interpret the FCA results, Figure 1.8 needs to be considered along with Figure 1.9. Each block in Figure 1.9 represents one of the nine traits considered and the stars represent the distribution of the different categories within that single trait. The centre of each star corresponds to the centre of gravity of all the species that display that trait

category and the rays link the species to their categories. While some traits such as migratory behaviour and carapace size explained variability in the data (i.e. they separate out along the two axes), most traits showed little separation among categories (e.g. substratum type).

Together with the correlation ratios (Table 1.4), Figure 1.9 was used to identify the most important traits driving the variation observed in Figure 1.8. Higher correlation values identify traits that explain higher levels of variability in the data and are reflected in Figure 1.9 as traits that have stars that separate out along the two axes. Carapace size was identified as being responsible for the most variation along the axes as it has the largest correlation ratios for both axes (Table 1.4). This is demonstrated by the categories separating out on both axes (Fig. 1.9). Other important traits causing variation along the axes included fecundity (also for both axes), migration for axis 1 and longevity, generation time and range size for axis 2. In contrast some categories (e.g. substratum type) did not separate out across the axes but rather clustered at the origin, indicating that these traits did not vary among species. Categories with many, elongated rays were those most commonly displayed, for example the category walking in the trait adult mobility is a trait possessed by all crabs.

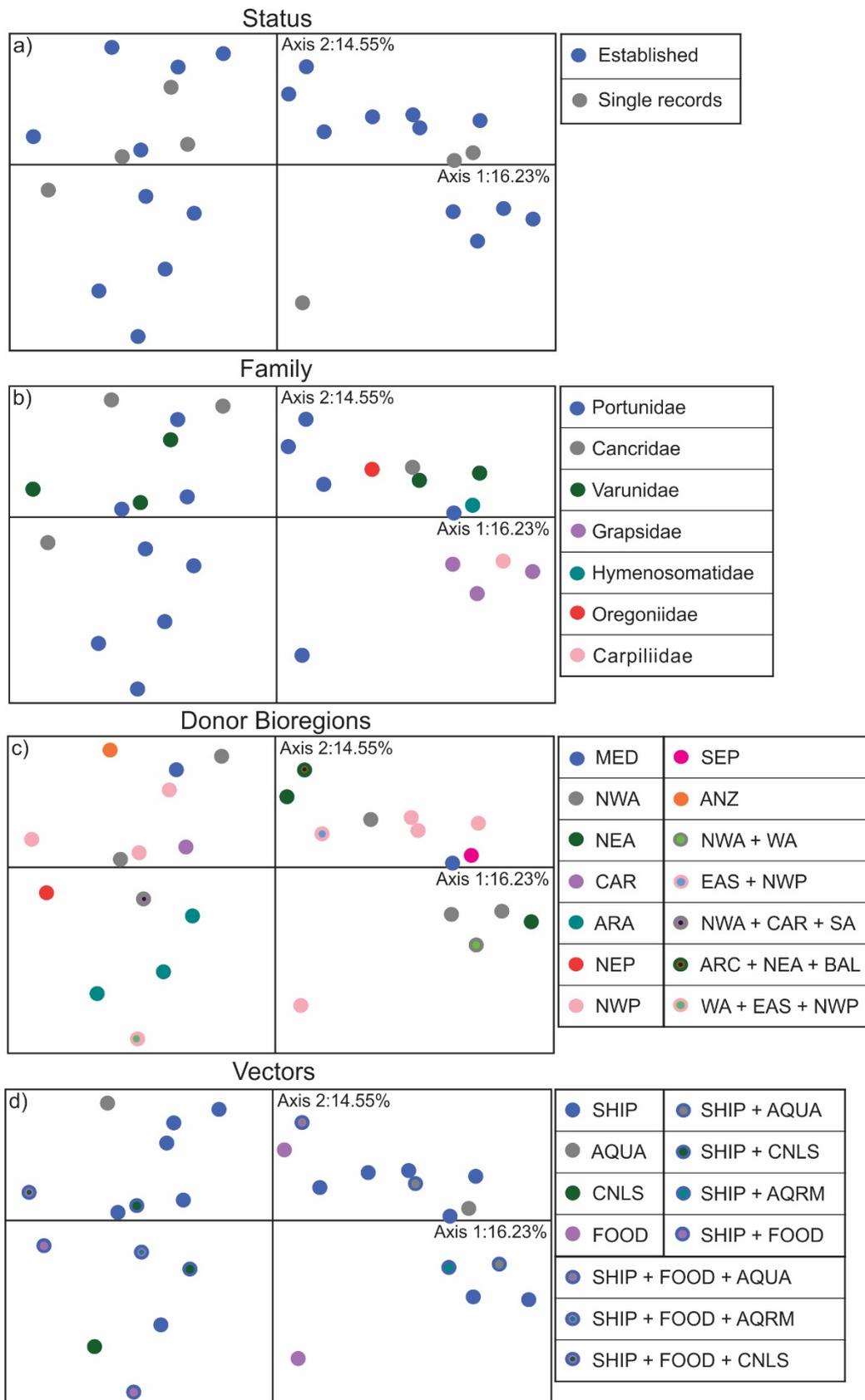


Figure 1.8 Fuzzy Correspondence Analysis (FCA) bidimensional plot where every dot represents one of the 28 alien crab species. Species are labelled according to (a) status, (b) family, (c) donating bioregion and (d) vector. Shipping: SHIP; Aquaculture: AQUA; Canals: CNLS; Food Industry: FOOD; Aquarium: AQRM.

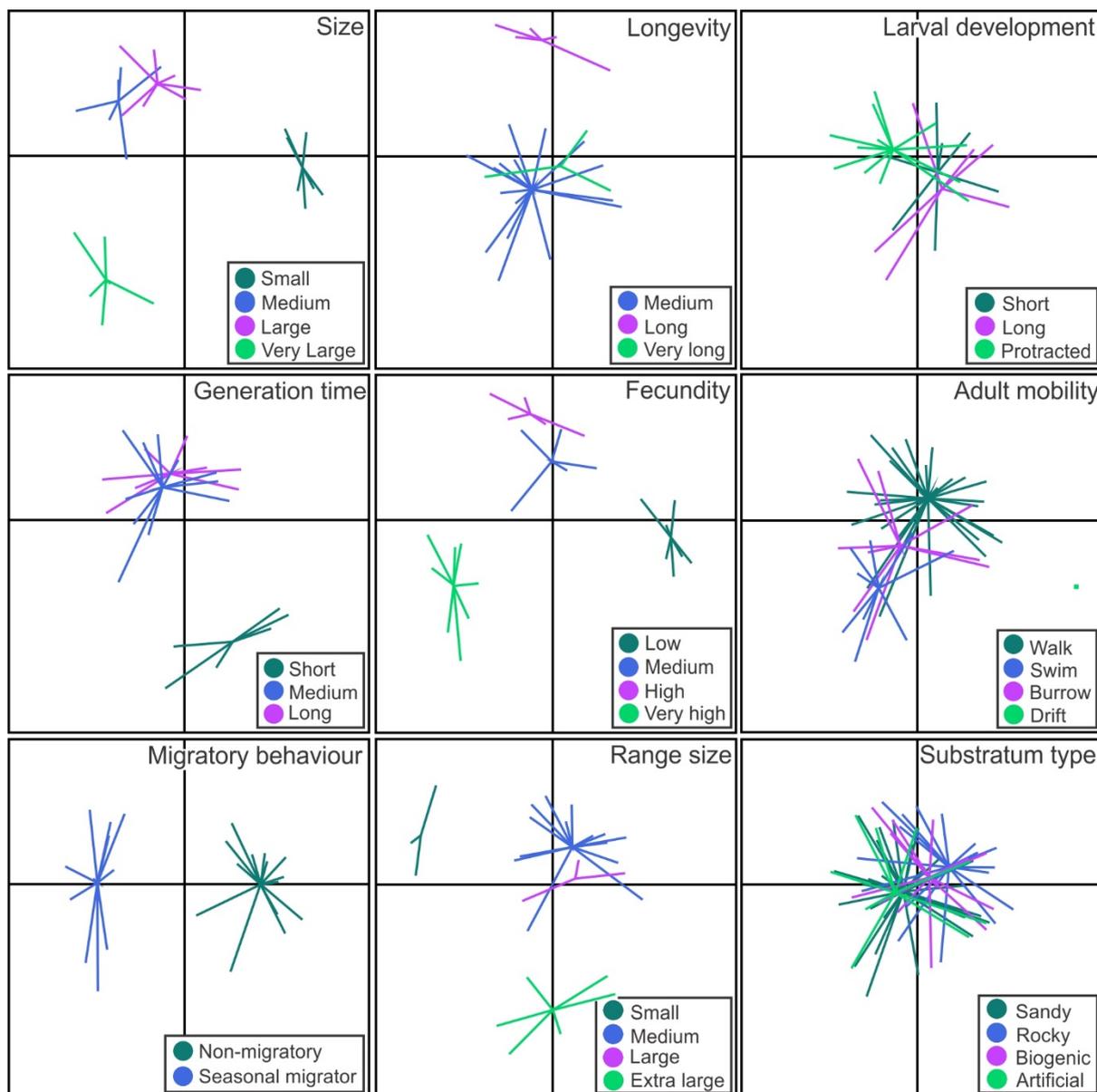


Figure 1.9 Fuzzy Correspondence Analysis bidimensional plot depicting the nine traits analysed. Each graph represents a single trait and the stars represent the categories within that trait.

Table 1.4 Correlation ratios per trait for the first two axes of the Fuzzy Correspondence Analysis (FCA). Traits highlighted in bold have highest correlation values for the respective axes.

Trait	Axis 1	Axis 2	Σ
Size	0.775	0.600	
Longevity	0.008	0.302	
Adult mobility	0.067	0.144	
Migratory behaviour	0.745	0.000	
Laval development	0.046	0.024	
Fecundity	0.716	0.414	
Generation time	0.073	0.428	
Range size	0.241	0.507	
Substratum type	0.050	0.017	
Variability explained (%)	16.23	14.55	30.78

Discussion

Due to the prevalence of and threats posed by aliens species (Simberloff et al. 2013), there is great value in understanding generalities governing invasions. Predatory crabs are amongst some of the most successful marine invasive taxa globally (Grosholz and Ruiz 2003; Kraemer et al. 2007; Brockerhoff and McLay 2011; Brousseau and McSweeney 2016). To better understand the complex drivers and traits behind the invasion success of these invaders, this chapter reviewed all reported invasions within this functional group and compiled a list of alien crabs, documented their global occurrence, identified vectors for their transfer, determined their rate of discovery and lastly, considered traits associated with their successful establishment. In total, 56 alien marine predatory crab species were identified from 15 families. There has been a significant increase in the rate of discovery of crabs over the past century with shipping being the most important pathway for the introductions of these crabs. The majority of alien crabs originated in the North West Pacific whereas the Mediterranean Sea was the recipient of the highest number of crab invasions, mainly resulting from the massive immigration of Red Sea crabs through the Suez Canal. Unexpectedly it was found that neither ecological nor biological traits were good predictors of the ability of alien crabs to use certain vectors and establish populations.

Patterns observed in crab invasions

The families from which the greatest number of alien brachyuran crab species were noted were the Portunidae, Varunidae, Cancridae, Pilumnidae and Grapsidae. The findings were somewhat similar to

that of Brockerhoff and McLay (2011) who also found these five families to be amongst the most common. It is notable that despite supporting the highest number of alien and established species, the Portunidae are not the largest family of brachyuran crabs. The most speciose family is actually the Xanthidae that constitutes more than double the number of species than the Portunidae, but has only two species known to be alien. While this may suggest that the Portunidae possess traits that predispose them to being successful invaders, this was not found during the detailed trait analysis undertaken in this study and the mechanism behind the high number of Portunid invasions remain unclear. It was, however, found that the number of established species is a function of the number of arriving species. This highlights that the management of pathways offers a promising means of preventing invasions by crabs.

It has been suggested that species with large native ranges are likely to be successful invaders (Ricciardi and Rasmussen 1998; Bates et al. 2013; Novoa et al. 2016). This is due to their tendency to have broad environmental and physiological tolerance ranges and the fact that they are, in many cases, food and habitat generalists (Vazquez 2006; Troost 2010), and thus able to survive within a variety of habitat types and climates around the globe. This study, however, found no correlation between native and invaded range size. This pattern may be reflective of alien crabs being restricted to small areas in provinces with vectors and not yet spreading to fill their full physiological tolerance ranges in their new regions. Once such regional spread takes place species with large native ranges may then realise large invasive ranges too.

The rate of discovery of alien marine predatory crabs has increased exponentially through time over the past 200 years. It is notable that numerous other studies considering marine species have reported the same exponential increase and trend in invasions over the past decades (Ruiz et al. 2000; Mead et al. 2011a; Howard et al. 2017; Seebens et al. 2017). Although the increase in discovery might reflect an increase in search effort (Ruiz et al. 2000), recent findings suggest that this increase might have resulted from an increase in the actual number of invasions due to globalization (Seebens et al. 2017). Search effort and reporting of marine alien species differs through time, across regions and taxa as a result of variability in the availability of scientific, financial and taxonomic resources (Costello et al. 2010). The Mediterranean Sea, for example, supports the most alien crab species and is one of the most studied regions in the world (Galil 2009; Zenetos et al. 2012; Katsanevakis et al. 2014a; Galil et al. 2015). Although, there has been an increase in survey effort in various countries over the past two decades (Carlton 1996; Hayes and Sliwa 2003; Costello et al. 2010) there is also a well-established trend of increasing global connectivity (Seebens et al. 2013) and it is likely an interplay between these two factors that has resulted in the high discovery rate of crabs over the last two decades.

The relationship between regions donating and receiving alien species can be complex, especially as receiving regions can themselves become donors (Grosholz and Ruiz 1995; Ruiz et al. 2000). Such a complex invasion network can be seen in the example of the European shore crab *Carcinus maenas* that has invaded western North America from several source regions including regions where this crab is alien (Carlton and Cohen 2003). The region that donated the majority of alien crabs (27 species) was the North West Pacific. The Western Central Pacific, which includes the North West Pacific bioregion, is one of the regions supporting the largest number of native crabs (Ng 1998; Ng et al. 2008), suggesting that the large number of species originating from this region simply reflects the high native diversity of crabs. In addition, the North West Pacific is central in the shipping network and undertakes a lot of trade with other regions (Wonham and Carlton 2005; Seebens et al. 2013). The large volume of shipping would thus increase the transfer opportunities for these crab species to reach other places. Introduction success of species is influenced by the duration of voyage and thus distance of the recipient region from the source region (Miller and Ruiz 2009). The majority of introduced species are introduced from regions that have an intermediate distance (8000–10 000 km) to the recipient port (Seebens et al. 2013) and could be one reason behind why most crabs from the North West Pacific are donated to the Australia and New Zealand bioregion, approximately 6800-9300 km away.

The bioregion that donated alien crabs to the greatest variety of regions was the North East Atlantic. One reason for this may be that *C. maenas* is present in this region and has spread from there (and the Baltic and Arctic regions) to surrounding bioregions and all but one continent, i.e. Antarctica. The North East Atlantic bioregion is also a well-known source region for many other marine alien species as it is very central in the shipping network and thus closely linked to many regions (Leppäkoski et al. 2013; Seebens et al. 2013). It is interesting to note that three bioregions did not donate any alien species. These include the East African, South Pacific and Antarctic bioregions, despite the former two receiving invasions. The fact that no crabs have been donated from the East African bioregion is likely reflective of its lower connectivity with distant regions when compared to other Indo-Pacific bioregions (Seebens et al. 2013). Like-wise, the majority of the islands constituting the South Pacific, are geographic isolated with large distances to mainlands and other regions (Gollasch 2007). This region also has a very low level of aquaculture exports (Gillett 2011) that could further reduce chances of species being donated. In contrast, the absence of crab introductions from Antarctica is most likely indicative of the very low native crab diversity in this region (Thatje et al. 2005; Aronson et al. 2007).

Reflecting the highly invaded nature of the marine environment in the Mediterranean Sea (Galil 2009; Zenetos et al. 2012) and the pattern observed for all crab species (Brockerhoff and McLay 2011), this region was found to support the most crab invasions. These high numbers are most likely because of its very central position in the shipping network, close proximity to many neighbouring regions, high

shipping connectivity with other regions (Seebens et al. 2013) and maybe most importantly, as a result of the Suez Canal (Katsanevakis et al. 2013; Galil et al. 2014). Most species alien to this bioregion arrived following the opening of the Suez Canal in 1869 (Galil and Zenetos 2002). The Suez Canal is thus among the most notorious pathways for the introduction of marine alien species (Galil et al. 2015), including crabs, to the Mediterranean region (Brockhoff and McLay 2011). This canal created a pathway from the Indo-West Pacific to the Mediterranean where the majority of crab species were introduced from the Arabian Seas, which incidentally only acts as a donating region to the Mediterranean Sea. No Mediterranean species are found in the Arabian seas or the Central Indian Ocean as the sea water flow in the Suez canal is from the Red Sea to the Mediterranean Sea and not vice versa (Rilov and Galil 2009). In fact, only five predatory crab species native to the Mediterranean occur in other regions. Furthermore, it has been found that specialised predators with a small native range size such as those in the Mediterranean Sea have reduced environmental resistance to disturbance (Borja et al. 2000). This could in turn reduce such species invasion success (Evans et al. 2006) as introductions normally occur in disturbed areas such as harbours (Wonham and Carlton 2005; Wonham et al. 2005). Estuaries, lagoons, ports and harbours are also common in the Mediterranean. As these areas are associated with frequent shipping and aquaculture activities (Ruiz et al. 2009; Bulleri and Chapman 2010), they serve as hotspots for numerous invasive species (Cardeccia et al. in press; Peters et al. 2017). Furthermore, these environments facilitate the survival and establishment of alien species (Coles and Eldredge 2002) firstly, by creating an ideal environment for species to thrive in by providing shelter from harsh environmental conditions and fluctuations (Bulleri and Chapman 2004) and secondly, by providing artificial, hard substrates such as docks, floats, piers pilings, pipes and aquaculture installations known to support alien marine and crab species (Ruiz et al. 2009; Lord 2017). The highly disturbed and invaded nature of the Mediterranean Sea has led to significant declines in native species, population extinctions, reduced genetic diversity, loss of habitat structure and increased homogenization (Galil et al. 2015). This possibly further facilitated the establishment of alien species due to reduced biotic resistance (Simberloff and Von Holle 1999).

Australia and New Zealand together form the second most invaded bioregion with more crabs having invaded New Zealand than Australia. As species distributions are limited due to their physiological tolerance ranges (Ruiz et al. 2000; Ashton et al. 2007), environmental matching of the donating and receiving habitat contributes to successful introduction (Peterson 2003; Facon et al. 2006). The Mediterranean and New Zealand are temperate regions. Temperate regions seem to be more suitable for invasions (Ruiz et al. 2000) firstly, due to more moderate temperatures and dampened temperature fluctuations when compared to other regions and secondly, as biotic resistance has been suggested to be less important in temperate regions further facilitating establishment success

(Freestone et al. 2013). Furthermore, the coast of New Zealand is, when compared to other coastlines, relatively depauperate of crab fauna (Dell 1968; McLay 1988; Gust and Inglis 2006) and might therefore be more vulnerable to invasion by alien crab species due to empty niches (Shea and Chesson 2002) and decreased biotic resistance (Udvardy 1969; Preisler et al. 2009). It is important, however, to acknowledge that the high search efforts and reporting of alien species in regions such as the Mediterranean Sea (Zenetos et al. 2012; Galil et al. 2015), Australia (Poore 2004; Hewitt et al. 2011) and New Zealand (Hewitt et al. 2004b; Hayden et al. 2009) might inflate the number of alien crabs recognised from these regions.

The South Pacific Ocean constitutes many islands and received species from 7 bioregions i.e. the greatest variety of donating regions noted in this study. The majority of these records are from the Hawaiian Islands which, like the Mediterranean, are a shipping hub connecting numerous regions (Carlton and Eldredge 2009). It is likely that this confluence of international shipping is responsible for the fact that this biogeographic region has been invaded by crabs from so many regions.

The fewest alien crab species were reported from the Arctic, Central Indian Ocean, East Africa, East Asian Seas, West Africa, South East Pacific, Wider Caribbean bioregions and Antarctica, none of which supported more than 3 alien crabs. The reasons behind this pattern are diverse and likely to vary in importance among regions: 1) regions with extreme environments may be inhospitable to the majority of species. An example of this can be seen in the fact that very few alien crab species have been recorded in Polar Regions, a pattern also seen in marine alien species in general (Tavares and De Melo 2004). In fact, the Atlantic Rock Crab *Cancer irroratus* is the only crab species that has been detected in the Arctic (Gíslason et al. 2014) while no alien predatory crab species have been detected in Antarctica. Establishment of crabs in these regions is probably limited due to the inability of crabs to survive in such cold conditions (Thatje et al. 2005; Aronson et al. 2007); 2) crab species from regions such as the Central Indian Ocean, East Africa and East Asian Seas bioregions often have large ranges as they occur across the Indo-Pacific Ocean (Carlton 2009). This together with the low level of knowledge held on the native ranges of these species (Brockerhoff and McLay 2011) makes it difficult to determine whether crabs are native or alien to any particular bioregion; 3) the low numbers of crabs recorded in some bioregions might reflect a lack of studies dedicated to the detection of marine alien species. An example of this can be seen in the fact that all of the crabs reported from the West Africa bioregion are known only from the west coast of South Africa (le Roux et al. 1990; Geller et al. 1997) which is well studied (Mead et al. 2011a, b; Robinson et al. 2016). It is, however, very unlikely that no invasions have taken place elsewhere, but to date no studies have been undertaken in neighbouring countries; 4) The low shipping intensity to surrounding source regions could contribute to the low invasion risk in regions like the West Africa and South East Pacific bioregions (Seebens et

al. 2013); 5) Some regions are considered very remote (e.g. the South East Pacific). As such species would also have to survive very long voyage times and numerous environmental stresses (Brockerhoff and McLay 2011) to reach these regions, which may ultimately reduce their invasion risk; 6) Regions in the Atlantic Ocean are connected to the Indo-Pacific, via the Panama Canal. As this canal runs through a freshwater lake, the invasion risk to such regions will be much lower for marine crabs (Brockerhoff and McLay 2011). This could explain the low number of invasions in the Caribbean which is linked to the Central Indo-Pacific, from which they are most likely to receive invasions (Seebens et al. 2013), via this canal.

Twelve vectors were identified in the transport of alien marine crabs, reflecting numerous opportunities for crab introductions, although it should be noted that solid ballast is no longer an active vector and unspecified shipping is not a vector in itself. Species that can be transferred by more than one vector are known as polyvectic species (Cohen 1997) and this characteristic is common in species with multiple life-stages that can be associated with different vectors. Crabs fall into this group having both pelagic (larval) and benthic (adult) life-stages that can be associated with different vectors (Fofonoff et al. 2003). Most crabs have been introduced through the pathway of shipping, following which the most important vectors have been the Suez Canal and transfer with aquaculture products. Gaining resolution on the relative importance of vectors associated with shipping is, however, challenging as ascribing an introduction to one or the other can be speculative (Ruiz et al. 2000; Gollasch 2007). Nonetheless, the dominance of shipping vectors is a pattern also reported for marine alien species in general (Ruiz et al. 1997; Gollasch et al. 2009; Hewitt et al. 2009). Since 1869 when it first opened, the Suez Canal has been responsible for the introduction of the majority of marine alien species present in the Mediterranean Sea (Galil 2009). This vector was also found to be one of the most important vectors responsible for the introduction of crabs to the Mediterranean by Brockerhoff and McLay (2011). Although fewer species have been introduced via this vector than through shipping, it is interesting to note that it has resulted in the transport of the greatest diversity of crab families. Species from the families Calappidae, Dairidae, Matutidae, Menippidae and Raninidae were only introduced via this vector. Transfer with aquaculture products such as oysters (for example see McLay 1988; Tavares 2003) was identified as the next most important vector. Internationally, this vector is considered a significant contributor in the introduction of marine species (Grosholz et al. 2015) and has resulted in the introduction of seven crab species around the world. Globally, the live seafood trade is also expanding and becoming an increasingly important vector (Naylor et al. 2001; Minchin 2007). Species from around the globe are introduced to numerous consumer markets (Ng 1998). From here, species can be released or can escape into the wild. Crabs such as the Chinese mitten crab, are very common seafood species which already had a market value of more than US\$1.25 billion year⁻¹

in 2002 (Wang et al. 2006). This species is exported internationally and its possible release or escape from markets has been identified as a threat (Dittel and Epifanio 2009). Crabs are popular culture species in some regions. Culturing can be an important contributing factor in the survival and successful establishment of alien species, as populations are restocked and introduced into carefully selected and suitable environments (Mack et al. 2000; Dittel and Epifanio 2009). To-date, four crab species are believed to have been intentionally released including *Callinectes sapidus*, *E. sinensis*, *Necora puber* and *Scylla serrata*, although not all have been successful to establish fisheries (Brockhoff and McLay 2011). Recently, yacht fouling has become an increasingly well recognised vector (Peters et al. 2014) and two crab species (*Percnon gibbesi* and *Hemigrapsus sanguineus*) have been introduced by this vector. However, due to the slow traveling speed of yachts it is unlikely that this vector is responsible for very long distance introductions. The introduction of marine species through freshwater water canals is not a common occurrence. However, two species from the family Varunidae (*E. sinensis* and *E. hepuensis*), both catadromous species from the North West Pacific, have been introduced via freshwater canals to inland Seas in Southern Iran, Iraq and Kuwait (Naser et al. 2012; Naderloo 2014). In addition, although the aquarium trade is sometimes overlooked as a vector, it has been responsible for the introduction of the crabs, *P. gibbesi* (Calado 2006) and *Callinectes sapidus* (Nehring et al. 2008).

The role of traits in crab invasions

In addition to the role of extrinsic factors in the success of biological invasions, it has been suggested that alien species possess certain characteristics important for their invasion success (Sakai 2001; Cardeccia et al. in press). Traits commonly thought to be associated with successful invaders include longevity, a large body size, high fecundity, long larval development, planktonic dispersal, generalist behaviour in terms of food and habitat preferences and broad environmental tolerance (Crawley 1989; Ehrlich 1989; Weis 2010; Hänfling et al. 2011).

Despite specific traits having been identified as important for the invasion success of taxa such as cacti (Novoa et al. 2015), bivalves (Nawrot et al. 2015) and amphipods (Grabowski et al. 2007), this study found no patterns in the traits of alien crabs that could be associated with their ability to establish, their taxonomic identity (i.e. at the family level) or the vectors through which they are transported. While this finding was unexpected, and offered no support to the *a priori* hypotheses that, crabs with established populations would be characterised by traits allowing them to survive under a variety of conditions and established and single record species would possess traits facilitating transfer by humans, these results could be explained by several factors.

The number of traits included in a trait analysis will influence the outcome (Bremner et al. 2006), with the inclusion of as many species as possible and the largest diversity of traits resulting in greatest resolution of important suites of traits. While this study strove to include crabs that have been recorded as alien as well as those that have not spread outside their native range and included as many traits as possible, the ability to do so was limited by the information available in the literature. As a result, nine traits were considered for 28 alien species. While this represents the first time that the traits of crabs have been assessed in such detail, the inclusion of more species and more traits in future analyses may result in the identification of traits important for invasion success not detected in the present study. Traits that have been identified as important for invasions, but which could not be included in the present study due to the lack of information, include aggression, growth rate (Weis 2010), salinity tolerance (Hänfling et al. 2011), feeding activity (Spilmont et al. 2015) and larval dispersal potential (Brousseau and McSweeney 2016). Future studies should strive to include these traits.

High levels of plasticity within traits enable species to adapt to a range of environmental conditions between and within the native and invaded habitats, thereby increasing their establishment success (Smith 2009). As such, the variability within traits and the plasticity with which they manifest might be key to invasion success. For example *E. sinensis* and *C. maenas* show a significant increase in body size in their introduced region (Grosholz and Ruiz 2003). Similarly, alien populations of *H. sanguineus* show earlier sexual maturation (Brousseau and McSweeney 2016), while *E. sinensis* shows significant variability in sexual maturation when compared to populations in their native range (Rudnick et al. 2005b). Unfortunately, not all traits have been assessed in this detail for all species and so this study was unable to consider variability in traits.

While some studies have highlighted traits that may be important in crab invasions, contrasting the findings of this chapter, it is important to consider the scale at which these were undertaken. These studies considered single species comparisons i.e. contrasting alien crabs between their native and invaded ranges (Grosholz and Ruiz 2003), or by comparing alien species with native species in a specific region (Brousseau and McSweeney 2016). While these studies are informative, it is important to acknowledge that their findings may be context dependent, potentially varying with individual introduction event, reflecting the genetic makeup of the founding population, the environmental conditions of the recipient region and the native fauna encountered (Crawley 1989). One of the strengths of multi-species analyses, such as the one undertaken in this study, is that they are able to elucidate general patterns present at a high taxonomic level. Nonetheless, the fact that this study was not able to identify a suite of traits important for invasion success in crabs does not mean that they do not exist for the reasons explained above.

Conclusion

This chapter has highlighted that 56 crab species from 15 families have been recorded outside their native ranges. These crabs come from many bioregions and have been introduced to all regions except Antarctica. The vectors through which they have been transported are varied, but shipping related transport has been responsible for the most introductions. The factors interacting to ultimately govern the invasion success of alien crabs, as with marine alien species in general, are complex and it was not possible to identify traits predisposing species to being successful invaders. Nonetheless, as more biological information becomes available for more species, such traits may become apparent. Notably, the rate of discovery of alien crabs is increasing exponentially, highlighting the importance of developing watch-lists for these invaders.

Chapter 2: What do we know about the impacts of marine alien crabs? Insights from a global assessment

Marine invasions can pose a threat to society and biodiversity alike. Although there is consensus that marine alien species need to be managed and impacts mitigated, resources are limited. A useful approach is to assess impacts and prioritise the management of those species associated with the most severe impacts. This chapter applied the Environmental Impact Classification for Alien Taxa (EICAT) to assess the environmental impacts of the 56 crab species previously identified as alien. In addition, all management efforts focused on these species were interrogated. Finally, traits potentially correlated with the severity of impact were investigated. Notably, only five of the 56 alien crab species could be assessed using the EICAT scheme, with the remaining 91% being excluded due to data deficiency. Even for the species for which impact had been quantified, studies had only been undertaken in 50% of the bioregions in which they occur. The Japanese shore crab *Hemigrapsus sanguineus*, was found to have the most severe impacts (Major impacts) as it alters the composition of native communities. Impacts of the remaining four species i.e. the Chinese mitten crab *Eriocheir sinensis*, European shore crab *Carcinus maenas*, Indo-Pacific swimming crab *Charybdis hellerii* and brush-clawed shore crab *Hemigrapsus takanoi*, were all categorised as Moderate as they manifest at the level of populations. Reflecting the predatory and competitive nature of these crabs, predation followed by competition were the main mechanisms through which the species impacted native biota. Management actions had only been executed for *C. maenas*, *E. sinensis* and *H. sanguineus* with the number of actions implemented being correlated with the time since discovery. Management actions were most often preventative, while eradication of established populations was most seldom attempted. No traits predisposing species to having more severe impacts were identified, although the scarcity of trait and impact data might have confounded these results. The general scarcity of data considering the impact of alien crabs might reflect a research bias towards 1) wide ranging conspicuous species with social or economic impacts; and 2) regions that have a biosecurity focus. Nevertheless, findings of this chapter demonstrate that alien crabs have the potential to cause severe ecological impacts and highlights the need for studies quantifying the impacts associated with this group.

Introduction

The rate of introduction of alien species is rising at an unprecedented rate around the globe (Ruiz et al. 2011) with many of these species thought to negatively affect society through their impacts upon socio-economic values (Binimelis et al. 2008; Jeschke et al. 2014) and human health (Hulme 2014).

However, these species can also have wide-spread, multifaceted and significant ecological impacts in their recipient environments (Measey et al. 2016; Kumschick et al. 2017a). Environmental impacts include effects on native individuals and measurable changes to the properties of indigenous populations, communities and ecosystems (Vitousek 1996; Parker et al. 1999; Blackburn et al. 2014). As such, the environmental impacts of alien species are recognised by scientists (Ojaveer et al. 2015; Kumschick et al. 2017a) and policy makers (CBD 2013) as a major threat to biodiversity that needs to be managed (Nentwig et al. 2010). As resources to manage alien incursions are limited (Hester et al. 2013), it is important to identify and prioritise species of greatest concern and thus minimise their associated impacts (Measey et al. 2016). However, how to prioritise potential target species is not always clear (Nentwig et al. 2010). One approach that has received increasing attention in the literature in recent years has been the prioritisation of species that cause the greatest impact (Blackburn et al. 2014; Evans et al. 2016; Measey et al. 2016).

A number of approaches and scoring systems for assessing and prioritising species based on their environmental impacts have been proposed and implemented. These include the Biopollution Assessment (Olenin et al. 2007), Invasive Species Assessment Protocol (Randall et al. 2008), Generic Impact-Scoring System (GISS) (Nentwig et al. 2010; Kumschick et al. 2012) and *Harmonia*⁺ and *Pandora*⁺ risk screening (D'hondt et al. 2014) and the most recent of these was proposed by Blackburn et al. (2014). Hawkins et al. (2015), proposed guidelines for the implementation of this framework and termed it the Environmental Impact Classification for Alien Taxa (EICAT). This is the formal system used by the IUCN (International Union for Conservation of Nature) to classify the threats that alien species pose to the environments they invade. It identifies twelve mechanisms through which impact can manifest, thus aligning with the IUCN Global Invasive Species Database. Ultimately, this system assigns species to one of five impact categories, ranging from Minimal Concern to Massive reflecting an increase in impact severity. EICAT is thus a simple standardised system that can be used to rigorously classify alien species in terms of the magnitude of their highest level of deleterious environmental impact, thereby supporting the identification of species of greatest concern. Although impact assessments have extensively been applied to terrestrial invasions (Kumschick and Nentwig 2010; Nentwig et al. 2010; Kumschick et al. 2015a; Evans et al. 2016), such assessments have rarely been applied for marine species (Ojaveer et al. 2015).

Predatory crabs are among some of the most successful marine invaders (Brockerhoff and McLay 2011; Hänfling et al. 2011; Jormalainen et al. 2016) with 56 species documented as introduced (see Chapter 1) and two of these, the European shore crab *Carcinus maenas* and the Chinese mitten crab *Eriocheir sinensis*, included on the world's 100 worst invasive alien species list (<http://www.iucngisd.org/gisd/>). As crabs are known for their voracious, competitive and predatory

nature, even in their native habitats (Forsström et al. 2015; Howard et al. 2017), it is not surprising that they have been highlighted as a source of ecological change in their invasive ranges (Grosholz et al. 2000; Epifanio 2013).

Considering the above, a global assessment of impact of all alien predatory crab species using a standardised scoring approach would be valuable. This study therefore aims to use the EICAT scheme to assess the environmental impacts of alien predatory crabs in order to identify species of greatest concern. Additionally, it aims to identify traits that may be associated with crabs that have high ecological impacts.

Methods

Literature search

Following Hawkins et al. (2015), all published information and grey literature recording the environmental impacts of the 56 alien species identified in Chapter 1 and the management strategies applied within their introduced ranges was collated and reviewed. Following a similar method to others (Nentwig et al. 2010; Measey et al. 2016), this was done by means of a literature search in Google Scholar®, using each species scientific and common name in isolation and in combination with the word “impact’ as search terms.

To identify if species with a longer invasion history and larger invaded range have been more extensively studied, the number of publications recording the impact of each species was correlated against 1) their date of first discovery; and 2) their invaded range size. This data was obtained from Chapter 1. To statistically consider these relationships, Spearman’s rank correlations were run in Statistica 13. This programme was used for all analyses in this chapter. For one species, *Halicarcinus planatus*, date of first discovery was not available and as such this species was excluded for this analysis.

EICAT assessment

Using EICAT through the application of the guidelines from Hawkins et al. (2015), crabs were classified according to their negative environmental impacts across their global introduced range. As it was not possible to assess current impacts based on the available literature only the maximum impact (i.e. greatest negative impact recorded) was considered. During classification, the impacts of each alien crab species was categorised under one of the 12 mechanisms by which impact can occur i.e. 1)

competition; 2) predation; 3) hybridization; 4) transmission of diseases to native species; 5) parasitism; 6) poisoning/ toxicity; 7) bio-fouling; 8) grazing/ herbivory/browsing (defined as grazing from this point); 9) chemical; 10) physical or 11) structural impact on ecosystem; and 12) interaction with other alien species (defined as interaction from this point). A Chi-squared test was used to compare the number of publications reporting each mechanism. For each species, reported impacts were assigned to one of five categories to obtain the impact rating (here after referred to as EICAT ratings). These EICAT ratings are, in order of ascending severity of impact, Minimal Concern (MC); Minor (MN); Moderate (MO); Major (MR) and Massive (MV). Species with known alien populations, but for which no or insufficient impact information was found, were classified as Data Deficient (DD; Table 2.1). A Chi-squared test was used to compare the number of species recorded in each EICAT category. A confidence rating (low, medium or high) was assigned to these impact categories to quantify uncertainty. This is based on the availability, type, quality and reliability of the data, degree of contradiction between data sources and the spatial scale at which impacts are recorded. For a detailed description of the mechanisms, impact categories and confidence ratings see Hawkins et al. (2015).

To gain an understanding of how impacts by alien crabs and studies considering these impacts vary geographically, the congruence between a species introduced ranges and the location of impact studies was considered. See Table 2.2 for a detailed listing of the bioregions.

Table 2.1 EICAT categories used to rate species based on their environmental impacts (as per Hawkins et al. (2015)).

EICAT categories	Abbreviation	Description of categories
Minimal Concern	MC	Negligible impact on native species individuals and no effect on fitness
Minor	MN	Reductions in fitness of individuals, but no declines in native population sizes
Moderate	MO	Declines in native population, but no changes in community composition
Major	MR	Reversible changes in community composition if the alien taxon is removed
Massive	MV	At least local extinction of native species and even with removal of alien species changes in community composition are irreversible
Data Deficient	DD	Species with known alien populations, but for which no or insufficient impact information was found

Table 2.2 The 18 IUCN bioregions (Kelleher et al. 1995 a, b, c, d) and abbreviated codes. (Refer to Figure 1.1 for a map).

Code	Bioregion	Code	Bioregion
ARC	Arctic	ARA	Arabian Seas
MED	Mediterranean	EAF	East Africa
NWA	North West Atlantic	EAS	East Asian Seas
NEA	North East Atlantic	SP	South Pacific
BAL	Baltic	NEP	North East Pacific
CAR	Wider Caribbean Sea	NWP	North West Pacific
WA	West Africa	SEP	South East Pacific
SA	South Atlantic	ANZ	Australia and New Zealand
CIO	Central Indian Ocean	ANT	Antarctica

Traits

To assess the potential role that biological and ecological traits may play in determining the severity of the impacts of alien crabs, carapace width (cm), longevity (years), fecundity (number of eggs/year) and native and invaded range size (defined as the number of IUCN bioregions in which they occur) were correlated against the EICAT rating for each species. Trait data was extracted from Chapter 1. Values for fecundity were logged transformed to correct for non-normal distributions. Spearman's rank correlations were used to determine the relationship between trait and impact severity.

Management actions

For each crab species for which an EICAT rating was generated, all management actions were extracted from the literature, while also documenting the geographic location where these were implemented. These management actions were then classified as monitoring, prevention, control or eradication (following Hawkins et al. (2015)). To identify if a species coverage in the literature, its invaded range size or the duration of its invasion history affected the number of management actions undertaken against the invader, the number of management actions for each species was correlated against 1) the number of publications detailing impact (Spearman's rank correlation); 2) the number of bioregions invaded by each species (Spearman's rank correlation); and 3) the date of first discovery of each species (Pearson's correlation).

Results

Quantification of impact in the literature

Only 9% (i.e. five out of 56) of the crab species reported as alien could be rated using the EICAT scheme due to the absence of quantified environmental impact information for the remaining 51 species (Fig. 2.1). It is notable that even for the five species for which impact has been quantified, few publications had documented their impact. In fact, fewer than four studies quantified the environmental impact of three of the species.

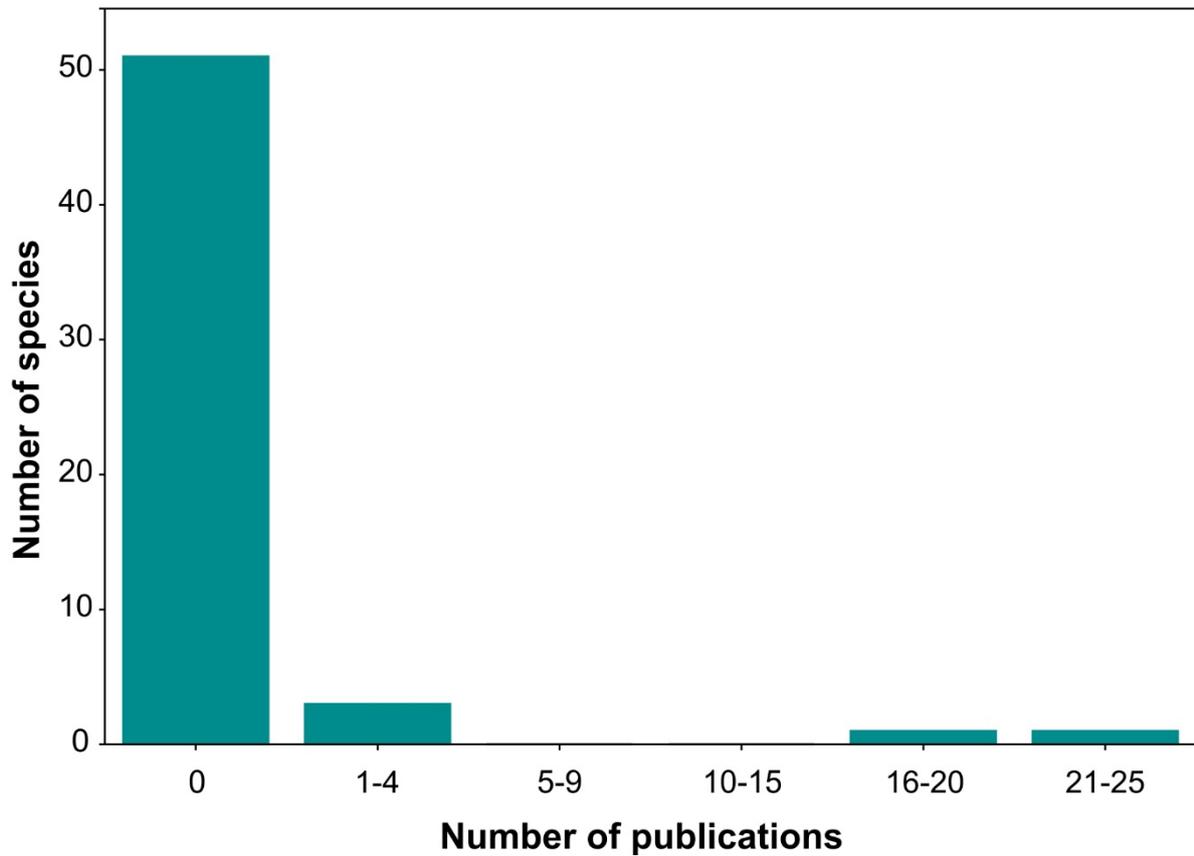


Figure 2.1 The number of alien crab species for which impact was considered by varying numbers of publications. The species for which publications were available are *Charybdis hellerii* (2 publications), *Hemigrapsus takanoi* (3 publications), *Eriocheir sinensis* (4 publications), *Hemigrapsus sanguineus* (16 publications) and *Carcinus maenas* (21 publications).

In total, only 46 publications were found to describe the impact of five species, *Hemigrapsus sanguineus*, *Eriocheir sinensis*, *Carcinus maenas*, *Charybdis hellerii* and *Hemigrapsus takanoi* (Table 2.3; see Appendix 2.1 and 2.2). Of these, 24% (11 publications) contained data describing the most severe impacts of these species and were used to allocate an EICAT rating to each based on their maximum impact reported.

Table 2.3 Number of publications reporting environmental impacts and those recording the highest impacts for each of the five crab species. See Appendix 2.1 and 2.2 for a list of references for each of the species.

Species	Environmental impact publications	Publications recording highest impact
<i>Carcinus maenas</i>	21	7
<i>Hemigrapsus sanguineus</i>	16	1
<i>Eriocheir sinensis</i>	4	1
<i>Hemigrapsus takanoi</i>	3	1
<i>Charybdis hellerii</i>	2	1

The paucity of studies documenting impact could not be explained by most species only recently having been recorded for the first time as there was no correlation between the date of first discovery and the number of publications reporting impact (Spearman's rank correlations; $r = -0.25$, $p > 0.05$; Fig. 2.2a). There was, however, a significant correlation between the number of impact studies and invaded range size of the species (Spearman's rank correlations; $r = 0.57$; $p < 0.05$; Fig. 2.2b).

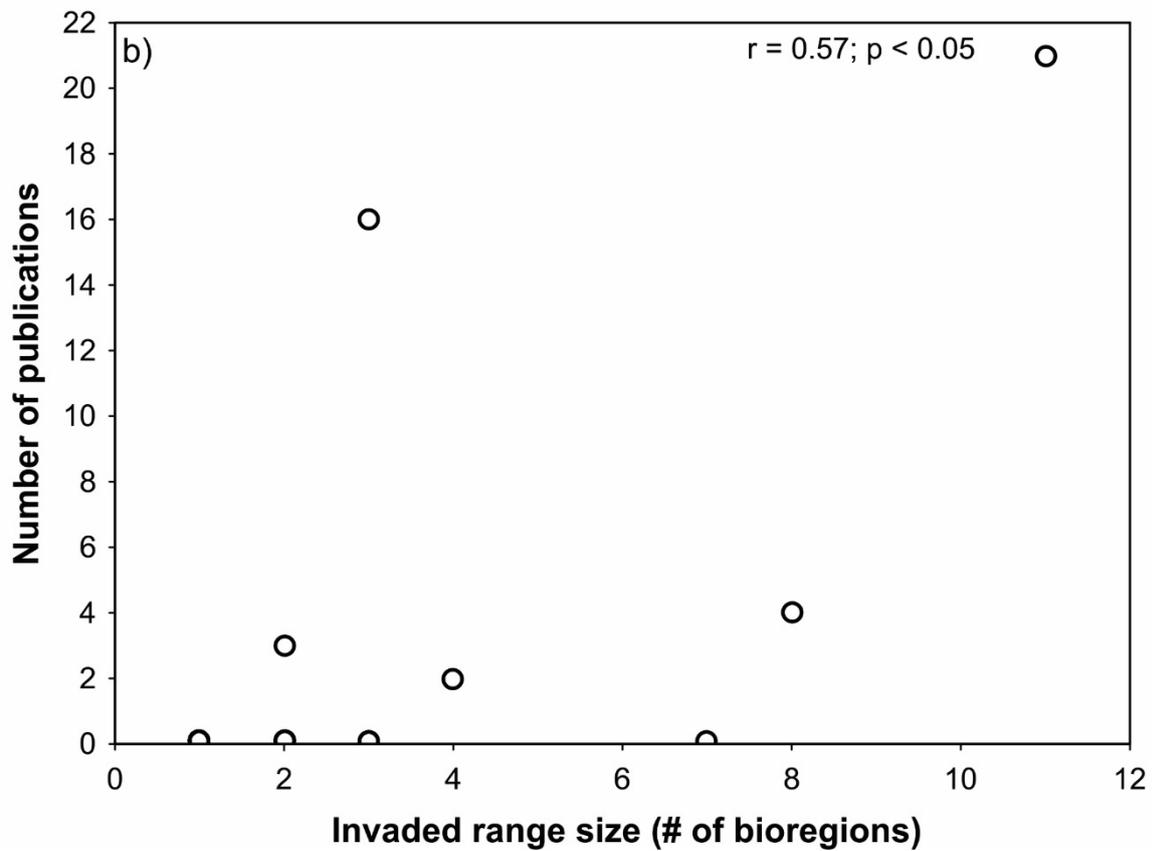
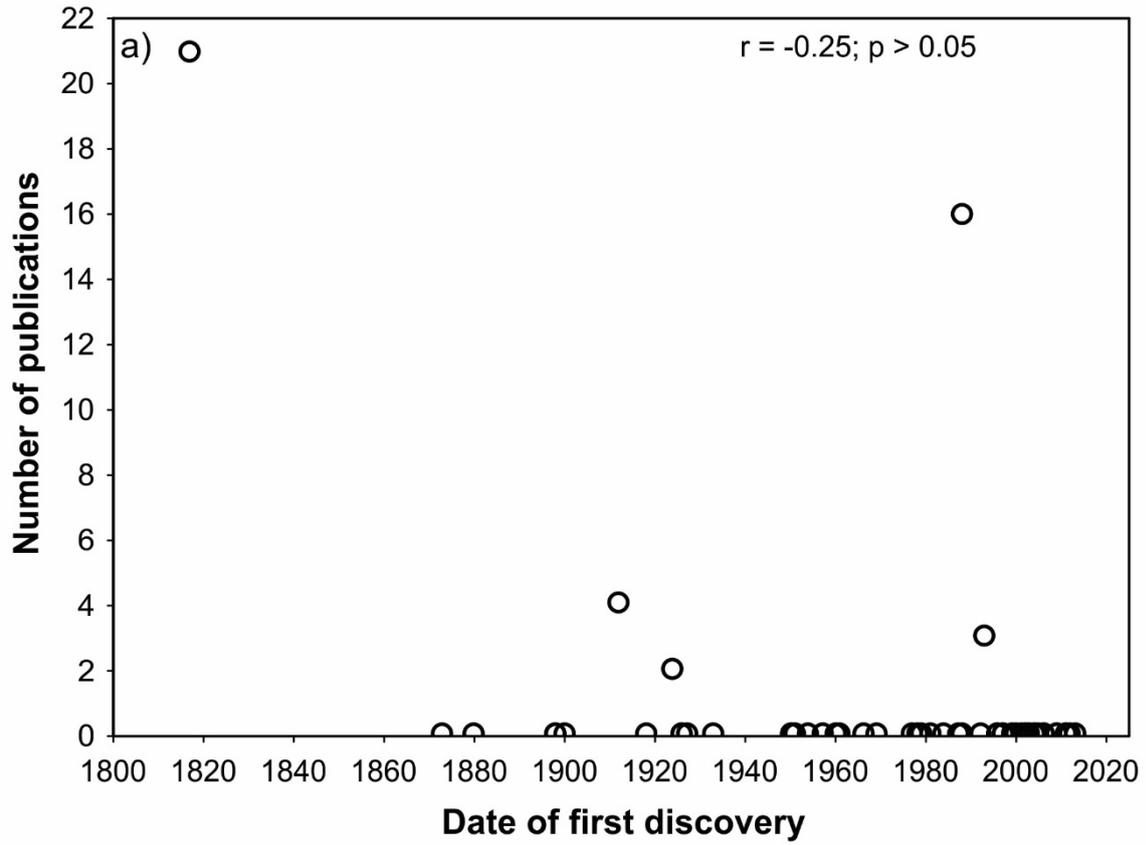


Figure 2.2 Scatterplots demonstrating the relationship between number of impact publications available for each of the 56 crab species and a) their date of first discovery and b) invaded range size.

EICAT assessment

The EICAT assessment of each alien crab species is summarised in Table 2.4. One species, the Japanese shore crab *Hemigrapsus sanguineus*, received an EICAT rating of MR (Major) while four were rated as MO (Moderate). No information was found on the impact of the remaining 51 species (i.e. 91% of crabs recorded outside of their native ranges) and these were therefore classified as DD (Data Deficient) (See Appendix 2.3). There was a significant difference in the number of species assigned to each EICAT category (Chi-squared; $X^2 = 232.89$; $df = 5$; $p < 0.001$; Fig. 2.3), with most of the species being Data Deficient. For a detailed description of the impacts caused by each species, and the rationale behind assigning species to the various mechanisms, EICAT ratings, and the allocation of confidence ratings see Appendix 2.4.

Table 2.4 EICAT assessment results for the five alien crab species based on their maximum impacts. Refer to Appendix 2.4 for a description of their impacts and detailed EICAT assessments.

Species	Mechanism	EICAT rating	Confidence	References used to assign ratings
Family Varunidae				
<i>Hemigrapsus sanguineus</i>	Competition	Major	Medium	Kraemer et al. 2007
<i>Hemigrapsus takanoi</i>	Competition	Moderate	Low	Dauvin et al. 2009
<i>Eriocheir sinensis</i>	Predation	Moderate	Medium	Rosewarne et al. 2016
Family Portunidae				
<i>Carcinus maenas</i>	Competition, predation, grazing, interaction	Moderate	Medium	Glude 1955; Grosholz and Ruiz 1995; Grosholz et al. 2000; Grosholz 2005; Kimbro et al. 2009; de Rivera et al. 2011; Garbary et al. 2014
<i>Charybdis hellerii</i>	Competition, predation	Moderate	Medium	Felder et al. 2009

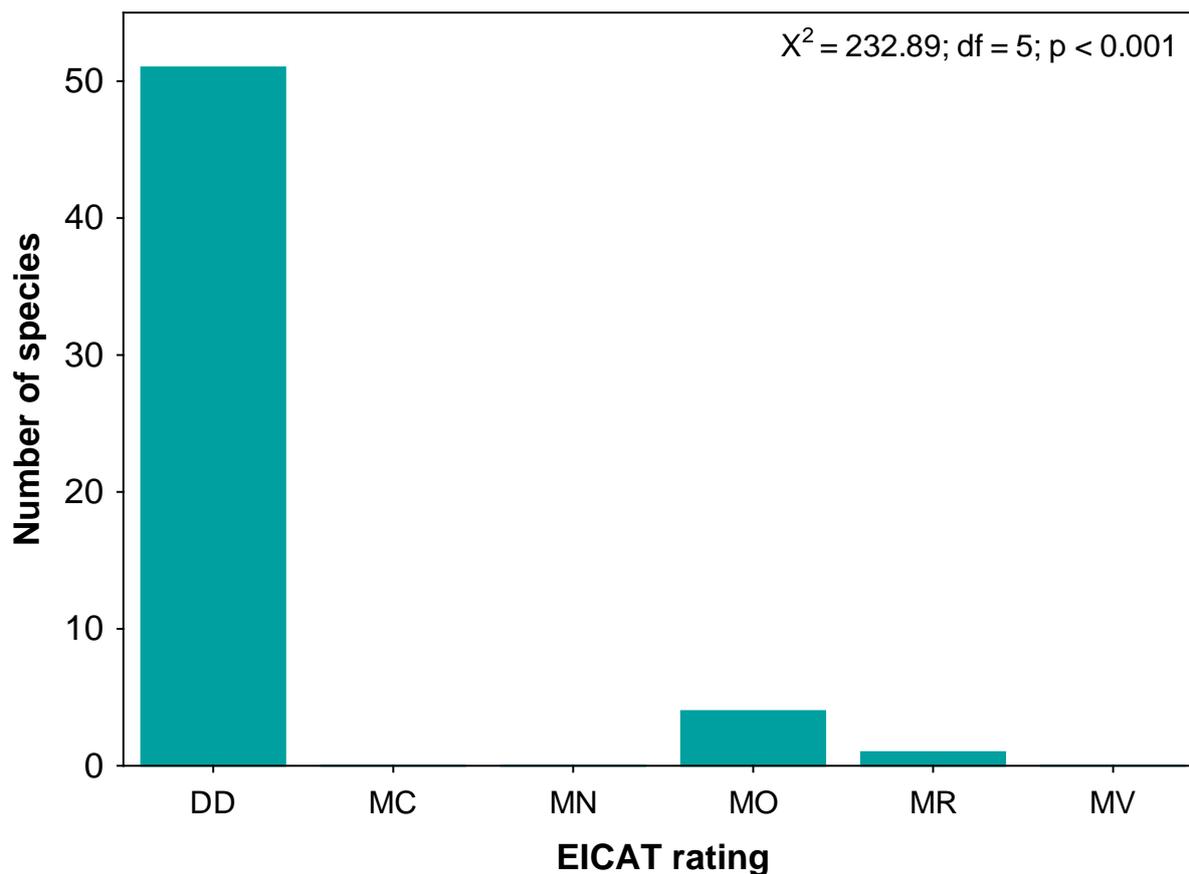


Figure 2.3 The number of crab species allocated each EICAT category. DD: Data Deficient; MC: Minimal Concern MN: Minor; MO: Moderate; MR: Major and MV: Massive.

The species that received the highest EICAT rating (i.e. Major) was *H. sanguineus*, with this level of impact being reported by a single publication. Similarly, for *H. takanoi*, *C. hellerii* and *E. sinensis* maximum impacts were noted by only single reports detailing Moderate impacts. In contrast, seven publications reported maximum impact of *C. maenas*, with this species being rated as having Moderate impact. It is notable that the mechanism through which the two *Hemigrapsus* species achieved their maximum impact was competition (Table 2.4). Despite not being found to have the most severe impacts of the crabs that were rated, *C. maenas* achieved impact through four mechanisms, more than any other species. None of the impact assessments received a high confidence rating. While four species were allocated a medium confidence rating, the rating of *H. takanoi* was assigned with low confidence due to the anecdotal nature of the literature. Although there was no significant difference in the number of publications that reported each mechanism (Chi-squared; $\chi^2 = 6.0; df = 3; p > 0.05$; Fig. 2.4), predation was noted most often. Although not the most frequently reported mechanism, competition was responsible for causing the greatest variety of

impact types (Fig. 2.5). Decreased abundance of native species was the most common type of impact recorded for alien crabs.

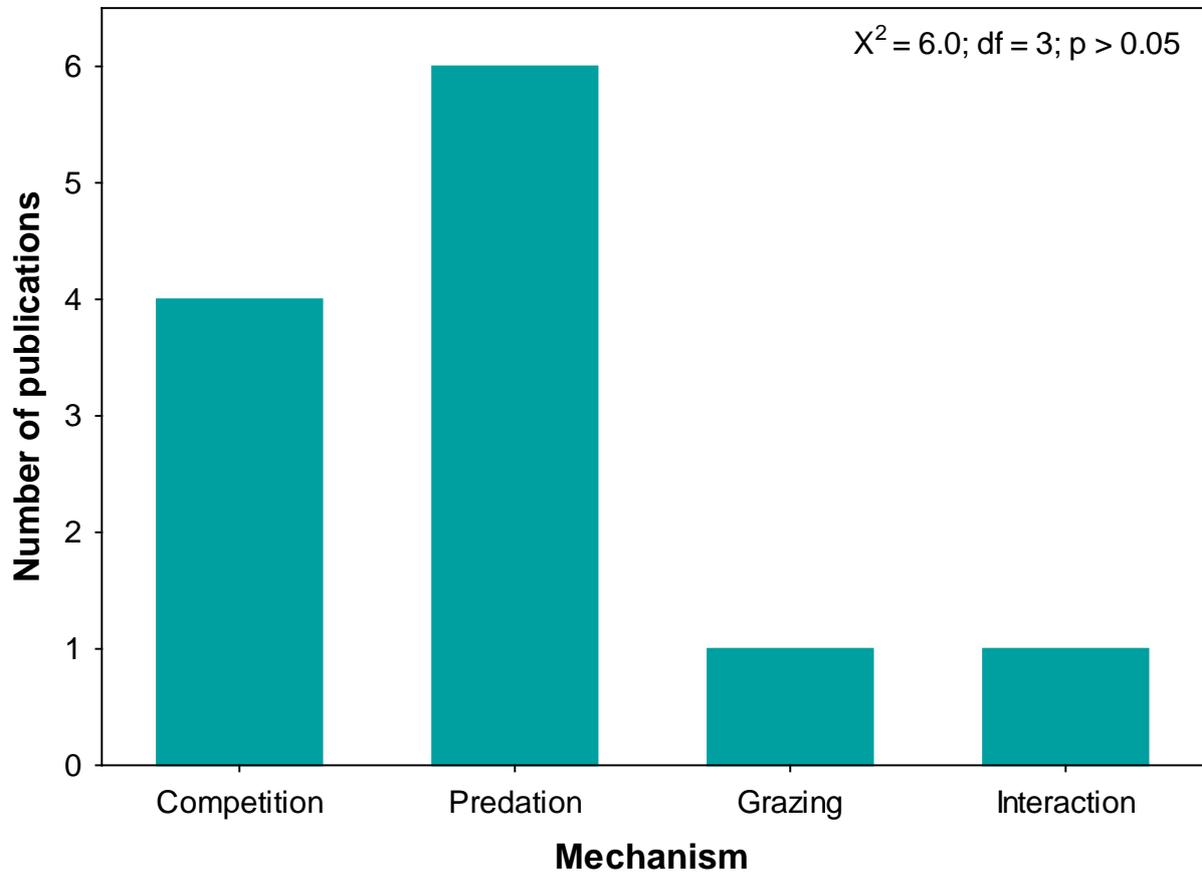


Figure 2.4 Number of publications reporting the various mechanisms involved in the maximum impacts of the five crab species rated by the EICAT scheme.

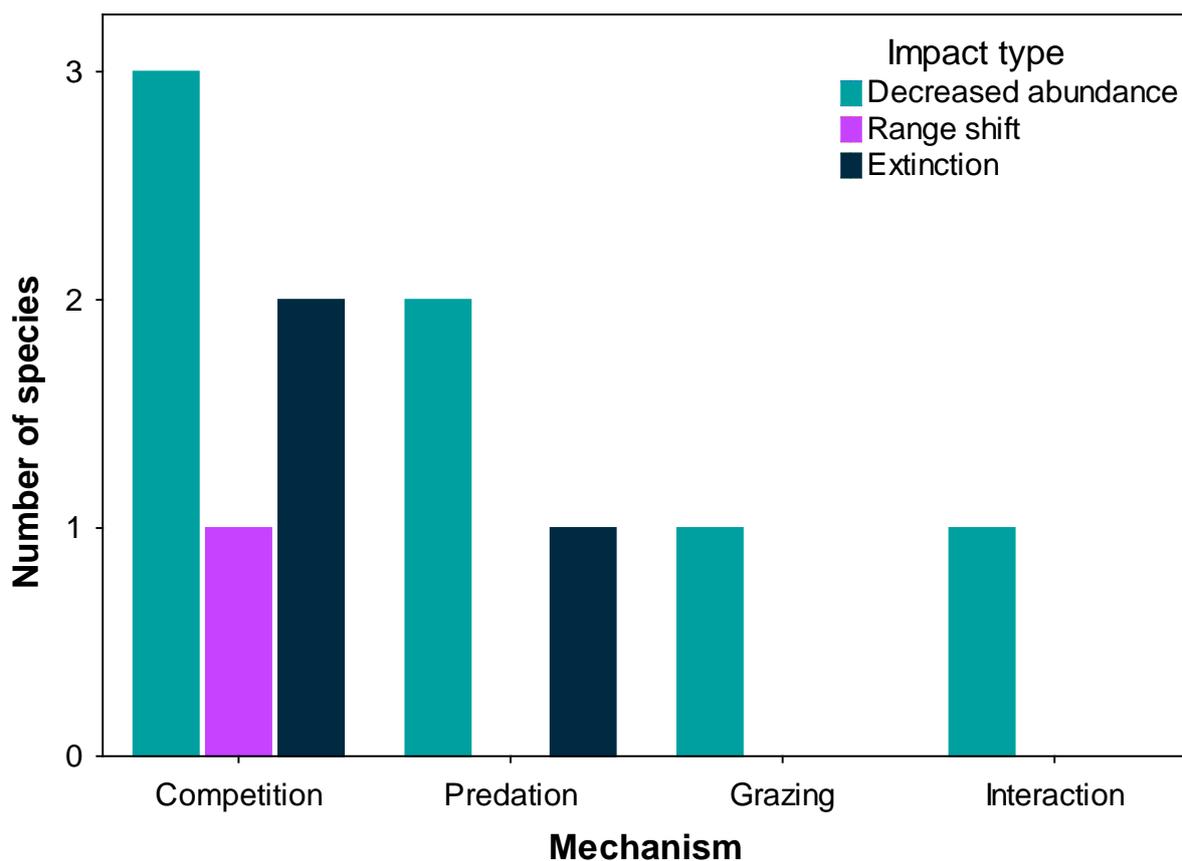


Figure 2.5 Types of impacts and the mechanism through which they manifest in alien crabs.

Alien crab species are known from 17 of the 18 bioregions (Fig. 2.6). Despite the wide geographical area over which these alien crabs have been recorded, impact has been quantified for only 9% of species and then in only 50% of bioregions in which they occur. The European shore crab *C. maenas* occurred in the most bioregions (11) and its impact had been quantified in four of these regions. Notably, its highest recorded impact was noted in two bioregions i.e. the North West Atlantic (NWA) and North East Pacific (NEP). For each of the remaining four species impact had been quantified in a minimum of two of the bioregions in which they occurred and their highest impacts were recorded in only one region. The impacts of alien crabs were most often quantified in the North East Atlantic bioregion (NEA). Even though the Mediterranean region (MED) supports the largest number of alien crab species (33 species, see Chapter 1), no assessments of impact have been undertaken in this bioregion. Additionally, no impacts have been considered in the ARC, CIO, ARA, EAF, EAS, SP, NWP or SEP bioregions despite alien crabs being present in these regions. Incidentally, the only two impact assessments conducted in the North West Atlantic (NWA) (one for *H. sanguineus* and one for *C. maenas*) were also the highest recorded impacts for these two species.

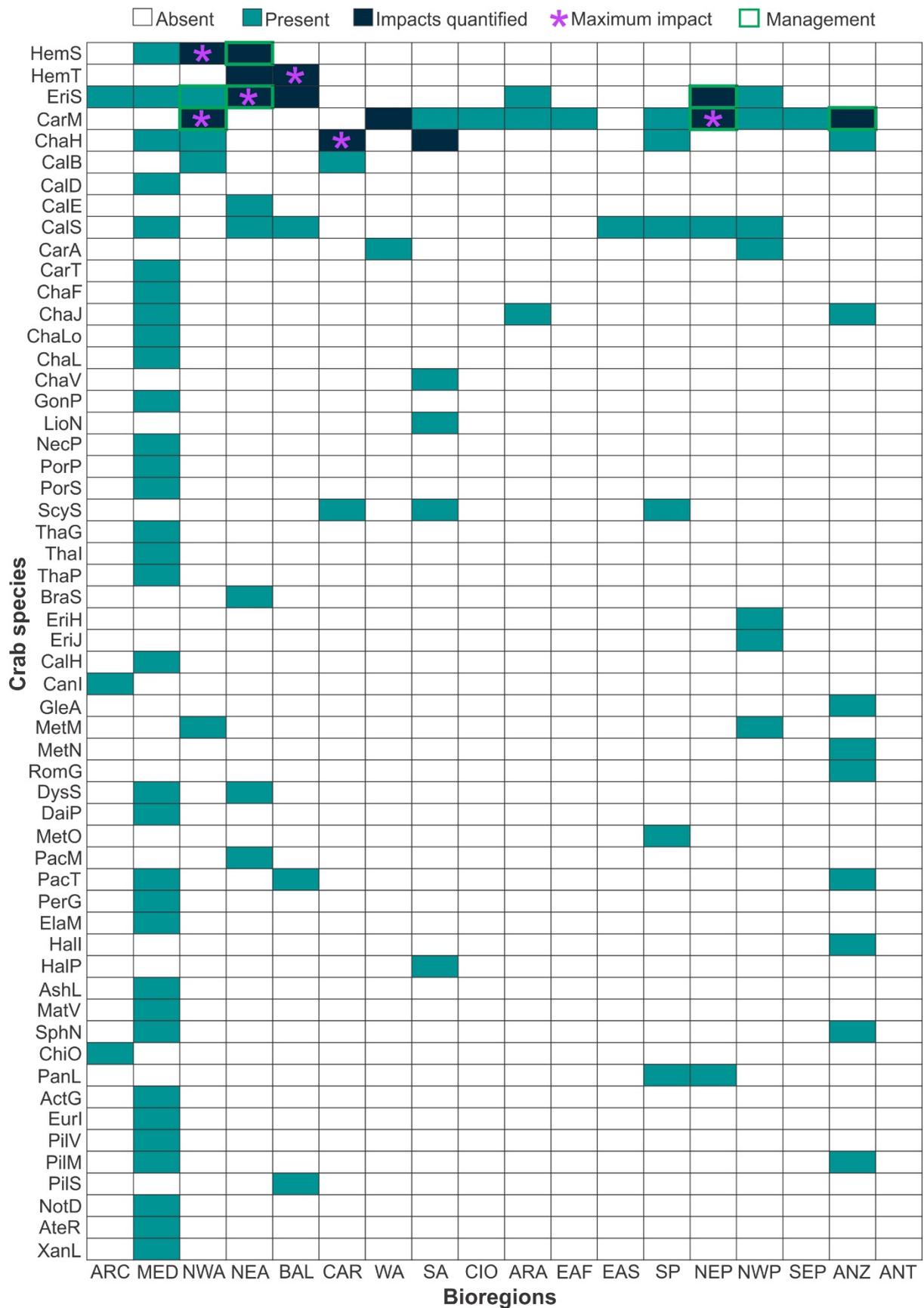


Figure 2.6 Distribution of species, assessments of impact and implementation of management actions across 18 bioregions (refer to Chapter 1, Table 1.3 for species names and Table 2.2 above for bioregion codes).

Traits

No relationship was found between carapace width (Spearman's rank correlation; $r = 0.19$; $p > 0.05$), longevity (Spearman's rank correlation; $r = 0.39$; $p > 0.05$) or fecundity (Spearman's rank correlation; $r = 0.13$; $p > 0.05$) and the severity of impact by alien crabs. Similarly no relationship was found between native (Spearman's rank correlation; $r = 0.20$; $p > 0.05$) or invaded range size (Spearman's rank correlation; $r = 0.19$; $p > 0.05$) and impact severity (Fig. 2.7).

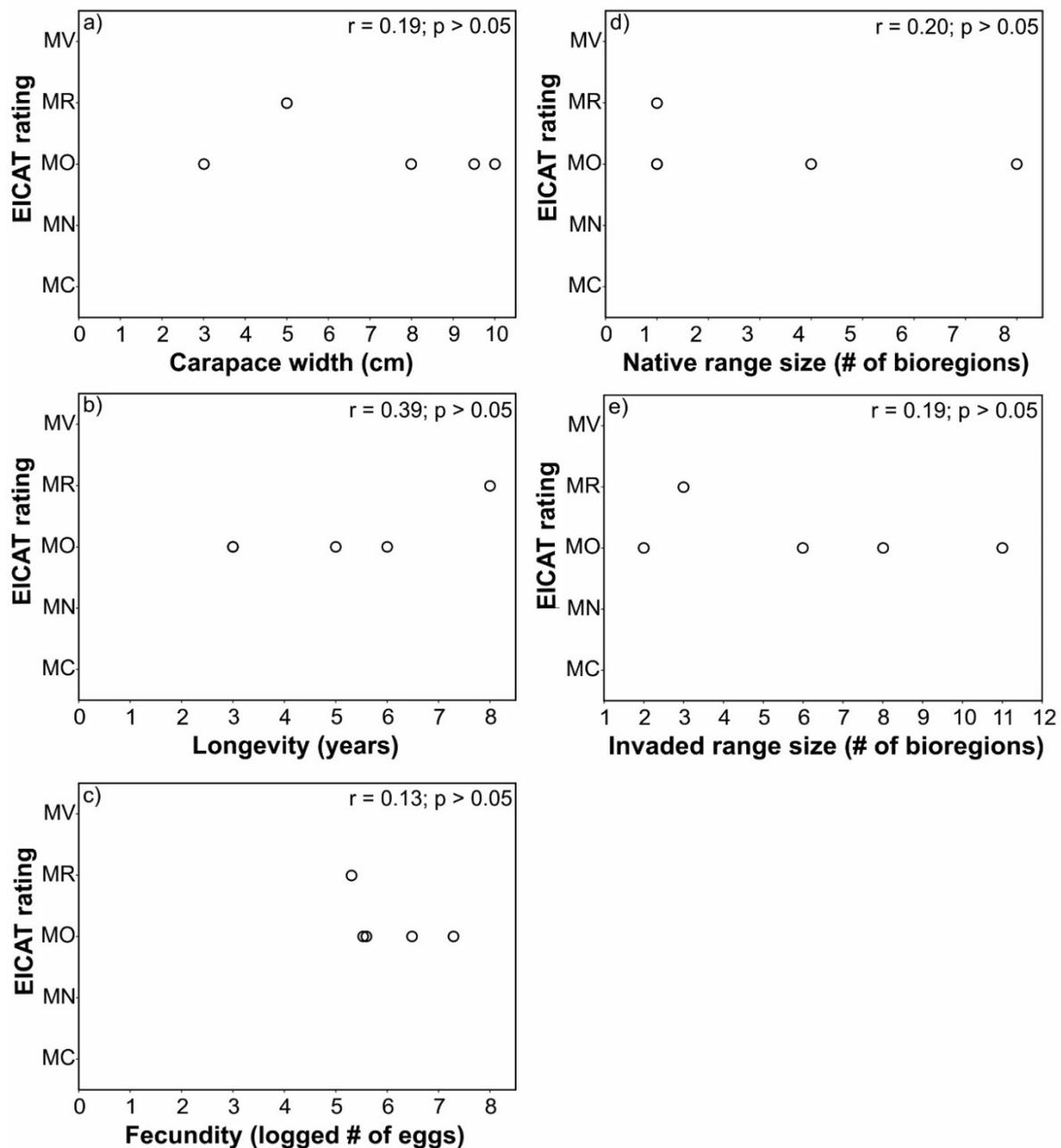


Figure 2.7 Correlations between EICAT ratings and the a) carapace width; b) longevity; c) fecundity; d) native; and e) invaded range size of the five crab species as reported in the literature.

Management actions

Management actions have been implemented for *C. maenas*, *E. sinensis* and *H. sanguineus* while none have been reported for *C. hellerii* or *H. takanoi* (Table 2.5). These management efforts were reported in 50% of the bioregions in which impact had been quantified for alien crabs and include the North West Atlantic (NWA), North East Atlantic (NEA), North East Pacific (NEP) and Australia and New Zealand (ANZ) (Figure 2.6). Prevention was the most commonly applied management action and has been reported for all three species. In contrast, eradication was most seldom implemented, only being reported in one instance for *C. maenas*. Physical/ mechanical removal was the approach most frequently used to control crabs once they are already present in a region. *Carcinus maenas* not only had the most management actions in place, but was the only species for which monitoring, prevention, eradication and control had been implemented. This species has been managed in numerous locations within three bioregions (North West Atlantic (NWA), North East Pacific (NEP) and Australia and New Zealand (ANZ)). Five of the management actions recorded for *E. sinensis* were implemented in numerous localities within the North East Atlantic (NEA; i.e. England, Ireland, Spain and Germany) whereas six of the management actions in the NEP were all implemented in California, USA. Notably, preventative management actions are present in the NWA even though no impacts have been quantified for this species in this bioregion. This is owing to the risk assessment that has been conducted for this species in Canada. In comparison, *H. sanguineus* only had one risk assessment undertaken in the United Kingdom.

Table 2.5 Management actions classified according to aim and the methods by which they are implemented. Management actions exist for only three of the five crab species with EICAT ratings. No management actions have been recorded for *Charybdis hellerii* or *Hemigrapsus takanoi*.

	<i>Carcinus maenas</i>		<i>Eriocheir sinensis</i>		<i>Hemigrapsus sanguineus</i>	
	Method	Location	Method	Location	Method	Location
Monitoring	Monitoring program	Washington, USA (WDFW 2008)	Surveys and monitoring program Trapping program for monitoring	California, USA (Holmes and Osmondson 1998; Veldhuizen 1997)	none	
	Targeted monitoring and sampling	Northern Territory, Australia (Marine Pest Monitoring 2010)		England, UK (Morrit et al. 2013)		
	Trapping program for monitoring	Southern Tasmania, Australia (Martin and Proctor 2000)				
Prevention	Risk assessment	Washington, USA (Colnar and Landis 2007)	Risk assessment	California, USA (Cohen and Weinstein 2001)	Risk assessment	UK (Clark 2015)
		Canada (Therriault et al. 2008a)		East & West coast, Canada (Therriault et al. 2008b)		
	Legal status	Australia (Currie et al. 1998)		Legal status		
		Washington, USA (WDFW 2008)	California, USA (ANSTF 2002)			
	Best practices	Australia (Aqenal 2008)	Best practices	California, USA (ANSTF 2002)		
				North Pacific coast of America, USA (Grosholz and Ruiz 2002)		
		Ireland (Kelly and Maguire 2009)				
Eradication	Trapping	California, USA (de Rivera et al. 2007b)	none		none	
Control	Physical/mechanical	Maine, Massachusetts, USA (Lindsay and Savage 1978)	Physical/ mechanical	Germany (Panning 1939; Veldhuizen 2001)	none	
		New York, Massachusetts, USA (Walton and Walton 2001)		California, USA (White et al. 2000)		
		Prince Edward Island, Australia (JCG Resource Consultants 2002)		California, USA (ANSTF 2002)		
		Massachusetts, USA (Buttner et al. 2004)		Southern Spain (Garcia-de-Lomas et al. 2010)		
		Washington, USA (WDFW 2008)				

The number of publications on the impacts of species did not influence the number of management actions implemented (Spearman's rank correlation; $r = 0.87$; $p > 0.05$; Fig. 2.8a). For example, impact had been reported for *H. sanguineus* 16 times, but only one management action has been applied to this species. Likewise, species with larger invaded ranges did not have more management actions (Spearman's rank correlation; $r = 0.82$, $p > 0.05$; Fig. 2.8b). Notably more management actions were put into place to address species with longer invasion histories (Pearson's correlation; $r = -0.91$; $p < 0.05$; Fig. 2.8c).

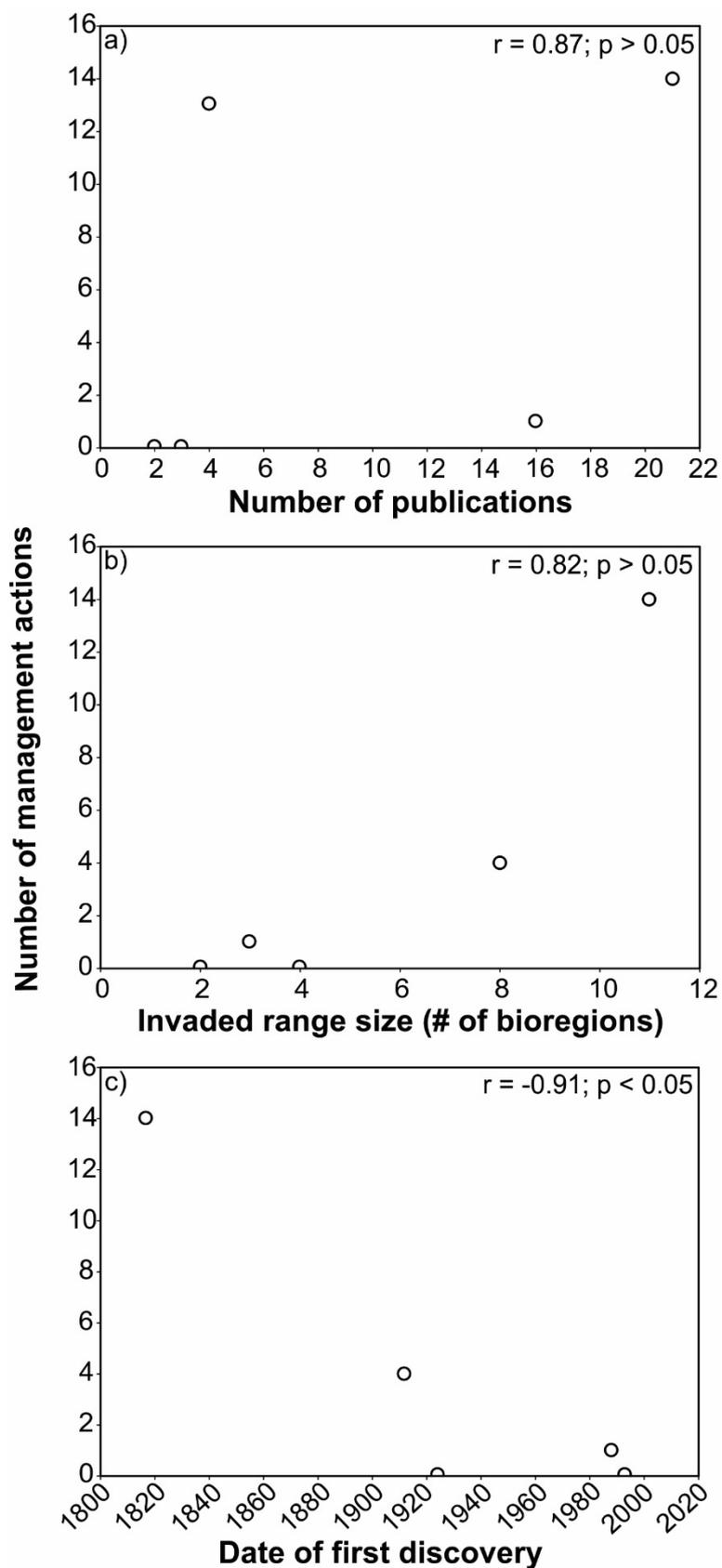


Figure 2.8 Scatterplots representing the relationship between the number of management actions implemented for each of the five EICAT rated crab species and a) publications documenting impact; b) invaded range size; and c) date of first discovery.

Discussion

The threat posed by alien species through the impacts they have in recipient regions is well recognised (Katsanevakis et al. 2014b; Kumschick et al. 2015a; Bellard et al. 2016) and consequently, the need to mitigate these impacts has been highlighted (Nentwig et al. 2010; Pyšek and Richardson 2010). One approach to achieving the goal of minimising impacts associated with invasions is to prioritise management of species causing the most severe impacts (Kumschick et al. 2012; Measey et al. 2016; Evans et al. 2016). Predatory crabs have been demonstrated to be successful invaders across the globe (Chapter 1), yet to date, little effort has been made to assess their environmental impacts on a global scale. In response, this study presents the first application of the IUCN endorsed EICAT scheme to a marine taxon. Most notably it was found that impacts had been quantified for only five of the 56 crabs that have been reported as alien. Thus, 91% of alien predatory crabs were considered data deficient and EICAT ratings could only be generated for the remaining five species. Of these species, the Japanese shore crab *Hemigrapsus sanguineus*, was found to have the most severe impact and was categorised as a species with Major impact. The remaining four species, the brush-clawed shore crab *Hemigrapsus takanoi*, Chinese mitten crab *Eriocheir sinensis*, European shore crab *Carcinus maenas* and Indo-Pacific swimming crab *Charybdis hellerii*, were categorised as having Moderate impact.

Despite their long history of introduction around the globe (see Chapter 1), the impacts of alien predatory crabs have seldom been quantified. While reflective of a general trend observed for marine alien taxa (Ojaveer et al. 2015; Ojaveer and Kotta 2015; Alexander et al. 2016; Robinson et al. 2017) there may be a number of factors driving this pattern. Firstly, invasions by crabs may truly result in few impacts. In this instance, the apparent data deficiency around quantification of impacts could be reflective of the fact that negative results are rarely published (Kumschick et al. 2015a; Evans et al. 2016; Kumschick et al. 2017a). There have, however, been few instances where experimental studies have detected no impacts by alien species (Davidson and Hewitt 2014) and it is thus considered unlikely that so many alien crabs have such few impacts across their invaded ranges. Secondly, it is possible that many of these species termed “data deficient” do in fact have impacts, but that these are yet to be quantified. The majority of literature on crab incursions simply reports on new records, abundances or population biology in new ranges (e.g. Sant’Anna et al. 2012a; Epifanio et al. 2013). Of the few studies that consider impact, most report on potential environmental impacts (e.g. Cohen et al. 1995; Gerard et al. 1999; Rudnick et al. 2000) with some being speculative without empirical evidence to support the conclusions drawn (e.g. Felder et al. 2009; Sant’Anna et al. 2012b). Thus, it is suggested that as more quantitative studies are undertaken to investigate impacts by these invasive predators, more ecological impacts are likely to become apparent.

Accepting that impacts have been quantified for few alien crabs, the question arises as to why impact has been measured for the five species that could be assessed using the EICAT scheme? This is likely a reflection of biases often observed in the field of invasion biology. The first bias relates to the fact that impact scoring of species is dependent on published data (Measey et al. 2016; Kumschick et al. 2017a). As wide ranging and conspicuous species are most often encountered, they may be studied most often (Pyšek and Richardson 2010), a process ultimately resulting in more published literature on such taxa (Olenin et al. 2010; Ojaveer et al. 2015). This is evidenced by the five species for which enough literature was available so as to assess their impacts being among the most wide-spread alien crabs. Additionally, their invaded range size was correlated with the number of studies considering their impact. The second bias stems from some regions being more actively engaged in biosecurity and the research that supports this important governmental function (Pyšek et al. 2008). In terms of crabs, this is reflected in the fact that impacts have been most often quantified in developed regions (for example the North West Atlantic (NWA), North East Pacific (NEP), Australia and New Zealand (ANZ), North East Atlantic (NEA) and Western Atlantic (WA) bioregions) which have been recognised for doing comparatively more research than developing regions (Vilà et al. 2010; Pyšek et al. 2008; Pyšek and Richardson 2010; Evans et al. 2016). It is notable, however, that despite supporting the highest number of alien crabs and being a largely developed region, the Mediterranean bioregion has produced no studies considering impact of alien crabs. The third bias reflects a research focus on alien species that cause more severe impacts (Hulme et al. 2013; Evans et al. 2016; Kumschick et al. 2017b). It has been suggested that this occurs because severe impacts are easily noticed and the data collected when assessing them is robust (Pyšek et al. 2008). Additionally, socio-economic (Pyšek and Richardson 2010) and human health impacts (Kumschick et al. 2015a; Ojaveer et al. 2015) have received more attention in the literature than environmental impacts. This is thought to be driven by these impacts being more apparent and thus more likely to be reported (Vilà et al. 2010), especially as they are perceived to have a greater impact upon society (Ojaveer et al. 2015). All the species that could be assessed using EICAT received relatively high EICAT ratings (i.e. Moderate or Major). Interestingly, *C. maenas*, *H. sanguineus* and *E. sinensis* are not only known for their negative environmental impacts, but also for their negative health and economic impacts (Glude 1955; Brousseau et al. 2001; Normant et al. 2002). As such these species might be perceived as carrying a greater cost to society (Ojaveer et al. 2015) and this could explain why their impacts have been studied.

The application of the EICAT scheme enabled some general patterns to be extracted about the impacts of alien predatory crabs. The impacts of these crabs resulted mainly in decreased abundance (extinction in extreme cases) and range shifts of native species (Kraemer et al. 2007; de Rivera et al. 2011; Rosewarne et al. 2016). The mechanisms through which these impacts manifested were

primarily predation and secondly competition. This finding was unsurprising as it reflects the predatory nature of the species chosen for this study and the competitive behaviour that has been reported for many species (Kraemer et al. 2007; MacDonald et al. 2007; Dauvin et al. 2009). While these generalities offer a first insight into the impacts of crabs outside their native ranges, it should be borne in mind that as impacts are quantified for more species, a more robust assessment will be possible for predatory crabs as a group. This is important as identifying the types of impacts and the mechanisms by which they occur are important for the management of these species (Kumschick et al. 2015a; Howard et al. 2017). While the impact ratings given to each species are important in themselves, they should be considered in light of the confidence with which these ratings were given. In this study, all ratings were allocated with medium confidence, excepting for the brush-clawed shore crab, *H. takanoi* where confidence was low. The medium confidence ratings were associated with various scenarios. Firstly, some of the studies were restricted to harbours or small locations that are not the typical spatial scale over which native communities can be characterised, although extrapolation under these circumstances is considered reliable (Hawkins et al. 2015). Secondly, although there was, in some cases, direct observational evidence in the field to support the assessment, these was not always coupled with experimental studies. Instead, results were inferred from these observations or from studies performed in laboratory settings. Thirdly, studies and evidence used to draw conclusions were scarce and / or circumstantial. The low confidence rating assigned to *H. takanoi* resulted from impact being inferred from observational and anecdotal information with no empirical data. As such, the evidence of impact was ambiguous and difficult to interpret. It is noteworthy that in the literature, impacts are often ascribed to alien species in this way (e.g. Molnar et al. 2008; de Greef et al. 2013; Katsanevakis et al. 2014b). As high confidence ratings are linked to large numbers of empirical studies (Hawkins et al 2015), low and medium ratings point to the dire need for more experimental studies to quantify the impacts of alien species (Kumschick et al. 2017a).

It has been suggested that a useful approach to understanding impacts by alien species is to identify traits correlated with the severity of their impacts (Nentwig et al. 2010; Measey et al. 2016; Novoa et al. 2016). Nonetheless, contrasting results have been attained for different taxa suggesting that the role of biological traits in regulating impacts is context dependent (Robinson et al. 2017). For example, fecundity has been found as a good predictor of magnitude of impact in amphibians (Measey et al. 2016) and mammals (Nentwig et al. 2010), but a weak predictor in birds (Evans et al. 2014). Size, on the other hand is strongly correlated with impact severity in amphibians (Measey et al. 2016), but weakly correlated for mammals (Nentwig et al. 2010) and birds (Evans et al. 2014). Despite traits having given insight into the impacts of some taxa, in this study, the traits of carapace width, longevity,

fecundity and native and invaded range size showed no association with the severity of impact by crabs. It is possible that other traits not assessed here (for example growth rate or habitat generalism), might show a relationship with severity of impact, but lack of detailed information on these traits for all species precluded their consideration. This lack of detailed biological information highlights another important gap in knowledge. Without foundational biodiversity knowledge, fields of applied ecology (like invasion biology) are unlikely to unlock their full potential.

The need to mitigate impacts by alien species is widely acknowledged (Nentwig et al. 2010; Blackburn et al. 2014). However, management actions directed specifically towards crabs have only been implemented for *H. sanguineus*, *C. maenas* and *E. sinensis*. It is interesting that the number of management actions taken for the five EICAT rated species showed no relationship with the number of studies considering their biological impacts or their invaded range sizes. Instead the greater the time since their first detection, the more actions were implemented to manage these species. These results are strongly influenced by the extensive management of *C. maenas* in North America and Australia and the fact that it was first recorded as alien in 1817. Markedly, these regions are well resourced and have well-developed biosecurity frameworks (Vilà et al. 2010; Azmi et al. 2015; Evans et al. 2016; Pyšek and Richardson 2010). The negative socio-economic and health impacts associated with *C. maenas*, *H. sanguineus* and *E. sinensis* might have been the motivation behind prioritising these species for management. Similar findings have been noted for alien mammals (Kumschick and Nentwig 2010). While these findings are based on an unavoidably small sample size, they suggest that the implementation of management likely occurs in response to perceived local threats and, at least for crabs, is not strategically undertaken in response to studies of biological impact. The fact that management actions have been implemented on the east and west coast of Canada for *E. sinensis*, even though no impacts have been quantified in these regions, provides further support for this notion.

Following such an approach where only species with high impact are managed, does however, increase the risk of a harmful invasion as any established species has the potential to cause an ecological impact (Pyšek and Richardson 2010; Ojaveer et al. 2015). Effective management should rather focus on a combination of approaches including prevention, early detection and rapid response (Meyerson and Reaser 2002; Hewitt et al. 2004b) with an awareness of species prioritised for their negative ecological impacts (Hulme 2006; Kumschick et al. 2015b). However, due to the paucity of studies quantifying the impacts of marine alien species (Ojaveer et al. 2015) together with practical and financial difficulties associated with management (Meyerson and Reaser 2002; Rejmánek and Pitcairn 2002), the successful management and eradication of marine alien species post-introduction is rare (Wotton and Hewitt 2004; Lehtiniemi et al. 2015; Ojaveer et al. 2015). Thus, preventative

strategies have been suggested as the most effective management approach towards minimising the risk of invasion by marine species (Wotton and Hewitt 2004; Hulme 2006; Ojaveer et al. 2014) and as such receive substantial attention in the literature (Ruiz et al. 2011, 2013). Thus a practical approach for the management of crabs would be a precautionary one, where efforts are focused on pre- and at-border management to mitigate introductions (Bax et al. 2001; Hulme 2006; Lehtiniemi et al. 2015). Commonly this is achieved through the management of potential pathways (Carlton and Ruiz 2005), the most common of which include ballast water (Gollasch and Leppäkoski 2007; David and Gollasch 2008) and hull fouling (Yebra et al. 2004; Roberts and Tsamenyi 2008). While prevention is better than cure, in terms of costs and avoidance of impacts (Ojaveer et al. 2014; Roy et al. 2014), species continue to breach borders. As such, management needs to be two pronged, aiming first to prevent invasions, but also addressing those incursions that do take place. It is in dealing with established alien species that management can benefit from prioritising those species that are associated with the worst impacts as suggested by the EICAT scheme (Blackburn et al. 2014). This can, however, only be achieved if impacts of alien species are quantified, not a common occurrence for marine alien species (Ojaveer et al. 2015). Thus, in the absence of information on species impacts, a precautionary approach should be applied whereby all alien species are considered high-risk (Ojaveer et al. 2015; Kumschick et al. 2017a). Additionally, studies quantifying impact should be strongly encouraged. Such studies would be of academic interest as they would support the development of our understanding of the context dependency of alien species impacts and they would also support efficient management of alien species incursions (Robinson et al. 2017).

Conclusion

This study represents the first application of the EICAT scheme to a marine taxon and the first global assessment of the impacts of alien crab species in their introduced range. This work revealed that the biological impacts of the majority of alien crab species have not been quantified, leaving 91% of species classified as Data Deficient. Even though only a small proportion of alien crab species could be rated by the EICAT scheme due to this scarcity of data, this study showed that alien crabs have the potential to cause severe ecological impacts. With the presently available data, no biological or ecological traits could be identified that correlate with impact severity. Maybe most importantly, this study has highlighted the dire need for quantification of impacts of alien crabs. While the aim of prioritising management of alien species based on impact is desirable, in the current situation where the impacts of few marine alien species have been investigated, the value of this approach is unfortunately diminished. As such it is recommended that empirical studies of impact be encouraged

to build up the depth of knowledge in this field. In the meantime, preventative management should be focused on addressing pathways of introduction so as to minimise introductions. In addition, the management of newly arrived and established species should apply a precautionary approach, whereby all alien crabs should be viewed as potentially harmful.

Chapter 3: Horizon scanning for alien predatory crabs: Insights for South Africa

As the South African coastline is considered vulnerable to invasion by predatory crabs and this group is associated with notable impacts elsewhere, it is important to mitigate the potential establishment of such crabs in this region. In response to this need, the aim of this chapter was to use horizon scanning to create an ordered watch-list of crabs, with known invasion histories that could establish along our coastline under both current and future predicted temperature scenarios. Due to South Africa's variable coastline, the susceptibility to invasion was considered for each of the four marine ecoregions i.e. the Benguela, Agulhas, Natal and Delagoa. This was done by 1) determining which alien crab species have pathways to reach South Africa; 2) comparing the temperature ranges experienced by these crabs in their native and introduced ranges to that of each of the four ecoregions; and 3) ranking potential invaders based on their EICAT rating. Chapter 1 revealed 56 crabs with an invasion history. The presence of pathways to South Africa was used to refine this list to 28 species that could reach our coastline. Four pathways (shipping, yacht fouling, aquaculture imports and the aquarium trade) were identified as potential routes of introduction. The notorious invaders the Japanese shore crab *Hemigrapsus sanguineus*, brush-clawed shore crab *H. takanoi* and the Chinese mitten crab *Eriocheir sinensis*, were placed on top of the watch-list due to their negative ecological impacts elsewhere. Incompatible temperature ranges excluded a maximum of two species from each ecoregion under current conditions. These patterns are expected to remain similar over the next half-century as predicted temperature increases are expected to only marginally make the Agulhas ecoregion more hospitable for potential invaders while excluding two species from the already warm Natal and Delagoa ecoregions. This study highlights that a variety of potential pathways exist for transporting crabs to South Africa, that the majority of alien crabs could survive along the South African coastline and that the entire coastline is vulnerable to their invasion. This watch-list should be used to support the early detection of alien crabs, an action that could minimise the chance of their successful establishment and ultimately help mitigate the negative impacts that may be associated with an incursion.

Introduction

The severity of the impacts associated with alien species and the difficulty associated with successfully managing marine invasions (Hopkins et al. 2011) highlights the urgent need to prevent future invasions. As prevention has been recognised as being more effective and less costly than control efforts, this approach is considered a priority (Ricciardi et al. 2011; Seekamp et al. 2016; Matthews et

al. 2017). Models predicting the identity and likely entry point of future invaders have been described as “the holy grail of invasion biology” (Enserink 1999), as knowledge of future invaders and an understanding of the drivers behind their invasion potential, possible invaded ranges and likely impacts will increase the efficacy of management efforts (Faulkner et al. 2014; Zaiko et al. 2014).

Horizon scanning is one pre-emptive approach to addressing impending threats such as invasive species. Defined as an organised investigation that gathers information on a wide range of potential threats within a given context to inform management and support decision-making (Habegger 2009; Roy et al. 2014), this approach has been applied in various arenas by government, industry and business (Sutherland and Woodroof 2009). Within the context of invasive species, horizon scanning investigates the potential introduction, establishment, and spread of alien species, as well as the consequences of impact by invaders (Gallardo et al. 2016), with the aim to support their early detection, ultimately to minimise the chances of successful establishments through increasing the probability of successful management (Shine et al. 2010). Numerous studies in Europe have implemented this method within the milieu of invasive species (Sutherland et al. 2008; Parrott et al. 2009). The most recent of these resulted in compilation of watch-lists of non-native species considered to pose a risk to the biodiversity (Roy et al. 2014; Gallardo et al. 2016). While many predictive models are time consuming and expensive (Simberloff 2005; Keller et al. 2007), watch-lists are a cost-effective, rapid method for identifying potential threats and are helpful in the development of preventative strategies and control efforts (Parrott et al. 2009). Watch-lists primarily identify species with an invasion history that are currently absent from the region of interest, but that can potentially invade the study area (Faulkner et al. 2014). Invasion history has been identified as a good predictor of future invasion potential for some alien taxa (Moyle and Marchetti 2006; Novoa et al. 2015). Although it is recognised that any species, even those without an invasion history, hold the potential to invade (Moyle and Light 1996; Hayes and Sliwa 2003), it is not always practicable to consider an entire taxon or group when pre-emptively considering invasions, as this approach is time consuming and information may not be available for all species within the group of interest. Thus, in the absence of other information, invasion history currently offers the most viable approach to identifying potential invaders (Hayes and Barry 2008; Faulkner et al. 2014). This approach is further strengthened when used together in combination with other important predictors such as the presence of vectors (Minchin 2006; Blackburn et al. 2011; Seebens et al. 2013), traits of species (Sakai et al. 2001; Novoa et al. 2015), the nature of recipient communities (Ruiz et al. 1997; Grosholz 2002; Ordóñez et al. 2013) and environmental and climatic suitability (Richardson et al. 2011; Faulkner et al. 2014; Matthews et al. 2017).

It is well recognised that empty niches can exist within communities (Walker and Valentine 1984; Whinam et al. 2005; Lloyd-Smith 2013). The ecological niche of a species can be viewed as its functional role within its community, often illustrated by its interaction with other species or its position within the trophic food web (Elton 1927; Pulliam 2000; Schoener 2009). Empty niches of such functional groups, specifically those at the top predator level, are not unusual (Chown et al. 1998; Whinam et al. 2005). Based on the empty niche hypothesis (Shea and Chesson 2002), if such a functional group is absent in an ecosystem and should a species with suitable characteristics be introduced (Pulliam 2000; Lekevičius 2009), it is likely that the species will successfully fill that empty niche and become invasive (Walker and Valentine 1984; Bergstrom and Chown 1999). Predators exert weak regulatory forces along the South African coastline (Bustamante and Branch 1996) rendering the region depauperate of dominant intertidal benthic marine predators characteristic of such systems elsewhere (for example see Connell 1970 and Menge 1976). As such, there are concerns that this region could be vulnerable to invasions by such predators. As predatory brachyuran crabs are considered one of the most invasive marine taxa (Brockerhoff and McLay 2011; Hänfling et al. 2011; Brousseau and McSweeney 2016), having invaded across the globe (see Chapter 1), potential invasions of the South African coast by this group are of great concern. To date there have been only two alien predatory crabs reported from this region i.e. the European shore crab *Carcinus maenas* (Le Roux et al. 1990) and the Mediterranean shore crab *Carcinus aestuarii* (Geller et al. 1997). Despite *C. maenas* having a wide-spread alien range at a global scale (Carlton and Cohen 2003), this crab is currently largely confined to two harbours along the Cape Peninsula (Mabin et al. in press) and appears to be excluded from open coast habitats by its inability to withstand high levels of wave movement (Hampton and Griffiths 2007) and through predation by native predatory fish (Mabin et al. in press). In contrast, *C. aestuarii* is thought to no longer occur in the region, not having been detected since 1997 (Robinson et al. 2005). Given the serious threat that alien crabs can pose to biodiversity (Grosholz et al. 2000; Rudnick et al. 2005b; Kraemer et al. 2007; Dauvin et al. 2009), the economic implications that they can have in recipient regions (Lovell et al. 2007) and the costs associated with managing problematic alien species (Hoffmann and Broadhurst 2016), it is important to pre-emptively consider future crab invasions and thus provide South African managing authorities the opportunity to institute monitoring and pro-active management plans.

The Blackburn framework for biological invasions (Blackburn et al. 2011) offers an ideal approach for guiding horizon scanning and developing watch-lists. It is a single unified model that can be applied to all human-mediated invasions (Blackburn et al. 2011; Fig. i). The framework recognises that the invasion process is divided into four stages which include transport (transferred from native habitat to new one), introduction (released in new habitat), establishment (survive and reproduce) and

natural range expansion (spreading in new habitat), all of which are separated by numerous biotic and abiotic barriers that must be overcome for a species to advance to the next stage. Thus, effective horizon scanning could apply this framework, using each stage as a filter to remove species from a starting list and thus ending with a watch-list of species of interest.

The global climate is changing at an unprecedented pace (IPCC 2014) and watch-lists founded on the ability of potential alien species to survive under present climatic conditions alone will be of little use as the climate continues to change. For example, South Africa has already experienced significant fluctuations in sea surface temperature over the past two decades (Rouault et al. 2010) and such changes are anticipated to continue (Jarre et al. 2015). When considering the climatic suitability of South Africa for potential alien species, it is important to consider the climatic similarity of the species current native and alien ranges to that of the current and predicted future climatic conditions of South Africa.

Against this background, this chapter aims to use horizon scanning to create an ordered watch-list of alien crabs with an invasion history that have the potential to arrive and establish along the South African coast under current and future temperatures. As shipping was highlighted as the dominant pathway by which alien crabs are introduced (see Chapter 1), and South Africa is deeply embedded within the international shipping network (Fraser et al. 2016), it was hypothesised that the vast majority of crabs with an invasion history will have a vector (or pathway) to reach South Africa and would thus be included on the list.

Methods

From the list of 56 alien predatory crab species developed in Chapter 1 (Table 1.3), those with a native range including South Africa (20 species), those currently present and recognised as alien to South Africa (1 species- the European shore crab *Carcinus maenas*) and those occurring offshore at depths greater than 60m (1 species – the snow crab *Chionoecetes opilio*) were excluded, leaving a new list of 34 potential invaders of the South African coastline. Using the Blackburn framework as a filter, a watch-list was developed in two steps (Fig. 3.1).

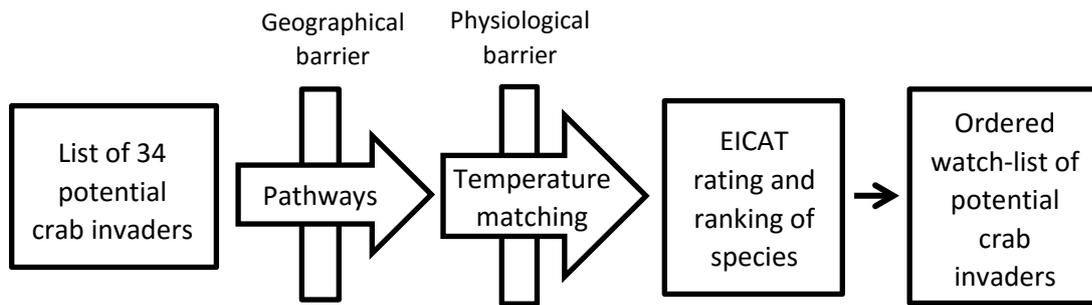


Figure 3.1 The horizon scanning framework implemented and the filtering process followed to create the watch-list of crab species of concern to South Africa.

Firstly, those species that could cross the geographical barrier (i.e. those with a pathway) were retained on the list of alien crabs. The existence of pathways to South Africa was identified from the literature review in Chapter 1. As it can sometimes be unclear which vector within the shipping pathway (ballast water or ship fouling) was responsible for the introduction of a species, the pathway of introduction rather than the vector was recorded for each species. Secondly, this list was further refined by excluding those species that could not cross the physiological barrier (i.e. temperature matching indicated that they would be unable to survive under current or future ambient climatic conditions). Temperature matching was interrogated by comparing the temperature between each species realised range (i.e. native and alien ranges of a species to account for potential plasticity in alien populations that may not be evident in native populations) and each of the four South African ecoregions (i.e. the Benguela, Agulhas, Natal and Delagoa ecoregions following Sink et al. (2012), Figure 3.2).

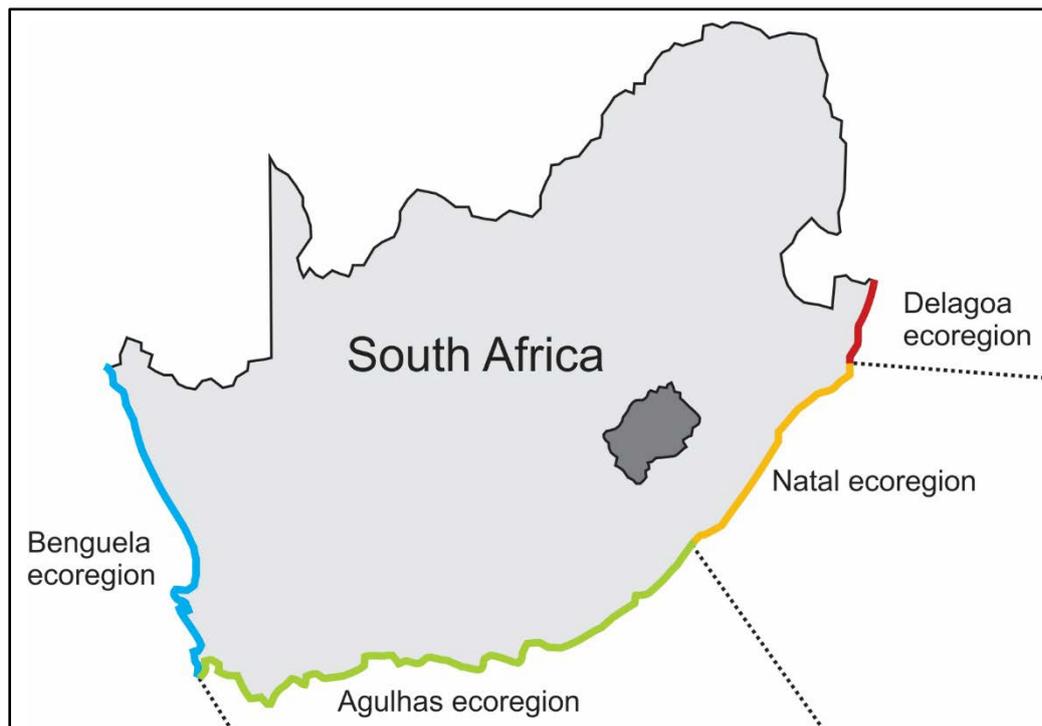


Figure 3.2 The four marine ecoregions of South Africa, ranging from the cool Benguela on the west coast, to the warm Delagoa ecoregion on the east coast. Note that the dashed lines are extended offshore for illustrative purposes only.

These four ecoregions reflect South Africa's variable coastline, ranging from the cool temperate west coast to the warm tropical east coast (Griffiths et al. 2010). The invasion potential of each species thus had to be considered for each ecoregion to account for the differences between these regions and the fact that they have the potential to support different suites of species with different environmental tolerances. Minimum and maximum sea surface temperatures (SSTs) of each species realised range, as well as that for the four South African ecoregions were extracted from the NASA Earth Observations Database. To capture seasonal variability in these measures, data were extracted for January and July for a seven year period (2010-2016). Using this data the mean and 95% confidence intervals (CI) for the minimum and maximum SSTs were calculated for each alien crab's range and each ecoregion. Minimum and maximum SSTs were chosen rather than mean SSTs because it is more likely that species will be constrained by the extreme conditions in new regions rather than their average environmental states. To account for future changes in temperature a predicted climate induced change in SSTs was extracted from IPCC (2014) scenario RCP4.5 which predicts a mean increase of 1.4 °C over the next 29-48 years (2046-2065). This value was then applied to current SSTs to provide a measure of future temperatures under a moderate emissions scenario. The degree of congruency between species

thermal ranges and the thermal characteristics of the four South African ecoregions was determined using the criteria in Table 3.1. This resulted in the ecoregions being classified as 1) too cold; 2) probably too cold; 3) possibly too cold; 4) suitable; 5) possibly too warm; 6) probably too warm; or 7) too warm to support each species. When the bioregion was too cold or too warm to support a species, that species was excluded from the watch-list for that specific ecoregion. In a cautionary approach, when ecoregions were probably or possibly too cold or too warm, the species was still included on the watch-list. While it would have been desirable to include other climatic variables such as salinity, the data was not available to support such an analysis.

Table 3.1 Criteria used to determine degree of congruency between the species thermal ranges and that of the South African ecoregions.

Description	Classification of ecoregion
Species minimum (min) and maximum (max) above the ecoregion min and max	Too cold
Species min 95% Confidence Interval (CI) overlaps with the ecoregion max CI	Probably too cold
Species max above the ecoregion max and species min mean falls between the ecoregion min and max (no overlap of species CI with the ecoregion min)	Possibly too cold
Species min and max fall below and above the ecoregion min and max respectively	Suitable
Species min below the ecoregion min and species max mean falls between the ecoregion min and max (no overlap of species CI with the ecoregion max)	Possibly too warm
Species max CI overlaps the ecoregion min CI	Probably too warm
Species min and max below the ecoregion min and max	Too warm

Lastly, to further refine the watch-list, the crabs were ranked from highest to lowest based on their Environmental Impact Classification for Alien Taxa (EICAT) rating they received in Chapter 2. This impact rating is a measure of the risk species pose to native biodiversity (Blackburn et al. 2014) and is important as it enables prioritisation of management efforts based on impact. These ratings were then used to create an ordered watch-list that indicated whether a species had a pathway to reach a certain ecoregion, whether it's climatically suited to survive in that ecoregion and its potential for impact.

Results

In total, 28 of the 34 crab species were found to have pathways to South Africa. Six species were excluded at this point for numerous reasons. The red swimming crab *Gonioinfradens paucidentatus*, was omitted from the watch-list due to no information being available on its potential pathway. The

remaining five species were excluded as they have previously only been introduced either by the Suez Canal (the swimming crab *Thalamita indistincta*, the lesser swimming crab *Charybdis longicollis*, the frog crab *Notopus dorsipes* and the pilumnid crab *Pilumnopus vauquelini*) or intentionally for food (the velvet crab *Necora puber*), both of which are not applicable pathways in the context of South Africa. Only four potential pathways were identified, i.e. shipping, yacht fouling, aquaculture imports and the aquarium trade (Fig. 3.3). Although the majority of species were found to previously have been transported via only one pathway, some species had multiple potential pathways (Fig. 3.4). When species had been transported by two pathways, this always involved shipping in combination with another pathway. The Sally Lightfoot crab *Percnon gibbesi*, was the only species previously transported by three potential pathways i.e. shipping, yacht fouling and the aquarium industry.

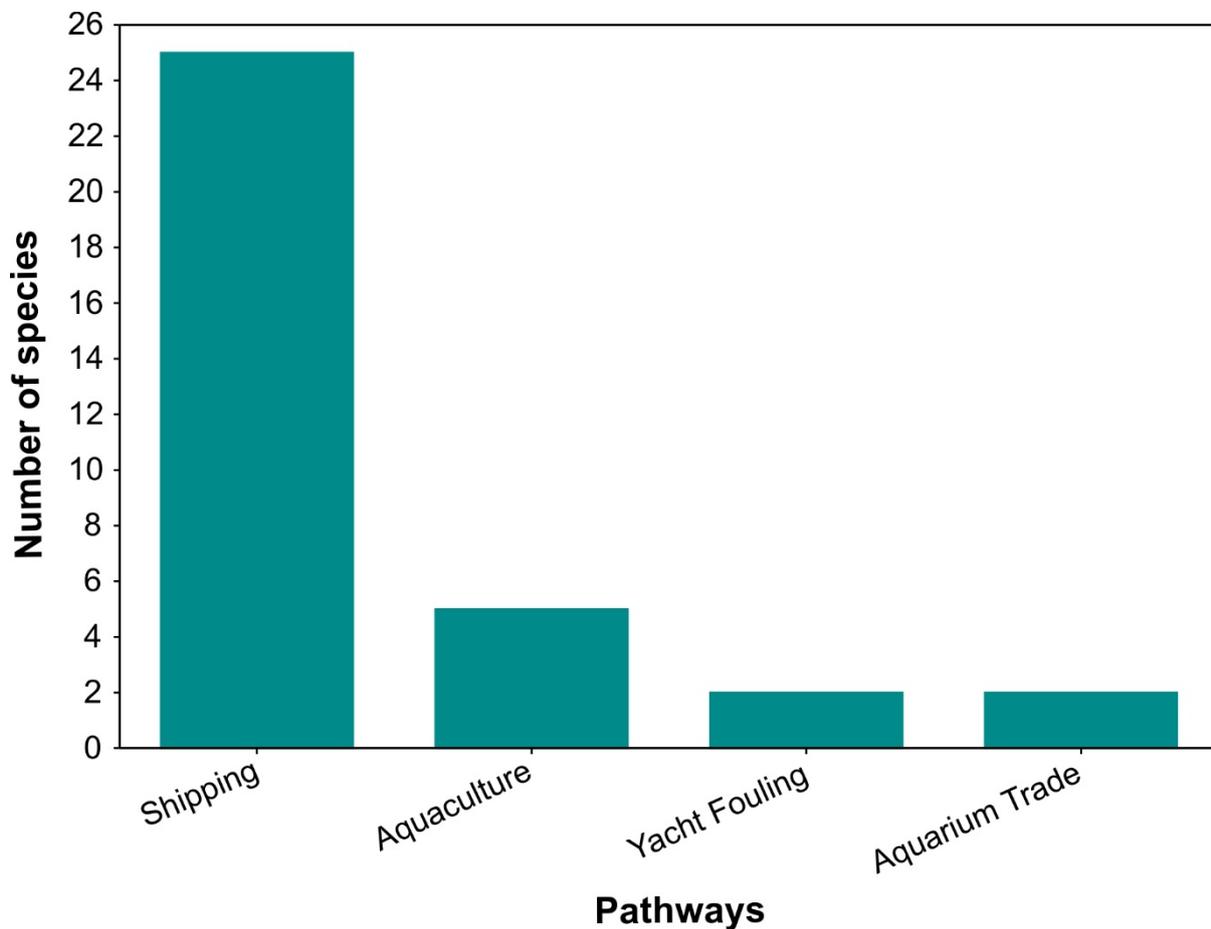


Figure 3.3 Potential pathways for the transport of the 28 crab species to South Africa. Note: Some species have the potential to be introduced by more than one pathway – see Fig. 3.4.

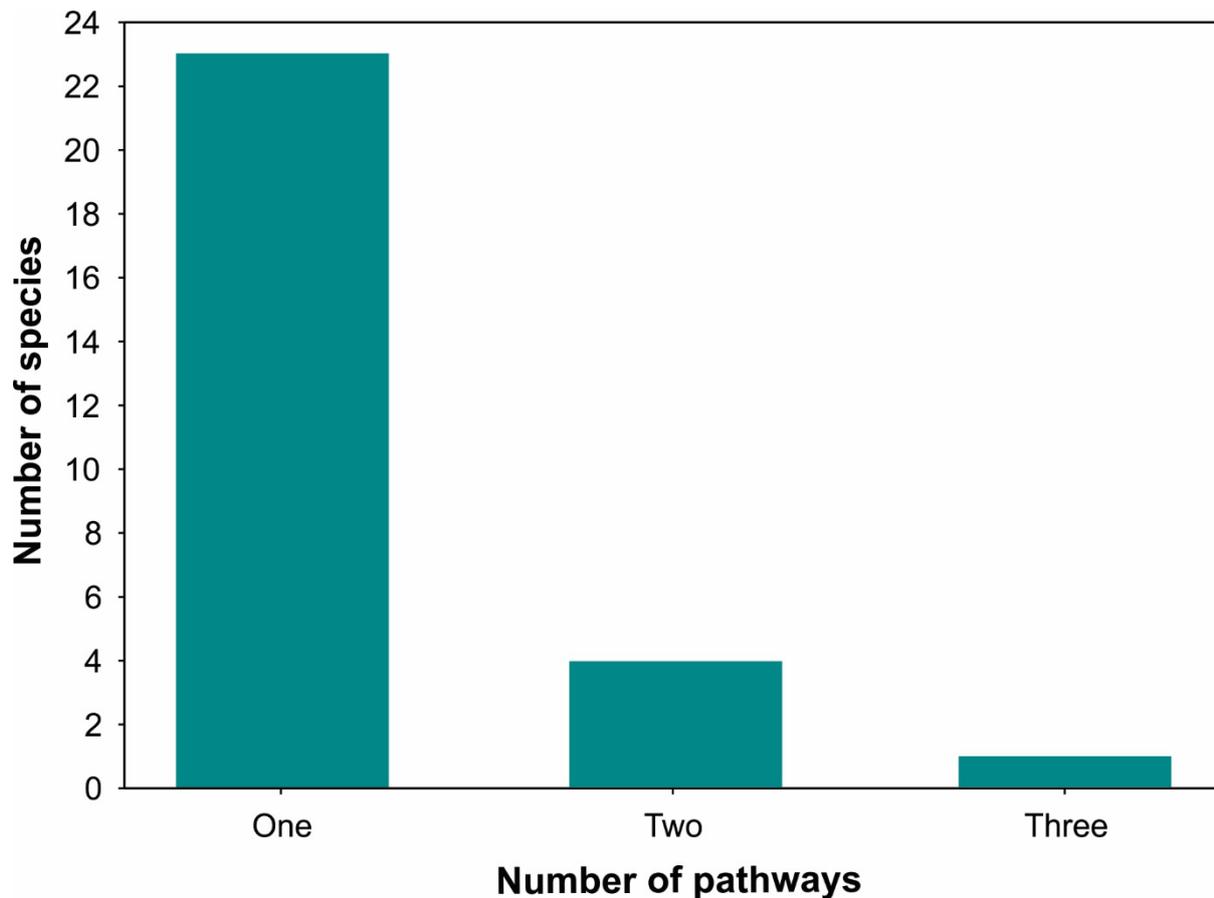


Figure 3.4. The number of crab species transported by single and multiple pathways.

The vast majority of crabs with invasion histories are likely to survive along the South African coast under both present and future conditions (Fig. 3.5, see Appendix 3.1 and 3.2 for the thermal ranges of each South African ecoregion and thermal tolerances of each species, respectively). Notably, typically warm water species are precluded from the cooler ecoregions while cold water species are excluded from the warm east coast. In total, 27 species have the potential to survive in the cold Benguela ecoregion under both current and future conditions. In particular, this ecoregion is too cold to support the purple climber crab *Metopograpsus oceanicus* and is probably too cold for both the pilumnid crab *Eurycarcinus integrifrons* and Hepu mitten crab *Eriocheir hepuensis*. In the slightly warmer Agulhas ecoregion, 27 species have the potential to survive under present conditions, while future temperature rises may make this ecoregion accessible to *M. oceanicus*. The Natal and Delagoa ecoregions have much higher mean minimum and mean maximum temperatures and a noticeably smaller temperature range than the former two ecoregions. As such, conditions are suitable for the survival of the warm water species *M. oceanicus*, *E. integrifrons* and *E. hepuensis*. In the Natal ecoregion, temperature regimes are currently too warm to support the pill box crab *Halicarcinus*

innominatus and as such 27 species are expected to survive in this ecoregion. With future temperature increases, however, only 26 species will be able to survive as this ecoregion also becomes too warm to support the Dungeness crab *Metacarcinus magister*. As the Delagoa ecoregion is warmer than the former three ecoregions, it is too warm to support both *M. magister* and *H. innominatus* under current and future conditions. As such, only 26 species have the potential to survive in this ecoregion.

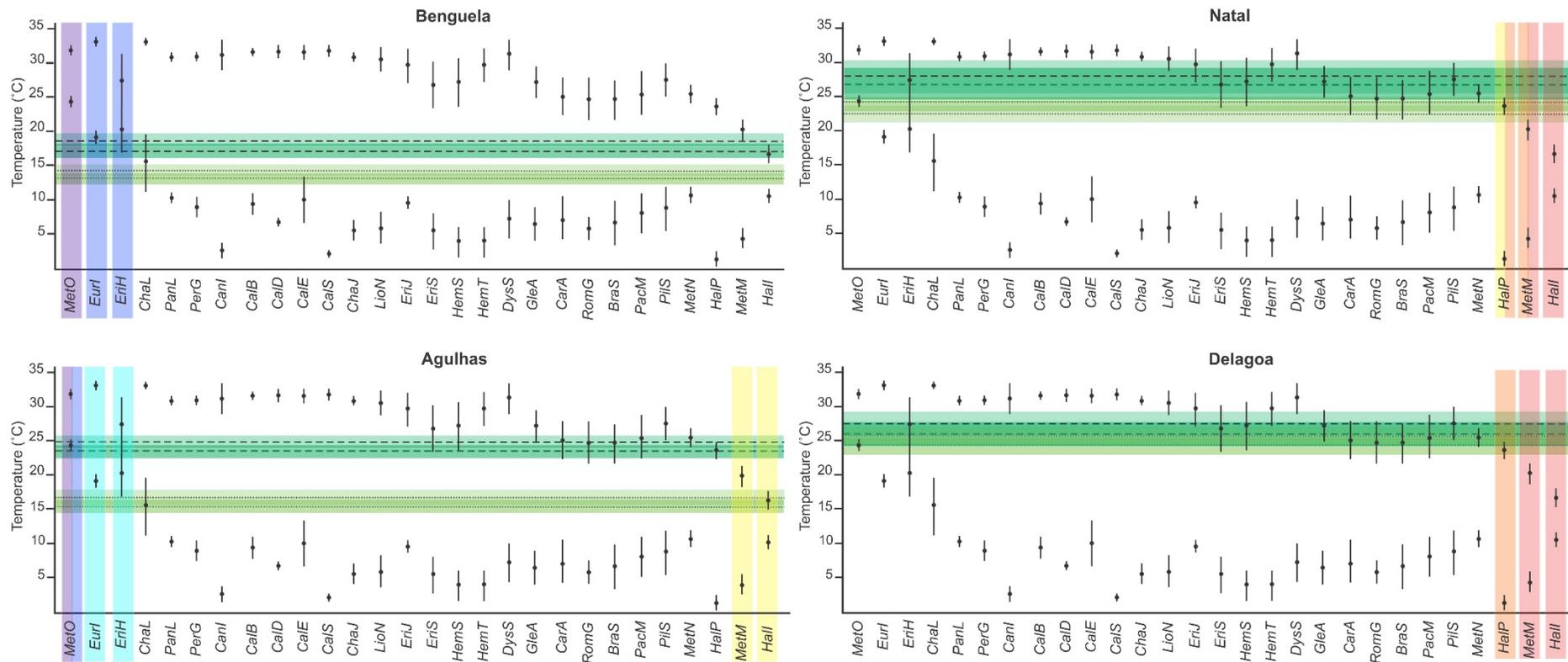


Figure 3.5 Mean minimum (horizontal dotted lines) and mean maximum SSTs (striped lines) $\pm 95\%$ CI (horizontal green bars) for each of the four South African ecoregions for both current (lower lines) and predicted temperatures (top lines). Mean minimum ($\pm 95\%$ CI) and mean maximum ($\pm 95\%$ CI) temperatures for each of the 28 crab species realised thermal range are also shown. Refer to Chapter 1, Table 1.3 for species names. Coloured vertical bars indicate the degree of congruency between each crab's thermal range and that of the ecoregion. Colours correspond to those in Table 3.1. Too cold ; probably too cold ; possibly too cold ; suitable ; possibly too warm ; probably too warm ; too warm . A single coloured bar represents congruency under both current and future temperature conditions. When a bar is split, the left side is indicative of matching with current conditions while the right side represents the future.

The complete watch-list with the 28 potential crab invaders is depicted in Table 3.2. Two families stand out due to the high number of alien crab species they support: the Portunidae (eight species) and the Varunidae (six species). Even though some pathways are specific to some ecoregions (e.g. oyster culture occurs only in the Benguela and Agulhas), intra-regional transfer between ecoregions can occur. Thus, all species with a vector to South Africa are considered to have the potential to ultimately reach all ecoregions. However, due to incompatible temperature ranges, three species (*M. oceanicus*, *M. magister* and *H. innominatus*) would not survive in some ecoregions (Fig. 3.5). Due to their negative ecological impacts elsewhere and their high EICAT ratings, the notorious Varunidae invaders, namely the Japanese shore crab *Hemigrapsus sanguineus*, brush-clawed shore crab *H. takanoi* and the Chinese mitten crab *Eriocheir sinensis* were placed at the top of the list.

Table 3.2 Watch-list depicting the alien crab species that can potentially survive in each South African ecoregion under present and predicted temperature conditions, their potential pathways (Shipping: SH; Yacht Fouling: YF; Aquaculture Products: AP; Aquarium Trade: AT) and EICAT rating (DD: Data Deficient). Colours correspond to those in Table 3.1 and illustrate the degree of congruency between each crab's thermal range and that of the ecoregion. Too cold ; probably too cold ; possibly too cold ; suitable ; possibly too warm ; probably too warm ; too warm . A cross (✖) indicates a species is expected to be excluded from the ecoregion due to regional temperatures being outside of their thermal tolerance range.

Crabs which can reach South Africa	Potential Pathway	Ability to survive environmental conditions								EICAT rating
		Present				Predicted				
		Benguela	Agulhas	Natal	Delagoa	Benguela	Agulhas	Natal	Delagoa	
Varunidae										
<i>Hemigrapsus sanguineus</i>	SH; YF	✓	✓	✓	✓	✓	✓	✓	✓	Major
<i>Hemigrapsus takanoi</i>	SH	✓	✓	✓	✓	✓	✓	✓	✓	Moderate
<i>Eriocheir sinensis</i>	SH	✓	✓	✓	✓	✓	✓	✓	✓	Moderate
<i>Eriocheir hepuensis</i>	SH			✓	✓			✓	✓	DD
<i>Eriocheir japonica</i>	SH	✓	✓	✓	✓	✓	✓	✓	✓	DD
<i>Brachynotus sexdentatus</i>	SH; AP	✓	✓	✓	✓	✓	✓	✓	✓	DD
Portunidae										
<i>Callinectes bocourti</i>	SH	✓	✓	✓	✓	✓	✓	✓	✓	DD
<i>Callinectes danae</i>	SH	✓	✓	✓	✓	✓	✓	✓	✓	DD
<i>Callinectes exasperatus</i>	SH	✓	✓	✓	✓	✓	✓	✓	✓	DD
<i>Callinectes sapidus</i>	SH; AT	✓	✓	✓	✓	✓	✓	✓	✓	DD
<i>Carcinus aestuarii</i>	SH	✓	✓	✓	✓	✓	✓	✓	✓	DD
<i>Charybdis japonica</i>	SH	✓	✓	✓	✓	✓	✓	✓	✓	DD
<i>Charybdis lucifera</i>	SH	✓	✓	✓	✓	✓	✓	✓	✓	DD
<i>Liocarcinus navigator</i>	SH	✓	✓	✓	✓	✓	✓	✓	✓	DD
Cancridae										
<i>Cancer irroratus</i>	SH	✓	✓	✓	✓	✓	✓	✓	✓	DD
<i>Metacarcinus magister</i>	SH	✓				✓				DD
<i>Metacarcinus novaezelandiae</i>	AP	✓	✓	✓	✓	✓	✓	✓	✓	DD

<i>Romaleon gibbosulum</i>	SH	✓	✓	✓	✓	✓	✓	✓	✓	DD
<i>Glebocarcinus amphioetus</i>	SH	✓	✓	✓	✓	✓	✓	✓	✓	DD
Grapsidae										
<i>Metopograpsus oceanicus</i>	SH	x	x	✓	✓	x	✓	✓	✓	DD
<i>Percnon gibbesi</i>	SH; YF;AT	✓	✓	✓	✓	✓	✓	✓	✓	DD
<i>Pachygrapsus marmoratus</i>	SH	✓	✓	✓	✓	✓	✓	✓	✓	DD
Hymenosomatidae										
<i>Halicarcinus innominatus</i>	AP	✓	✓	x	x	✓	✓	x	x	DD
<i>Halicarcinus planatus</i>	AP	✓	✓	✓	✓	✓	✓	✓	✓	DD
Pilumnidae										
<i>Eurycarcinus integrifrons</i>	SH	✓	✓	✓	✓	✓	✓	✓	✓	DD
<i>Pilumnus spinifer</i>	SH	✓	✓	✓	✓	✓	✓	✓	✓	DD
Carpiliidae										
<i>Dyspanopeus sayi</i>	SH; AP	✓	✓	✓	✓	✓	✓	✓	✓	DD
Panopeidae										
<i>Panopeus lacustris</i>	SH	✓	✓	✓	✓	✓	✓	✓	✓	DD

Discussion

In the face of increasing rates of invasions, systems that have empty niches are particularly at risk of invasion and the negative impacts associated with alien species (Shea and Chesson 2002; Forsström et al. 2015). The South African coastline is one such a system in relation to intertidal benthic predators (Bustamante and Branch 1996). As crabs are considered one of the most successful marine invasive taxa (Grosholz and Ruiz 2003; Kraemer et al. 2007; Brousseau and McSweeney 2016) with predatory, crabs comprising the majority of these invaders (Brockerhoff and McLay 2011), the threat posed by this group along this coastline is notable. Preventing the invasion of these crabs should thus be considered a priority. Within this context, the present study aimed to identify alien crabs that could invade the South African coastline and so support their early detection. A total of 28 alien crabs were found to have pathways to reach South Africa and were included on the watch-list. The notorious Varunidae invaders, the Japanese shore crab *Hemigrapsus sanguineus*, the brush-clawed shore crab

H. takanoi and the Chinese mitten crab *Eriocheir sinensis* were placed on top of the list due to their high EICAT ratings. Four potential pathways to South Africa were identified with shipping being the most common. Temperature matching revealed that incompatible temperature ranges are likely to exclude a maximum of two species from each of the four ecoregions under both current and future conditions.

Identifying invasion pathways important in the introduction of species is essential. This enables the appropriate management of these pathways in order to prevent, reduce and manage future invasions (Lodge et al. 2006; Hulme et al. 2008). Shipping, yacht fouling, aquaculture imports and the aquarium trade were identified as potential pathways of crab species to South Africa. In total, 28 potential crab invaders have been introduced through pathways that exist in the South African context and could thus reach these shores. The fact that multiple potential pathways exist highlights the risk of invasion by crabs. Shipping, which includes fouling and ballast water, has not only been the most important pathway for the introduction of crab species around the globe (see Chapter 1), but also for marine alien species to South Africa (Mead et al. 2011a). Due to the increasing complexity and densification of the shipping network, the emergence of new regional ports, and growing trade volumes and shipping traffic to southern African countries from Europe, America, Asia and Australia (Fraser et al. 2016), the introduction of crab species via this pathway should be anticipated. It should, however, be noted that the IMO Ballast Water Management (BWM) Convention came into force on 8 September 2017. As South Africa is a signatory of this Convention, we will be forced to better regulate ballast water in the future and as such the risk of ballast water as a vector might decrease. Nevertheless, as this Convention has only recently been enforced and the ballast water management standards are still being phased in, in addition to hull fouling still being an active vector, shipping can still act as a potential pathway for the transport of crabs. The identification of aquaculture as the second most important potential pathway can be attributed to its increased importance around the globe over the past few decades (Seo and Lee 2009; Grosholz et al. 2015). This pathway has historically been the second most important pathway for the introduction of marine species to South Africa (Mead et al. 2011a). Although aquaculture as a pathway for the introduction of alien species is being regulated in South Africa, this pathway is also actively being promoted by our government as an important avenue for supporting socio-economic development in South Africa. The expansion of the industry is the focus of a national programme, Operation Phakisa (www.operationphakisa.gov.za/). As such, it is expected that this pathway will grow in the future and so will the risk of invasion associated there with.

Yacht fouling has also recently become an increasingly well recognised vector (Peters et al. 2014; 2017). Due to the slow travelling speed of yachts, however, it is unlikely that yachts will be responsible for the introduction of crabs from distant localities. However, this vector could operate between neighbouring countries. Additionally, yachts have been identified as an important pathway for the intra-regional transfer of species (Peters et al. 2014) and this pathway could be important for the transfer of crabs along the South African coast. Although the aquarium trade has been identified as a potential pathway to South Africa, its importance for the introduction of marine species to this country has not been assessed. Nevertheless, it remains a threat as this is a large and growing industry (Williams et al. 2012) and its importance as a pathway for the introduction of marine species has been identified as increasing through time (Semmens et al. 2004; Katsanevakis et al. 2013).

As temperature has a significant influence on the distribution of species (Tittensor et al. 2010), the invasion potential of a species is expected to be greatest in areas thermally similar to that of its current range (Williamson 1996; Peterson 2003). Temperature matching has thus been identified as important in predicting the invasion potential and distribution of novel biota (Matthews et al. 2017). When applied in this study, temperature matching revealed that the majority of crab species with an invasion history are likely to be able to survive along the South African coast, with all 28 species having the potential to survive in at least two ecoregions. Only three species (the purple climber crab *Metopograpsus oceanicus*, Dungeness crab *Metacarcinus magister* and pill box crab *Halicarcinus innominatus*) are expected to be excluded in specific ecoregions due to incompatible temperatures.

With the predicted alterations in global climate (Rahel and Olden 2008; Rouault et al. 2010), changes in sea temperature could influence native community composition and diversity (Helmuth et al. 2002; Lord 2017) and facilitate the establishment of invasive species (Stachowicz et al. 2002a; Walther et al. 2009; Sorte et al. 2010). With South Africa already experiencing changes in sea surface temperatures (Rouault et al. 2010), it is likely that alien species currently in the region will change their distributions in the future, while new incursions are expected to be supported under new conditions. Temperature matching of potential alien crabs to future climatic conditions in the medium-term did, however, yield similar results to those gained when considering current temperatures, with one warm water crab *M. oceanicus* being excluded from the cool Benguela ecoregion while the more temperate *M. magister* and *H. innominatus* were excluded from the warmer regions. The fact that overall the South African coast was found to be suitable for most species is largely reflective of the broad range of climates supported (i.e. from cool temperate on the west coast to warm tropical on the east coast) and the fact that this coastline experiences relatively stable water temperatures that never approach freezing and rarely reaching above 30°C. Nonetheless, it is important to be cautious when considering these results

as they could no doubt be made more accurate by detailed physiological studies on the crabs in question. Additionally, crabs might be able to invade, expand or adapt to ranges currently assumed to be unsuitable for their survival for various reasons. Firstly, alien species are known to exhibit phenotypic plasticity that can enable adaptation to a range of environmental conditions currently considered unsuitable (Rosecchi et al. 2001; Prentis et al. 2008). Notably, such adaptive behaviour has previously been observed in alien crabs (Thatje et al. 2005; de Rivera et al. 2007a). Secondly, alien species are believed to have enhanced eurythermality. As such species might be able to survive over a wide range of temperatures and be favoured, especially under higher temperatures associated with predicted climate change (Zerebecki and Sorte 2011). Thus their realised ranges might not be an accurate representation of their entire physiological tolerance range and the temperature ranges in which they can survive (Tingley et al. 2014). Lastly, higher genetic diversity might facilitate survival and range expansion into areas not anticipated to be suitable for their survival. This phenomenon has been observed in some alien populations of the European shore crab *Carcinus maenas* (Roman 2006).

A few of the crab species included in this study are not solely marine, but known for their catadromous lifestyle, spending most of their adult life in river systems and only migrating downstream to brackish or marine waters to breed (Veilleux and de Lafontaine 2007). Such species include *E. sinensis* (Anger 1991), the Japanese mitten crab *E. japonica*, (Veilleux and de Lafontaine 2007), the Hepu mitten crab *E. hepuensis* (Naser et al. 2012), the blue crab *Callinectes sapidus* (Millikin and Williams 1984) and the Bocourt swimming crab *C. bocourti* (Perry et al. 1992). Many of the harbours along the South African coastline occur in rivers and despite not being as big as many northern hemisphere rivers, these rivers could still provide suitable habitat for the survival of these catadromous crabs. Examples of some of the harbours in river systems which could provide habitat for these crabs include Richards Bay Harbour in the Delagoa region, Durban Harbour in Natal and East London harbour in the Agulhas ecoregion. Within the Benguela, the large Table Bay Harbour does not lie in a river itself but is close to Milnerton Lagoon.

The watch-list revealed that the families Portunidae (swimming and shore crabs) and Varunidae (mitten crabs) support the greatest number of potential crab invaders to South African shores. This reflects the pattern seen for these families globally (See Chapter 1). Their successfulness is believed to be attributed to their great dispersal and migratory abilities (Brousseau and McSweeney 2016; Grosholz and Ruiz 1996; Herborg et al. 2005) and ecologically diverse nature which enables them to inhabit a variety of habitats (Millikin and Williams 1984; Dittel and Epifanio 2009).

Impacts previously noted for an alien species can be suggestive of potential impacts in new regions and thus be used to inform management actions (Branch and Steffani 2004; Ricciardi 2007; Kulhanek

et al. 2011). For example, similar impacts have been noted for established populations of *C. maenas* in most of its invaded ranges (Grosholz and Ruiz 1996). However, impacts of marine species are rarely quantified (Ojaveer et al. 2015; Robinson et al. 2017) and it does therefore not come as a surprise that the ecological impacts have not been quantified for the majority of crab species. In fact, impacts have been quantified for only three of the 28 crab species identified as having the potential to reach South Africa (i.e. *H. sanguineus*, *H. takanoi* and *E. sinensis*) resulting in only these three species receiving EICAT ratings and being placed at the top of the watch-list. This highlights the concerns raised in Chapter 2 and by others (Measey et al. 2016; Evans et al. 2016), that despite the value of the ideology behind the EICAT scheme, its use may presently be of limited value in the marine context due to the paucity of information quantifying impacts of marine alien species (Ojaveer and Kotta 2015; Ojaveer et al. 2015). Despite the fact that information on impacts was only available for *H. sanguineus*, *H. takanoi* and *E. sinensis* the introduction of any of the listed predatory crabs to South Africa should be considered worrisome. This is because through their predatory nature, invasive crabs can cause trophic cascades, altering food webs (Grosholz et al. 2000; Kimbro et al. 2009), community and habitat structure (Rudnick et al. 2005b; Brousseau et al. 2014; Garbary et al. 2014), biotic interactions (Forsström et al. 2015) and ecosystem functioning (Grosholz and Ruiz 1995). Additionally, predatory species introduced to areas depauperate of such species can cause prominent ecological impacts (Forsström et al. 2015) as the native species have not evolved anti-predator responses against the new predator (Sih et al. 2010).

Conclusion

This study provides the first South African horizon scanning assessment to identify and prioritise potential marine alien species. It revealed that 28 alien crab species have potential pathways to South Africa and most are expected to be able to survive along this coastline. This serves to highlight the risk posed by this group along the South African coast. Three crabs from the family Varunidae i.e. the Japanese shore crab *Hemigrapsus sanguineus*, the brush-clawed shore crab *H. takanoi* and the Chinese mitten crab *Eriocheir sinensis* were placed on the top of the watch-list based on their negative ecological impacts. Nevertheless, as any of the crabs have the potential to cause impacts in South Africa, all 28 species should be considered potentially harmful. When taken up by authorities this list will support the development of appropriate management actions including monitoring, early detection and rapid response to potential crab invasions in South Africa. It is, nonetheless, important to note that despite the value of this watch-list, crabs that have no previous invasion history could still be introduced and pose a threat along this coast. As such, monitoring programmes should look out for

the species on the watch-list, but should also highlight the detection of any unrecognised crabs to authorities immediately.

Synthesis

Introductions of marine alien species beyond their native ranges are escalating at an unprecedented rate (Grosholz 2002; Wonham and Carlton 2005; Simberloff et al. 2013) due to an increase in suitable pathways, global connectedness and intensification of global trade (Whinam et al. 2005; Wilson et al. 2009; Ruiz et al. 2011). Successful invasions are often associated with the interaction of numerous exogenous factors such as pathways (Hulme et al. 2008), propagule pressure (Lockwood et al. 2005), the recipient abiotic environment (Faulkner et al. 2014; Airoidi et al. 2015) and endogenous traits of the invader (Crawley 1989; Ehrlich 1989; Troost 2010). With so many of these species recognised as having negative impacts upon the economy (Binimelis et al. 2008; Jeschke et al. 2014), human health (Hulme 2014) and ecology of recipient environments (Katsanevakis et al. 2014b), marine alien species are recognised as a major threat to both biodiversity and society (Ojaveer et al. 2015).

Predatory brachyuran crabs are considered a successful invasive taxa (Grosholz and Ruiz 2003; Brockerhoff and McLay 2011; Hänfling et al. 2011; Brousseau and McSweeney 2016) with some species being associated with significant economic (Lafferty and Kuris 1996; Normant et al. 2002), human health (Chakraborty et al. 2002) and ecological impacts in their invaded ranges (Kraemer et al. 2007; Rudnick et al. 2005b; Dauvin et al. 2009; Garbary et al. 2014). When considering the prevalence of impacts and threats posed by alien species, it is of great importance to understand the drivers governing their successful invasion. Such information can ultimately be used to understand how we can mitigate the introduction and manage the impacts of invasive species in invaded ranges (Novoa et al. 2015; Cardeccia et al. in press). Despite this, until now no studies have considered predatory crabs in a multi-species and multi-trait approach to gain insight into the drivers of and trait profiles associated with their successful invasion.

Thus in an effort to better understand the complex drivers, patterns, vectors and traits behind the invasion success of these predatory crab invaders, Chapter one aimed to review all global invasions by predatory crabs. This study identified a total of 56 predatory marine alien crab species from 15 families as introduced to regions outside their native ranges. The family Portunidae stood out in supporting the highest number of established alien crab species. While numerous vectors have been involved in the transfer of crabs to various regions around the globe, it was notable that the majority of crabs were introduced by multiple vectors within the shipping pathway. Introduction via the Suez Canal was the next most common vector. Although these alien crabs have been introduced to and from numerous bioregions, the majority originate from the North West Pacific while the Mediterranean bioregion is the recipient of the most crab invaders. This study was, unexpectedly, not able to identify

any predictors of invasion success or suites of traits that predispose crabs to becoming successful invaders. The paucity of trait data is likely to have contributed towards this outcome and as more information on basic biological data becomes available for more species, ecological traits behind the invasion success of crabs may become evident. The outcomes of this study are important not only as they revealed an important gap in the literature with regards to the paucity of trait information for crabs, but also because they provide clarity on the source regions of introductions and the important vectors of transfer for crabs. Such information is a key requirement for the development of management strategies aimed at minimising the risk of introduction.

Since crabs are associated with significant negative impacts within their invasive ranges (Grosholz et al. 2000; Epifanio 2013) it is of great importance to not only mitigate their introduction, but also to manage species already present outside of their native ranges. However, as resources to manage alien species are limited (Hester et al. 2013), it is not possible to manage all incursions. It has been suggested that the best approach would be to prioritise species based on their impacts and manage those of greatest concern (Pyšek and Richardson 2010; Blackburn et al. 2014; Evans et al. 2016). Chapter two therefore used the Environmental Impact Classification for Alien Taxa (EICAT) to assess the environmental impacts of all 56 alien predatory crab species in order to identify species of greatest concern. Results revealed that impacts have only been quantified for 9% of the 56 alien crab species across less than half of the 18 IUCN bioregions in which these species occur. The remaining 91% of species are considered Data Deficient. As such, EICAT could only be used to assess five species for which impact had been quantified. The Japanese shore crab *Hemigrapsus sanguineus* received the highest EICAT rating i.e. one of Major impact. This rating resulted from this species causing changes in the composition of native communities. The remaining four species, the Chinese mitten crab *Eriocheir sinensis*, European shore crab *Carcinus maenas*, Indo-Pacific swimming crab *Charybdis hellerii* and brush-clawed shore crab *Hemigrapsus takanoi* were all rated as having a Moderate impact as they negatively affected native populations, but not community composition. Notably, direct observational evidence and empirical studies of impacts on native biota over large invaded geographical areas in the field was scarce even for these five species. Findings of this study supported suggestions by others that invasion research is often taxonomically and geographically biased. Such biases are observed in the fact that studies most often focus on 1) species that are wide-spread and conspicuous (Pyšek and Richardson 2010; Ojaveer et al. 2015), cause more severe impacts (Hulme et al. 2013; Evans et al. 2016; Kumschick et al. 2017b) or are associated with socio-economic and health impacts (Ojaveer et al. 2015); or 2) developed regions associated with more research (Vilà et al. 2010; Pyšek and Richardson 2010; Evans et al. 2016) and a focus on biosecurity (Pyšek et al. 2008). Management actions have been implemented for only three species (i.e. *C. maenas*, *E. sinensis* and *H. sanguineus*) that are restricted

to well-resourced regions and are associated with negative socio-economic and health impacts. Notably, species with a longer invasion history tended to have more management actions against them. This chapter highlights that alien crabs have the potential to cause severe ecological impacts in their invaded ranges and emphasises the need for studies quantifying the impacts of alien crabs so as to improve our understanding of impacts associated with incursion and in order to support prioritisation of management actions aimed at mitigating the impacts of established species.

The South African coastline has been described as depauperate of marine benthic predators and thus may be vulnerable to invasions by predatory crabs. Considering the open niche present in this system, together with the ability of crabs to cause impacts in their introduced ranges (Kraemer et al. 2007; Rudnick et al. 2005b; Dauvin et al. 2009; Garbary et al. 2014), it provides impetus to institute preventative management to limit invasions and associated impacts along the South African coast. Chapter three applied horizon scanning to create an ordered watch-list of alien crabs that could arrive and establish along the South African coast under current and future temperature regimes. Results revealed that 28 alien crab species have potential pathways to reach South African shores. Shipping was highlighted as the most important pathway, followed by yacht fouling, aquaculture imports and the aquarium trade. Although not all pathways act in each ecoregion, all four pathways should be considered equally important in terms of management as species can be polyvetric and intra-regional transfer can enable the transport of species between ecoregions. Temperature matching revealed that at least 26 crab species are expected to be able to survive in each ecoregion under both present and future conditions, while three species, the Japanese shore crab (*Hemigrapsus sanguineus*), brush-clawed shore crab (*H. takanoi*) and Chinese mitten crab (*Eriocheir sinensis*) were placed highest on the watch-list due to their negative ecological impacts identified in Chapter two. Nevertheless, all 28 species should be considered a potential threat to the native biota along South African shores as any species have the potential to cause impacts even if impact has not previously been reported. As the eradication of species are difficult, expensive and can be of low ecological value once a species has become established in a marine system (Mack and Lonsdale 2002; Britton et al. 2011), it is considered more useful to pre-emptively manage species both pre-border (i.e. the management of pathways (Ruiz et al. 2011) and at-border (i.e. the early detection of alien species (Roy et al. 2014; Ojaveer et al. 2015)). The watch-list developed in this chapter could enable such an approach by supporting the implementation of effective early detection and risk assessments of these predatory crabs. These actions could in turn facilitate the fast response to incursions and minimise chances of establishment along South African shores.

This thesis has reviewed global crab invasions, assessed the impacts of these alien species and developed a watch-list to support the early detection of alien crabs in the South African context. The

insights gained during this work suggest that despite apparently opposing approaches to the management of marine invasions being progressed in the literature (for example see Blackburn et al. (2014) vs Ojaveer et al. (2015)) both approaches form a vital cog in a holistic approach to management. It is thus suggested that a two prong approach be applied, aiming firstly to prevent introductions by managing pathways and borders (Ojaveer et al. 2015), and secondly (where possible) to prioritise post-border management actions based on the impact associated with invasions (Blackburn et al. 2014). While pre-border and at-border management can be facilitated by tools like the watch-list developed in this thesis, it is notable that the scarcity of information quantifying impacts in marine systems poses challenges to the use of tools like EICAT to support post-border management. As alien species impacts are often context dependent, varying in both space and time (Thomsen et al. 2011; Robinson et al. 2017), more quantitative studies are needed to improve our understanding of the threat they pose and support evidence based management.

This thesis has highlighted important gaps in knowledge in relation to crab invasions. We do not presently know enough about the drivers and traits associated with invasion success or impacts of alien crabs to successfully mitigate their introduction or manage them in an insightful way. There is thus an urgent need for studies to improve our understanding of invasion success and impacts of these invaders. Until such time as this body of work emerges, it is suggested that a precautionary approach be applied to managing crab incursions. This work has adopted novel approaches to exploring and understanding the drivers governing successful invasions and their associated impacts and the development of watch-lists of potential problematic species. As such, this study can serve as a model for other similar studies considering other taxonomic groups and regions.

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Appendices

Appendix 1.1 Databases and publications used in the compilation of the list of predatory marine crabs and information on their distribution, vectors and traits.

Databases and websites (All accessed between September 2015 and February 2016)

ABRS (2009) Australian Faunal Directory. Australian Biological Resources Study, Canberra:
<http://www.environment.gov.au/biodiversity/abrs/online-resources/fauna/afd/index.html>

Animal Diversity Web (ADW): <http://animaldiversity.org/accounts/Animalia/>

Centre for Agriculture and Biosciences International (CABI): <http://www.cabi.org/>

Crustaceology: <http://www.crustaceology.com/>

Global Invasive Species Database (GISD): <http://www.iucngisd.org/gisd/>

Information System on Aquatic Non-indigenous and Cryptogenic Species (AquaNIS): <http://www.corpi.ku.lt/databases/index.php/aquanis/species/all>

International Union for Conservation of Nature and Natural Resources (IUCN) red list:
<http://www.iucnredlist.org/>

Marine Species Identification Portal: <http://species-identification.org/search.php>

MarLIN: <http://www.marlin.ac.uk/>

National Exotic Marine and Estuarine Species Information System (Nemesis): <http://invasions.si.edu/nemesis/>

National Introduced Marine Pest Information System (NIMPIS): <http://data.daff.gov.au/marinepests/>

Ocean Biogeographic Information System (OBIS): <http://www.iobis.org/>

SeaLifeBase: <http://www.sealifebase.org/>

Smithsonian Marine Station (SMS) at Fort Pierce: http://www.sms.si.edu/irlspec/Compl_Reports.htm

The Mediterranean Science Commission (CIESM) Atlas of exotic crustaceans in the Mediterranean:
<http://www.ciesm.org/atlas/index.html>

World Register of Marine Species (WoRMS): <http://www.marinespecies.org/>

World Register of Introduced Marine Species (WRIMS): <http://www.marinespecies.org/introduced/>

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in the Mediterranean Sea by 2012. A contribution to the application of European Union's Marine Strategy Framework Directive (MSFD). Part 2. Introduction trends and pathways. *Mediterranean Marine Science*, 13: 328–352.

Appendix 2.1 The list of environmental impact publications reviewed and those recording the highest environmental impact of each species.

Environmental impact publications	Papers recording highest impact
<p><i>Hemigrapsus sanguineus</i> Bourdeau and O'Connor 2003 Brousseau et al. 2001 Brousseau et al. 2014 DeGraaf and Tyrrell 2004 Dauvin et al. 2009 Freeman and Byers 2006 Gerard et al. 1999 Griffen and Byers 2009 Griffen and Williamson 2008 Jungblut et al. 2017 Lohrer and Whitlach 2002a Lohrer and Whitlach 2002b MacDonald et al. 2007 Peterson et al. 2014 Tyrrell et al. 2006</p>	<p>Kraemer et al. 2007</p>
<p><i>Eriocheir sinensis</i> Czerniejewski et al. 2010 Gilbey et al. 2008 Rudnick et al. 2005b</p>	<p>Rosewarne et al. 2016</p>
<p><i>Hemigrapsus takanoi</i> Landschoff et al. 2013 Van den Brink et al. 2012</p>	<p>Dauvin et al. 2009</p>
<p><i>Carcinus maenas</i> Beal 2014 Breen and Metaxas 2008 Breen and Metaxas 2009 DeGraaf and Tyrrell 2004 Floyd and Williams 2004 McDonald et al. 2001 MacDonald et al. 2007 Ross et al. 2004 Taylor 2005 Tyrrell et al. 2006 Walton et al. 1999 Walton and Walton 2001 Walton et al. 2002</p>	<p>Glude 1955 Grosholz and Ruiz 1995 Grosholz et al. 2000 Grosholz 2005 Kimbro et al. 2009 de Rivera et al. 2011 Garbary et al. 2014</p>
<p><i>Charybdis hellerii</i> Sant'Anna et al. 2012a</p>	<p>Felder et al. 2009</p>

Appendix 2.2 Detailed list of references cited in Appendix 2.1.

Beal BF (2014) *Green crab, Carcinus maenas, trapping studies in the Harraseeket River, and manipulative field trials to determine effects of green crabs on the fate and growth of wild and cultured individuals of soft-shell clams, Mya arenaria*. Downeast Institute for applied marine research and education, University of Maine, Maine, pp. 76.

Bourdeau PE and O'Connor NJ (2003) Predation by the nonindigenous Asian Shore Crab *Hemigrapsus sanguineus* on macroalgae and molluscs. *Northeastern Naturalist*, 10: 319–334.

Breen E and Metaxas A (2008) A comparison of predation rates by non-indigenous and indigenous crabs (juvenile *Carcinus maenas*, juvenile *Cancer irroratus*, and adult *Dyspanopeus sayi*) in laboratory and field experiments. *Estuaries and Coasts*, 31: 728–737.

Breen E and Metaxas A (2009) Effects of juvenile non-indigenous *Carcinus maenas* on the growth and condition of juvenile *Cancer irroratus*. *Journal of Experimental Marine Biology and Ecology*, 377: 12–19.

Brousseau DJ, Filipowicz A and Baglivo JA (2001) Laboratory investigations of the effects of predator sex and size on prey selection by the Asian crab, *Hemigrapsus sanguineus*. *Journal of Experimental Marine Biology and Ecology*, 262: 199–210.

Brousseau DJ, Goldberg R and Garza C (2014) Impact of predation by the invasive crab *Hemigrapsus sanguineus* on survival of juvenile blue mussels in western Long Island Sound. *Northeastern Naturalist*, 21: 119–133.

Czerniejewski P, Rybczyk A and Wawrzyniak W (2010) Diet of the Chinese mitten crab, *Eriocheir sinensis* H. Milne Edwards, 1853, and potential effects of the crab on the aquatic community in the river Odra/Oder Estuary (N.-W. Poland). *Crustaceana*, 83: 195–205.

Dauvin JC, Rius AT and Ruellet T (2009) Recent expansion of two invasive crabs species *Hemigrapsus sanguineus* (de Haan, 1835) and *H. takanoi* Asakura and Watanabe 2005 along the Opal Coast, France. *Aquatic Invasions*, 4: 451–465.

DeGraaf JD and Tyrrell MC (2004) Comparison of the feeding rates of two introduced crab species, *Carcinus maenas* and *Hemigrapsus sanguineus*, on the blue mussel, *Mytilus edulis*. *Northeastern Naturalist*, 11: 163–167.

de Rivera CE, Grosholz ED and Ruiz GM (2011) Multiple and long-term effects of an introduced predatory crab. *Marine Ecology Progress Series*, 429: 145–155.

Felder DL, Dworschak PC, Robles R, Bracken HD, Windsor AM, Felder JM and Lemaitre R (2009) Obvious invaders and overlooked infauna: unexpected constituents of the decapod crustacean fauna at Twin Cays, Belize. *Smithsonian Contributions to the Marine Sciences*, 38: 181–188.

Floyd T and Williams SJ (2004) Impact of green crab (*Carcinus maenas* L.) predation on a population of soft-shell clams (*Mya arenaria* L.) in the Southern Gulf of St. Lawrence. *Journal of Shellfish Research*, 23: 457–462.

Freeman AS and Byers JE (2006) Divergent induced responses to an invasive predator in marine mussel populations. *Science*, 313: 831–833.

Garbary DJ, Miller AG, Williams J and Seymour NR (2014) Drastic decline of an extensive eelgrass bed in Nova Scotia due to the activity of the invasive green crab (*Carcinus maenas*). *Marine Biology*, 161: 3–15.

Gerard VA, Cerrator RM and Larson AA (1999) Potential impacts of a western Pacific grapsid crab on intertidal communities of the northwestern Atlantic Ocean. *Biological Invasions*, 1: 353–361.

Gilbey V, Attrill MJ and Coleman RA (2008) Juvenile Chinese mitten crabs (*Eriocheir sinensis*) in the Thames estuary: distribution, movement and possible interactions with the native crab *Carcinus maenas*. *Biological Invasions*, 10: 67–77.

Glude JB (1955) The effects of temperature and predators on the abundance of the soft-shell clam, *Mya arenaria*, in New England. *American Fisheries Society*, 84: 13–26.

Griffen BD and Williamson T (2008) Influence of predator density on nonindependent effects of multiple predator species. *Oecologia*, 155: 151–159.

Griffen BD and Byers JE (2009) Community impacts of two invasive crabs: the interactive roles of density, prey recruitment, and indirect effects. *Biological Invasions*, 11: 927–940.

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Grosholz ED and Ruiz GM (1995) Spread and potential impact of the recently introduced European green crab, *Carcinus maenas*, in central California. *Marine Biology*, 122: 239–247.

Grosholz ED, Ruiz GM, Dean CA, Shirley KA, Maron JL and Connors PG (2000) The impacts of a nonindigenous marine predator in a California bay. *Ecology*, 81: 1206–1224.

Jungblut S, Beermann J, Boos K, Saborowski R and Hagen W (2017) Population development of the invasive crab *Hemigrapsus sanguineus* (De Haan, 1853) and its potential native competitor *Carcinus maenas* (Linnaeus, 1758) at Helgoland (North Sea) between 2009 and 2014. *Aquatic Invasions*, 12: 85–96.

Kimbrow DL, Grosholz ED, Baukus AJ, Nesbitt NJ, Travis NM, Attoe S and Coleman-Hulbert C (2009) Invasive species cause large-scale loss of native California oyster habitat by disrupting trophic cascades. *Oecologia*, 160: 563–575.

Kraemer GP, Sellberg M, Gordon A and Main J (2007) Eight-year record of *Hemigrapsus sanguineus* (Asian shore crab) invasion in western Long Island Sound estuary. *Northeastern Naturalist*, 14: 207–224.

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Lohrer AM and Whitlatch RB (2002b) Relative impacts of two exotic brachyuran species on blue mussel populations in Long Island Sound. *Marine Ecology Progress Series*, 227: 135–144.

MacDonald JA, Roudez R, Glover T and Weis JS (2007) The invasive green crab and Japanese shore crab: behavioral interactions with a native crab species, the blue crab. *Biological Invasions*, 9: 837–848.

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Ross DJ, Johnson CR, Hewitt CL and Ruiz GM (2004) Interaction and impacts of two introduced species on a soft-sediment marine assemblage in SE Tasmania. *Marine Biology*, 144: 747–756.

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Sant'Anna BS, Watanabe TT, Turra A and Zara FJ (2012a) First record of the non-indigenous portunid crab *Charybdis variegata* from the western Atlantic coast. *BioInvasions Records*, 1: 11–16.

Taylor DL (2005) Predatory impact of the green crab (*Carcinus maenas* Linnaeus) on post-settlement winter flounder (*Pseudopleuronectes americanus* Walbaum) as revealed by immunological dietary analysis. *Journal of Experimental Marine Biology and Ecology*, 324: 112–126.

Tyrrell M, Guarino PA and Harris LG (2006) Predatory impacts of two introduced crab species: inferences from microcosms. *Northeastern Naturalist*, 13: 375–390.

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Appendix 2.3 List of 51 species that were classified as data deficient (DD) during the EICAT assessment.

Family	Species	Family	Species
Portunidae	<i>Callinectes bocourti</i> <i>Callinectes danae</i> <i>Callinectes exasperatus</i> <i>Callinectes sapidus</i> <i>Carcinus aestuarii</i> <i>Carupa tenuipes</i> <i>Charybdis feriata</i> <i>Charybdis japonica</i> <i>Charybdis longicollis</i> <i>Charybdis lucifera</i> <i>Charybdis variegata</i> <i>Gonioinfradens paucidentatus</i> <i>Liocarcinus navigator</i> <i>Necora puber</i> <i>Portunus pelagicus</i> <i>Portunus segnis</i> <i>Scylla serrata</i> <i>Thalamita gloriensis</i> <i>Thalamita indistincta</i> <i>Thalamita poissonii</i>	Carpiliidae	<i>Dyspanopeus sayi</i>
		Dairidae	<i>Daira perlata</i>
		Grapsidae	<i>Metopograpsus oceanicus</i> <i>Pachygrapsus marmoratus</i> <i>Pachygrapsus transversus</i> <i>Percnon gibbesi</i>
		Hymenosomatidae	<i>Elamena mathoei</i> <i>Halicarcinus innominatus</i> <i>Halicarcinus planatus</i>
		Matutidae	<i>Ashtoret lunaris</i> <i>Matuta victor</i>
		Menippidae	<i>Sphaerozium nitidus</i>
		Oregoniidae	<i>Chionoecetes opilio</i>
Varunidae	<i>Brachynotus sexdentatus</i> <i>Eriocheir hepuensis</i> <i>Eriocheir japonica</i>	Panopeidae	<i>Panopeus lacustris</i>
Calappidae	<i>Calappa hepatica</i>	Pilumnidae	<i>Actumnus globulus</i> <i>Eurycarcinus integrifrons</i> <i>Pilumnopeus vauquelini</i> <i>Pilumnus minutus</i> <i>Pilumnus spinifer</i>
Cancridae	<i>Cancer irroratus</i> <i>Glebocarcinus amphioetus</i> <i>Metacarcinus magister</i> <i>Metacarcinus novaezelandiae</i> <i>Romaleon gibbosulum</i>	Raninidae	<i>Notopus dorsipes</i>
		Xanthidae	<i>Atergatis roseus</i> <i>Xanthias lamarckii</i>

Appendix 2.4 Detailed description of the impacts resulting in the assigned mechanisms and EICAT ratings, as well as the associated confidence ratings and justifications.

Impact caused by species and mechanism of impact	Confidence rating and justification
<i>Hemigrapsus sanguineus</i>	EICAT rating: Major
<p>Competition</p> <p>A census of crab populations from 1998-2005 at Edith Read Wildlife sanctuary in Rye, NY, revealed a 95% decrease in the abundance of the flatback mud crab <i>Eurypanopeus depressus</i>, a 80% decrease in the lower intertidal density of the periwinkle <i>Littorina littorea</i> and declines in populations of the Atlantic rock crab <i>Cancer irroratus</i>, shore crab <i>Carcinus maenas</i>, and spider crab <i>Libinia emarginata</i> that coincided with the with the expansion of the Japanese shore crab <i>Hemigrapsus sanguineus</i>. In 1998 and 1999, Atlantic rock crab and shore crab were uncommon and in 2000 large areas were devoid of shore and Atlantic rock crabs with few flatback mud crabs (Kraemer et al. 2007).</p>	<p>Medium</p> <p>The impacts are based on observations in the field over long periods of time (1998 - 2005) and on inferred data. From the fact that the area were devoid of some species one could assume that <i>H. sanguineus</i> caused local population extinction of these species. Studies and evidence are scarce. Impacts are recorded at a spatial scale which may not be relevant to the scale over which original native communities can be characterized, but extrapolation or downscaling of the data to relevant scales is considered reliable or to embrace little uncertainty.</p>
<i>Eriocheir sinensis</i>	EICAT rating: Moderate
<p>Predation</p> <p>Laboratory feeding trials revealed that the Chinese mitten crab <i>Eriocheir sinensis</i> is a predator of chironomids, isopods, eggs of two fish species and the freshwater shrimp <i>Gammarus pulex</i>. Juvenile <i>E. sinensis</i> predated on <i>G. pulex</i> more than the native Atlantic stream crayfish <i>Austropotamobius pallipes</i>. Outdoor mesocosms experiments in 2012 at a meadow at the University of Leeds Field Research Unit, UK further revealed declines in the abundance of amphipods, isopods, chironomids and gastropods when <i>E. sinensis</i> was present. Together with the feeding experiments this infers that predation by <i>E. sinensis</i> is responsible for declines (Rosewarne et al. 2016).</p>	<p>Medium</p> <p>Laboratory experiments were conducted for four weeks to determine the diet of <i>E. sinensis</i>. Outdoor mesocosms experiments revealed a decline in abundance of invertebrates in the presence of <i>E. sinensis</i>. This data was then used to infer that these changes occur in natural communities. Impacts are recorded at a spatial scale which may not be relevant to the scale over which original native communities can be characterized, but extrapolation or downscaling of the data to relevant scales is considered reliable or to embrace little uncertainty. The data is reliable and not contradictory to any other studies</p>

Impact caused by species and mechanism of impact	Confidence rating and justification
<i>Hemigrapsus takanoi</i>	EICAT rating: Moderate
<p>Competition</p> <p>In 2008, alien populations of the brush-clawed shore crab <i>Hemigrapsus takanoi</i> and <i>H. sanguineus</i>, which is present along the Opal coast on the French side of the Dover Strait, were found to inhabit similar habitats to that of the native shore crab <i>Carcinus maenas</i>. Where <i>H. takanoi</i> was present in high densities (Dunkirk harbour) it was found to significantly dominate <i>C. maenas</i> which showed extreme declines in abundance. In contrast, in areas with low abundance of <i>H. takanoi</i> (Boulogne-sur-mer), <i>C. maenas</i> dominated (Dauvin et al. 2009).</p>	<p>Low</p> <p>It is inferred that <i>H. takanoi</i> caused the reduction in population densities of <i>C. maenas</i> from the observational evidence. The study just states that <i>C. maenas</i> was not dominant in areas where <i>H. takanoi</i> was, not that the densities declined. The interpretation of data/information is difficult and not direct or clear and the evidence thus not of good quality.</p>
<i>Carcinus maenas</i>	EICAT rating: Moderate
<p>Predation</p> <p>A study in Sagadahoc Bay, Maine, USA revealed a 50% decrease in soft-shell clam populations between 1949 and 1953 that coincided with an increase in <i>Carcinus maenas</i> abundance (Glude 1955).</p>	<p>Medium</p> <p>Studies and evidence were accessible, of good quality and reliable. The impacts are based on 1) well-documented observations in the field over long periods of time (14 years for de Rivera et al. (2011); 20 years for Grosholz (2005) and 4 years for Glude (1955)) in conjunction with lab experiments to confirm that the marked changes are as a result of <i>C. maenas</i> invasion; 2) observations in conjunction with experimental field studies (Garbary et al. 2014; Grosholz and Ruiz 1995); and 3) before and after studies (Grosholz et al. 2000) and experimental designs set up in mesocosms within the field (Kimbrow et al. 2009). Most of the studies were recorded in harbours or in small locations which are not the typical spatial scale over which original native communities can be characterised, but extrapolation or downscaling of the data to relevant scales is considered reliable. Data from the studies were not contradictory.</p>

Impact caused by species and mechanism of impact	Confidence rating and justification
<p>Predation</p> <p>Enclosure experiments at Bodega Bay harbour during 1993 revealed that <i>Carcinus maenas</i> significantly reduced the densities of the once abundant cumacean <i>Cumella vulgaris</i>, Pacific clam <i>Nutricola tantilla</i>, confusing dwarf-venus clam <i>N. confusa</i> and the amphipod <i>Corophium</i> sp. Abundances of the tanaid <i>Leptochelia dubia</i>, syllid polychaete (<i>Exogene</i> sp.), and a spionid polychaete (<i>Pseudopolydora</i> sp.) was also reduced but not significantly. Cracked shells in the experimental cages were an indication of predation (Grosholz and Ruiz 1995)</p>	
<p>Predation</p> <p>A nine year monitoring study in central California revealed that <i>Carcinus maenas</i> significantly reduced the abundance of 20 invertebrate species and the densities of the native clams <i>Nutricola confusa</i> and <i>N. tantilla</i> and that of native shore crab <i>Hemigrapsus oregonensis</i>, by 5 to 10 times within three years of its arrival. This suggests top-down control (Grosholz et al. 2000).</p>	
<p>Predation</p> <p>Based on data for nearly 30 years (since early 1970's -2002) at Bodega Harbor, CA, there has been a drastic decrease in the dominance of the clams <i>Nutricola tantilla</i> and <i>N. confusa</i> (<i>Nutricola</i> sp.) which has been suggested to be as a result of <i>Carcinus maenas</i> predation. Lab experiments confirmed that <i>C. maenas</i> strongly prefers <i>Nutricola</i> sp. (Grosholz 2005).</p>	

Impact caused by species and mechanism of impact	Confidence rating and justification
<p>Interaction with other alien species</p> <p>The replacement of the native rock crab <i>Cancer antennarius</i>, and whelk <i>Acanthinucella spirata</i> by invasive <i>Carcinus maenas</i> and an invasive whelk <i>Urosalpinx cinerea</i> in Tomales Bay, California, resulted in the drastic decline of native oysters <i>Ostreola conchaphila</i>. In a system of native crabs and whelks, oyster populations are maintained as crabs consume whelks and alter their foraging behaviour. When replaced by the invasive whelks, although whelks did not avoid crabs due to naivety, native crabs could still reduce densities of invasive whelks and reduce oyster consumption. However, when replaced by the invasive whelks and crabs, oyster populations were depleted as a result of predator naivety of invasive whelks to crabs and the reduced ability of <i>C. maenas</i> to reduce densities of invasive whelks (Kimbrow et al. 2009).</p>	
<p>Competition</p> <p>14 years of field surveys (1993 to 2006) and experimental setups at Gaffney Point, Bodega Harbor, California revealed that the abundance of native <i>Hemigrapsus oregonensis</i> declined when that of alien <i>Carcinus maenas</i> increased and increased when that of <i>C. maenas</i> declined. <i>H. oregonensis</i> populations exhibited range shift which coincided with shifts in the abundance of <i>C. maenas</i> (de Rivera et al. 2011).</p>	
<p>Grazing</p> <p>Observations in 2001 and 2002 in estuaries along the Nova Scotia coast of the southern Gulf of St. Lawrence, revealed a 75% decline in shoot density of the common eelgrass <i>Zostera marina</i>. As similar declines were noted for</p>	

Impact caused by species and mechanism of impact	Confidence rating and justification
<p>experimental setups in eelgrass beds in Benoit Cove in which <i>Carcinus maenas</i> was present, the foraging behaviour of <i>C. maenas</i>, which involved the tearing of shoots and the digging of large pits, was suggested as the reason behind the severe decline (Garbary et al. 2014).</p>	
<p><i>Charybdis hellerii</i> EICAT rating: Moderate</p>	
<p>Competition and predation</p> <p>Sampling in 1983 and 2002 revealed that spiny lobsters (<i>Panulirus</i> sp.), swimming crabs (<i>Callinectes</i> sp.), stone crabs (<i>Menippe</i> sp.), and large spider crabs (<i>Mithrax</i> sp.) were present and common in habitats of large bottom debris and cavities under coral heads at both Carrie Bow Cay and Twin Cays. During 2007 sampling, none of these species were present. As seven individuals of the alien swimming crab <i>Charybdis hellerii</i> were present and dominated cavities under coral heads, it is believed to have displaced these species. This crab has also been observed to feed on individuals of <i>Callinectes</i>, and one species of <i>Panulirus</i> (Felder et al. 2009).</p>	<p>Medium</p> <p>The study is based on before and after observations, lending some direct observational evidence in the field to support the assessment. As there were no quantifying studies, some information is inferred. Impacts are recorded at a spatial scale which may not be relevant to the scale over which original native communities can be characterized, but extrapolation or downscaling of the data to relevant scales is considered reliable or to embrace little uncertainty. Data is not contradictory.</p>

Appendix 3.1 Mean ($\pm 95\%$ CI) minimum and maximum SSTs for current and predicted climate for each South African ecoregion.

Ecoregions	Current		Predicted	
	\bar{Y} min (CI)	\bar{Y} max (CI)	\bar{Y} min (CI)	\bar{Y} max (CI)
Benguela	12.93 (12.20-13.65)	17.02 (15.71-18.33)	14.33 (13.60-15.05)	18.42 (17.11-19.73)
Aghulhas	15.27 (14.08-16.47)	23.42 (22.47- 24.38)	16.67 (15.48-17.87)	24.82 (23.87-25.78)
Natal	22.28 (21.25-23.32)	26.57 (24.25-28.88)	23.68 (22.65-24.72)	27.97 (25.65-30.28)
Delagoa	24.15 (22.76-25.54)	25.91 (24.08-27.73)	25.55 (24.16-26.94)	27.31 (25.48-29.13)

Appendix 3.2 Mean ($\pm 95\%$ CI) minimum and maximum SSTs for each alien crab species across its geographic range.

Species	\bar{Y} min (CI)	\bar{Y} max (CI)	Species	\bar{Y} min (CI)	\bar{Y} max (CI)
<i>Metopograpsus oceanicus</i>	24.83 (24.44-25.23)	32.05 (31.66-32.43)	<i>Eriocheir sinensis</i>	5.3 (2.54-8.05)	26.65 (23.19-30.10)
<i>Eurycarcinus integrifrons</i>	18.83 (17.73-19.93)	33.02 (32.26-33.79)	<i>Hemigrapsus sanguineus</i>	3.84 (1.70-5.97)	27.06 (23.17-30.94)
<i>Eriocheir hepuensis</i>	20.57 (17.47-23.67)	27.41 (23.53-31.29)	<i>Hemigrapsus takanoi</i>	3.84 (1.70-5.97)	29.53 (26.96-32.09)
<i>Charybdis lucifera</i>	15.45 (11.08-19.82)	32.87 (32.37-33.36)	<i>Dyspanopeus sayi</i>	7.04 (4.30-9.77)	31.01 (28.58-33.45)
<i>Panopeus lacustris</i>	10.09 (9.64-10.54)	30.84 (30.11-31.56)	<i>Glebocarcinus amphioetus</i>	6.67 (4.26-9.07)	27.01 (24.64-29.38)
<i>Percnon gibbesi</i>	8.77 (7.30-10.23)	30.95 (30.36-31.53)	<i>Carcinus aestuarii</i>	7.07 (3.36-10.78)	24.82 (21.99-27.65)
<i>Cancer irroratus</i>	2.48 (1.23-3.73)	30.97 (28.77-33.10)	<i>Romaleon gibbosulum</i>	5.70 (4.15-7.26)	24.78 (21.85-27.71)
<i>Callinectes bocourti</i>	9.13 (7.63-10.62)	31.41 (31.19-31.63)	<i>Brachynotus sexdentatus</i>	6.44 (3.08-9.80)	24.55 (21.88-27.23)
<i>Callinectes danae</i>	6.63 (6.04-7.21)	31.53 (30.57-32.50)	<i>Pachygrapsus marmoratus</i>	8.55 (5.69-11.41)	25.58 (22.49-28.66)
<i>Callinectes exasperatus</i>	9.92 (6.47-13.37)	31.53 (30.57-32.50)	<i>Pilumnus spinifer</i>	8.73 (5.29-12.10)	27.49 (25.02-29.97)
<i>Callinectes sapidus</i>	2.03 (1.51-2.55)	31.53 (30.57-32.50)	<i>Metacarcinus novaezelandiae</i>	10.64 (9.40-11.88)	25.25 (23.36-27.13)
<i>Charybdis japonica</i>	5.82 (4.57-7.06)	30.82 (30.06-31.58)	<i>Halicarcinus planatus</i>	1.66 (1.08-2.23)	23.24 (22.00-24.48)
<i>Liocarcinus navigator</i>	5.61 (3.15-8.06)	30.41 (28.60-32.21)	<i>Halicarcinus innominatus</i>	10.45 (9.24-11.67)	16.53 (15.28-17.77)
<i>Eriocheir japonica</i>	9.34 (8.18-10.50)	29.53 (26.94-32.11)	<i>Metacarcinus magister</i>	4.13 (2.69-5.58)	20.24 (18.30-22.17)