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Biological and ecological attributes of a population of the
invasive Asian paddle crab, *Charybdis japonica*, in
northeastern New Zealand

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of Doctor of Philosophy in Marine Science,
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Abstract

This thesis describes biological and ecological characteristics of the invasive Asian paddle crab, *Charybdis japonica* and is the first such study of the species in its invaded habitat. Based on the first appearance of gravid females in November, mating begins at the end of winter and continues throughout the summer. After attaining a reproductive size of between 40 and 50mm carapace width after one year, females hatch at least one brood of up to 400,000 eggs between austral spring and autumn (November to April) with a peak in austral summer. Young crabs that hatch early in the reproductive season attain recruitment size in autumn and settle into estuaries. Comparisons of zoeal survival rates to historical sea surface temperatures and salinities show that *C. japonica* Stage 1 zoeae tolerate broad environmental ranges and could survive natural conditions and continue to spread throughout New Zealand. Throughout its life, *C. japonica* is an opportunistic omnivore with a preference for sessile and slow moving macroinvertebrate prey items, based on diet analysis. Starved *C. japonica* preferentially prey upon smaller bivalves and can consume up to 42 juveniles of recreationally and ecologically important bivalve species in 24h. In one-on-one competition for food, male *C. japonica* behaviourally dominated both male and female native New Zealand paddle crabs, which were not successful in defending or acquiring the prey items from *C. japonica*. Surprisingly, despite its predatory and competitive abilities, field experiments and comparisons with historical surveys did not detect an impact of *C. japonica* on native fauna. With a long larval life that facilitates dispersal, rapid growth to maturity, high fecundity, a broad voracious diet, high competitive ability, and broad environmental tolerances, it appears that *C. japonica* has biological and ecological attributes that have aided their integration into a novel New Zealand habitat.

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Chapter One

General Introduction

Overview

Marine invasions, defined as the introduction and successful establishment of marine species outside their natural ranges, have been recorded in increasing numbers over the past 25 years (e.g. Cohen and Carlton 1998, Mack et al. 2000, Ruiz et al. 2000, Hewitt et al. 2004, Galil 2007, Lockwood et al. 2007). Indeed, there are over 500 marine invasive species established in the coastal waters of the USA alone (Grosholz 2005). Once established, introduced populations can spread quickly over large distances, either by human mediated means or unaided adult and/or larval dispersal (e.g. Cohen et al. 1995, Grosholz 1996, Ruiz et al. 1997, Cohen and Carlton 1998, Mack et al. 2000, Ruiz and Carlton 2003, Minchin 2007). Many introduced species have caused severe ecological and economic impacts (e.g. Carlton 1996, Mack et al. 2000, Pimentel et al. 2000, Carlton 2001, Crooks 2002, Wallentinus and Nyberg 2007), which are now considered one of the most important threats to natural biodiversity, on par with the effects of global climate change (Lubchenco et al. 1991, Vitousek et al. 1997, Carlton 2001, Hewitt 2003, Grosholz 2005). The failure to address the pressing problem of marine invasions could result in the loss of fishery resources, disruption of natural ecological processes, and the creation of homogenous impoverished oceans composed of cosmopolitan species (Mack et al. 2000).

Many questions regarding the processes and patterns of successful invasions remain unanswered due to the plethora of factors that contribute to the overall establishment, spread, abundance, and demography of invasive species (deRivera et al. 2005). These factors include propagule supply, environmental conditions, and the recipient community. It is estimated that only 10% of all introduced species establish themselves in a new environment, and, of these, only 10% expand their ranges (Williamson 1996). While many studies have examined the role of the recipient community (low diversity of native species, empty niches, disturbed environments, etc.) in defining whether or not a species will be successful, the biological and ecological traits of the invader are equally important. There is no definitive list of characteristics that describe successful invaders; however, certain biological and ecological traits concerning physiological tolerances, life history characteristics, population level variability, biogeographic attributes, and behaviour reappear consistently (Kolar and Lodge 2001). Overall, the most successful marine invasive species have high fecundities, short generation times, high genetic variability, a large native range, eurytopy, polyphagy, phenotypic plasticity (i.e. broad environmental tolerances), and human commensalism (Lodge 1993, Fofonoff et al. 2003). However, in order for an exotic species to become established, the invaded ecosystem must be compatible with the physiological and ecological requirements of the invader.

Species with narrow specialist requirements are unlikely to succeed in new environments that present novel challenges.

Because it is unethical to experimentally transplant species into a new habitat, it is imperative to study successful invaders in their novel environments to understand those characteristics that may have aided their introduction. Describing such attributes can also be employed to predict their future spread and possible impacts on native species. This thesis aims to describe the biological and ecological characteristics that have aided the introduction of an invasive species of crab into northeastern New Zealand.

Biological characteristics of successful invaders

There are two stages to any invasion: (1) introduction, colonization and establishment of a species in a new area, and (2) spread and replacement of, or coexistence with, native species. The most important factor affecting the success of invasive organisms is their ability to be transported to new habitats both as larvae and adults (Kolar and Lodge 2001). While there are several examples of human-assisted transportation vectors for invasive organisms, a large proportion of marine invasions are proposed to have been facilitated by the international commercial shipping industry and ballast water exchange (Gollasch 2007). As most commercial shipping ports are located within harbours, bays and estuaries, the ballast that is exchanged in these waterways inadvertently uptakes and later discharges both adult and larval stages of marine species that have evolved to be extremely tolerant to natural fluctuations of various factors (i.e. salinity, temperature, turbidity) (MacIsaac et al. 2002).

The ability to tolerate natural environmental fluctuations in the form of physiological plasticities selectively allow some species to successfully establish and spread even if they have been transported long distances from their native range (Carroll 2007). During the journey to new ecosystems, microcosms in ballast tanks perform species selections of their own; temporal studies of species diversity and abundance show a dramatic decline of live organisms after 10 days (Gollasch et al. 2000, Olenin et al. 2000). Although many species do not survive the trans-oceanic journeys, those that do survive tend to be able to withstand a plethora of variables (MacIsaac et al. 2002). Once they have arrived in a new environment, exotic species may become locally adapted over time in response to selective pressures associated with environmental conditions (Crandall et al. 2000, Lee 2002). This post-invasion evolutionary response has been suggested as a possible explanation for the time lag observed between the initial invasion event and the subsequent population and range explosion (Williamson 1996, Mooney and Cleland 2001). Founding populations can spread at any time through adult migration or larval dispersal, as a highly successful reproductive year may increase the number of propagules and the chance of further invasion throughout the country. Some invasive species exhibit

lag periods between the first and secondary invasions that can last years or decades (Crooks and Soule 1999). For example, Grosholz (1996) reports annual rates of expansion for introduced portunid and grapsid crabs of between 12 and 55km/y, although annual and geographical variation can influence these rates.

However, due to a number of variables, founding populations may be small and vulnerable to extinction by demographic, environmental, and/or general stochasticity (MacArthur and Wilson 1967, Lockwood et al. 2005). Not only does the number of births need to outweigh the deaths, but the population itself needs to increase at such a rate to reduce the time in which it is at risk of stochasticity (Sol 2007). Understanding the life history of any species requires knowledge of such aspects as the development of sexual maturity, changes in allometric growth, and fecundity. Collectively, these factors ultimately influence population dynamics by affecting reproductive output, demographics, and recruitment rates (Williams 1966, Stearns 1992) and contribute to the ability of invasive species to spread in a new location. Therefore, such biological and life history attributes of *r*-selected species (i.e. relatively young age at maturity, large numbers of independent young, fast intrinsic growth) may influence the ability of some organisms to escape the critical founding stage and become successful invaders.

Marine invasions of island ecosystems and ecological characteristics of successful invaders

While the ability to establish populations may be mostly due to the physiological and /or biological attributes of the invader, long-term success depends on the ecological structure of the invaded habitat. The success or failure of a species, once it has dispersed to a new environment, is influenced by at least three factors: (1) the amount of resources available to the invader and their ability to utilize these resources, (2) the pattern of resource use among native organisms that the invader must compete against, and (3) the strength and organization of interspecific competition within the community, influencing the ability of the invader to successfully enter the community structure (including both positive and negative interactions) (Bruno et al. 2003, Dunstan and Johnson 2007). Those species that have a broad habitat range and/or diet tend to fare well as invaders (Lefebvre et al. 2004, Vazquez 2006, Weis 2010), as do those species that are able to compete strongly with native species for resources such as food and space (Dunstan and Johnson 2007).

New Zealand has been an isolated island for at least 80 million years (Gordon et al. 2010). It is conventional wisdom that island ecosystems are highly susceptible to invasions, and that invasions on islands are more detrimental than continental invasions (Elton 1958, Wilson 1965, Carlquist 1974). Its nearest neighbour is Australia, which is 1600 - 2250 kilometres away; Antarctica and South America are 2570 and 6240 kilometres away, respectively. In fact, in a global comparison of the numbers of

successful marine invasions, the island nations of New Zealand and Hawaii accounted for two of the four most invaded coasts (Inglis et al. 2006). This may be due to the commonly held belief that the relative isolation of island communities, such as New Zealand, has led to few and competitively inferior functional groups, which are not able to fill all of the ecological niches, (i.e. the “vacant niche hypothesis”) (Elton 1958, MacArthur and Wilson 1967, Carlquist 1974, Towns and Ballantine 1993, Sax and Brown 2000). For example, compared with other temperate coastlines around the world (i.e. 218 species of brachyurans in West Africa (Manning and Holthuis 1981), over 1500 species along the US coast with 429 species off the coast of Texas, USA alone, and over 1400 species along the South American coastline (Boschi 2000)), New Zealand has only 63 intertidal and subtidal crab species (McLay 1988). While 82% of the genera are represented by a single species, 53% of these are endemic to New Zealand (Inglis et al. 2006). In some cases, the depauperate species assemblages of island ecosystems have effectively reduced the number of functional groups, allowing a new species the opportunity to fill an empty niche (Simberloff 1995). This is especially true for the marine environment, as it has been estimated that there are at least 150,000 empty niches in marine ecosystems worldwide (Walker and Valentine 1984).

With the increases in globalization and the plethora of human-aided invasion vectors, geographically and ecologically isolated ecosystems are being inundated with hundreds of new species, and islands lacking high species diversity may be especially prone to invasions due to the lack of native competitors, predators or pathogens (i.e. the enemy release hypothesis, Keane and Crawley 2002). Having evolved in a more competitive environment, invasive species may have an upper hand in competing against species that have not co-evolved to interact with them (Sax and Brown 2000). Due to the decreased number of island species, there is a lack of competition for resources, which effectively renders island species naïve to competitive interactions and in a poor position to compete with a similar invader (Elton 1958, Simberloff 1995). Their release from enemies in new environments allows exotic species to spend more energy on growth and reproduction, and may ultimately influence their competitive superiority (Laffetty and Kuris 1996, Torchin et al. 2001, 2003). The combination of ecological characteristics, including a broad diet, effective predation strategies in a new environment, and the ability to compete successfully with native organisms, is instrumental in predicting whether or not an invasive species will survive and spread in a novel ecosystem.

Invasive crabs

Crabs are among the most widespread taxa in the oceans (Poore 2004), and they have many life history traits that enable them to be successful invaders. Many successful invasive crabs exhibit biological traits of *r*-selected species, including rapid growth, early sexual maturation, high

reproductive rates, and production of large broods (Weis 2010). Invasive crabs can be an important structuring force in marine communities by altering habitats and ecosystem function (i.e. primary production, decomposition, hydrology, nutrient cycling, disturbance regimes), and/or altering abundance, distribution and behaviours of native species and other exotic species (Glude 1955, Hanks 1961, Lubchenco 1978, Grosholz and Ruiz 1995, Grosholz et al. 2000, Brousseau et al. 2001, Walton et al. 2002, Ross et al. 2004, Rudnick et al. 2005, Hollebone and Hay 2008, Kimbro et al. 2009). Many successful invasive crabs have been shown to have opportunistic, generalist feeding approaches that enable them to survive in various ecosystems (e.g. *Carcinus maenas* (Cohen et al. 1995), *Charybdis hellerii* (Dineen et al. 2001), *Eriocheir sinensis* (Rudnick and Resh 2005), *Hemigrapsus sanguineus* (Ledesma and O'Connor 2001)). Earlier studies on crab predation in estuaries have provided strong evidence that they are important predators of juvenile bivalves (Landers 1954, Carriker 1967, Ropes 1968, Jensen and Jensen 1985, Hines et al. 1990), supporting the hypothesis that crabs tend to choose relatively small prey (Seed and Hughes 1995). High juvenile mortality has important implications for prey population maintenance and is a serious threat to the successful management of commercial bivalve resources (Belding 1930, Hanks 1961, Galtsoff 1964). For several species of invasive crabs, the ability to effectively compete with native species for resources, such as food and shelter, has been instrumental to their success (McDonald et al. 2001, Jensen et al. 2002, deRivera et al. 2005, Williams et al. 2006, MacDonald et al. 2007, Roche and Torchin 2007, Gibley et al. 2008, Dauvin et al. 2009). In several cases, it is a matter of the invasive being a larger, competitively superior species (Grosholz et al. 2000), but even smaller or equally sized invasives have been shown to be competitively dominant over native species for resources (McDonald et al. 2001, deRivera et al. 2005, Williams et al. 2006). The superior competitive ability of some populations of invasive crabs has been shown to restrict the distributions of similar native crabs or even other invasive crabs (Lohrer and Whitlatch 2002, Hunt and Behrens Yamanda 2003, deRivera et al. 2005, Kraemer et al. 2007, Belair and Miron 2009, Breen and Metaxas 2009).

Not all successful crab invaders fulfill all the biological and ecological attributes listed above. However, by studying all applicable characteristics of successful invaders, we can determine those traits that are the most important to the continued residency and spread of species in new environments. Collating this data will allow more accurate predictions of the likelihood of a new species becoming established and may be able to forecast the impact they will have on native ecosystems.

A marine invader in New Zealand: *Charybdis japonica*

More than 175 non-indigenous species have become established in New Zealand waters over the past 200 years and continue to appear (Gordon et al. 2010). There have been reports of non-native

crab species found in New Zealand waters previously; larvae and adults of the swimming crabs *Scylla serrata* and *Portunus pelagicus* have been found infrequently but are unable to breed due to the cooler sea surface temperatures (Dell 1964, Wear and Fielder, 1985, Webber, 2001). Recently, however, New Zealand has been colonized by a new species of crab from east Asia, *Charybdis japonica* (Crustacea: Decapoda: Portunidae), which has been able to establish populations and expand its range along the northeastern coast.

C. japonica, growing up to 110mm carapace width (Kim 2001), is a relatively new invader and was first discovered in the Waitemata Harbour, Auckland, New Zealand in 2000 (Webber 2001); its identity was confirmed using DNA and morphological identification in 2002 (Smith et al. 2003). This is the first record of *C. japonica* establishing populations outside its native range, and it is believed to have been transported via ballast water in container ships from east Asia (Gust and Inglis 2006). During 2002, numerous *C. japonica* individuals were found throughout the Waitemata Harbour, while none were found in the offshore regions of the Hauraki Gulf (Gust and Inglis 2006). *C. japonica* has been trapped in a variety of habitats and substrata that are exposed to a range of salinities and do not have distinct habitat associations (Gust and Inglis 2006). Due to several factors, including ineffective methods of control, *C. japonica* has become established in other estuaries around coastal northeastern New Zealand. Established populations of *C. japonica* currently occur as far north as the Weiti River and as far south as the Whitford embayment (Gust and Inglis 2006, Jones and Browne 2006). In May 2009 the Ministry of Agriculture and Forestry Biosecurity New Zealand (MAFBNZ) discovered 3 female *C. japonica* (non-gravid) and 5 males in the Whangarei Harbour, 134 km north of the Waitemata Harbour (J. McDonald, MAFBNZ, personal communication). However, due to the lack of trapped gravid females, the assumption that there is an established population remains unproven.

Although there are no other known established *C. japonica* populations north of the Weiti River, as indicated by the lack of gravid females, it does not mean that this species will stop spreading. Anticipating future invasions requires the prediction of possible areas of spread and establishment of non-native species, which can lead to management strategies to combat the invasion if it occurs (Kolar and Lodge 2001, deRivera et al. 2007, Vander Zanden and Olden 2008). Temperature and salinity are two of the most influential abiotic factors that may affect distribution ranges of invasive species like *C. japonica* as they strongly influence survival, growth and development of crab larvae (Brett 1979, Sulkin et al. 1996, Anger 2001, Baylon and Suzuki 2007, Bravo et al. 2007). As such, these abiotic factors have been highlighted as ultimately impacting the successful establishment of a species in a new environment (Epifanio et al. 1998, Rudnick et al. 2000, Gilman 2006, Sanford et al. 2006, deRivera et al. 2007, Storch et al. 2009). Testing the survival of *C. japonica* larvae at experimental

environmental conditions may highlight specific areas of concern around New Zealand that should be monitored for range expansion.

Having evolved in a more competitive environment, invasive species may have an upper hand in competing against species that have not co-evolved to interact with them (Sax and Brown 2000). Throughout the Indo-West Pacific, there are 61 species of *Charybdis* reported, 19 species in Malaysia alone (Ng et al. 2008), and it is thought that species originating from highly diverse ecosystems are intrinsically better competitors (Allendorf and Luikart 2007). As New Zealand has a relatively depauperate crab fauna compared to other coastlines around the world (McLay 1988), there is no equivalent to *C. japonica* in estuaries, harbours or bays. However, juveniles and adults of the commercially important and similarly sized indigenous portunid crab *Ovalipes catharus* are known to sporadically use estuaries, harbours and bays where *C. japonica* is found (Wear 1982, Osborne 1987a, 1987b, Gust and Inglis 2006). Gut analyses for *C. japonica* and *O. catharus* indicate significant dietary overlap, and both species are known to cannibalize conspecifics and consume other crab species (Wear and Haddon 1987, Davidson 1987, Weimin et al. 1998). Experimentally analyzing the inter- and intra-specific interactions between *C. japonica* and *O. Catharus* may uncover possible changes in the behaviour of either species.

***Charybdis japonica* in its native range**

Despite the large population of *C. japonica* throughout its native range, little is published about this species' natural history and few comparative data are available for life histories of other species of this genus. *C. japonica* is indigenous to intertidal and subtidal estuaries, harbours, and bays of China, Japan, Korea, Taiwan and Malaysia to a depth of 15 m in oceanic and estuarine waters (Sakai 1976, Dai and Yang 1991, Kim 2001, Ng et al. 2008). In China, *C. japonica* inhabit waters with mean monthly SST's ranging from 4-34°C and have a wide salinity tolerance, acclimating to salinities as low as 14ppt (Wang et al. 1996, Hong-Yu et al. 2008). In Korea, *C. japonica* females produce up to three larval broods each season, with between 94,000 and 473,000 eggs in each brood (Kim 2001); in China they lay an average of 85,000 eggs (Wang et al. 1996). In China, *C. japonica* spawn in the early spring (April-May) and late summer (August-September) when sea surface temperatures (SST's) are between 20 and 28°C (Wang et al. 1996). *C. japonica* females have also been shown to store sperm from multiple males for up to seven days (Kim 2001). Not including the megalopa stage, the six zoeal stages of *C. japonica* remain in the water column for a total of at least 18 days (Yatsuzuka 1952), allowing for the potential of spread by ocean currents during this time. In its native range, *C. japonica* is an omnivore that preys upon a large variety of benthic species including bivalves, crustaceans, fish, and cephalopods (Dai and Yang 1991, Weimin et al. 1998, Kimura 2005, Sudo et al. 2008, Quan et al.

2010). Although not extensive, the literature does portray *C. japonica* as a highly fecund and fast maturing predator with a broad range of prey items that is exposed to a large spectrum of environmental variables in its native range. These data indicate that *C. japonica* may have biological and ecological attributes that contribute to their success as invaders in New Zealand.

Scope of thesis

Marine ecological systems are inherently complex, and there are numerous factors that contribute to the success or failure of an invasive organism to establish, naturalize and /or spread. Limited knowledge of the ecological and biological attributes of *C. japonica* in its native range describes an aggressive and dominant species that is capable of a large geographic range, producing large numbers of recruits, plasticity with respect to fluctuations in environmental factors, and consumption of a broad range of prey items (Sakai 1976, Dai and Yang 1991, Wang et al. 1996, Weimin et al. 1998, Kim 2001, Kimura 2005, Hong-Yu et al. 2008, Ng et al. 2008, Quan et al. 2010). It can be predicted that most successful invaders are able to spread quickly due to broad environmental tolerances and habitat preferences, the presence of suitable conditions for establishment, their ability to competitively dominate native species, and a lack of natural enemies (Weis 2010). Ultimately, their success will be limited by secondary factors, including their ability to find an empty niche and become a facilitator in their new habitat, and will determine whether the species will actually proliferate (Weis 2010). Indeed, while an organism may survive the transit to a new environment, the probability that it will survive and flourish is very low; and, even if they are able to reproduce, their descendants may only survive a few generations before becoming locally extinct (Williamson 1996). As *C. japonica* is a successful invader that is expected to increase in distribution and abundance along the coast of New Zealand, this thesis aimed to characterize important biological and ecological parameters of this population in its invaded range. Nationally, these data will serve as baselines for the reproduction, spread, and impact of *C. japonica* throughout New Zealand, and provide a basis for subsequent management strategies. Globally, the information generated from this thesis may be incorporated into overall global predictions of successful invasive species and their ecosystem effects.

Thesis Outline

This thesis combines novel field (Chapter 3) and laboratory (Chapters 2, 3, 4, and 5) investigations to describe the biological and ecological characteristics that make *Charybdis japonica* a successful invader in New Zealand and the potential impact of this species on native species. Each chapter contains its own introduction, methods, results, and discussion.

Due to the established status of *C. japonica* in northeastern New Zealand, it becomes imperative to examine the population biology of this species in its newly invaded habitat. Chapter 2

describes the biological parameters of an established population of *C. japonica* from the Weiti River including information on population structure and spawning period, relative growth and sexual maturity, fecundity estimates, and diet composition.

As a large portunid crab, *C. japonica* has the capability of becoming a significant predator on several ecologically and recreationally important benthic invertebrates. Using both field and laboratory experiments, Chapter 3 examines the interactions between *C. japonica* and native prey items to determine what prey items *C. japonica* consumes and the possible impact on the ecosystem.

As nothing is known about the physiological tolerance levels of *C. japonica* in New Zealand, the temperature and salinity tolerance ranges of *C. japonica* Stage 1 zoeae were determined in Chapter 4 to predict its possible range expansion by larval recruitment. This manuscript has been accepted into the peer reviewed journal *Biological Invasions*.

The potential for niche and habitat overlap between *C. japonica* and the native New Zealand paddle crab, *Ovalipes catharus*, indicates the need to assess, for predictive purposes, the possible effects of this invasive portunid on its indigenous competitor. In Chapter 5, similarly sized native and invasive paddle crabs were paired in the presence of a single food source to determine the behavioural interactions between the species and elucidate the possible effects of *C. japonica* on *O. catharus* distribution patterns.

A synthesis of the findings of the separate parts of the thesis is provided in the General Discussion (Chapter 6). The various biological and ecological attributes of *C. japonica* studied in this thesis are discussed with relevance to how they may have aided *C. japonica* in becoming a successful invader in New Zealand.

Chapter Two

Population biology and diet analysis of an invasive population of *Charybdis japonica* in northeastern New Zealand

Introduction

One goal of ecological research on invasive species is to elucidate how exotic species, with initially small and genetically constrained populations, are able to establish in environments to which they had no prior exposure (Sax and Brown 2000). Theory suggests that successful invasive organisms have biological and/or ecological attributes that aid their integration into novel environments (Mayr 1965). Comparing these attributes of novel invaders to those of successful past introductions has become a widely used tool to estimate the success of invasions that are already occurring, as well as forecasting the risk of possible future invaders (Duncan et al. 2003). However, few studies have accounted for failed introductions because these are rarely documented; therefore a null hypothesis associated with unsuccessful invasions is problematic.

The most important stage following the invasion of a novel organism is the establishment of a self-sustaining population. Due to a number of factors, initial populations tend to be small and vulnerable to extinction by demographic, environmental, and/or general stochasticity (MacArthur and Wilson 1967, Legendre et al. 1999, Lockwood et al. 2005). Not only does the number of births need to outweigh the deaths, but the population itself needs to increase at such a rate to reduce the time in which it is at risk of stochasticity (Sol 2007). Therefore, such biological and life history attributes of *r*-selected species (i.e. relatively young maturity, large numbers of independent young, fast intrinsic growth) may influence the ability of some organisms to escape the critical founding stage and become successful invaders.

In order to describe the population dynamics of an established community of *C. japonica* in one estuary in northeastern New Zealand, the temporal patterns of abundance and size composition for this species were established. The potential influence of annual temperature fluctuations on *C. japonica* abundance was also assessed.

Understanding the life history of any species requires knowledge of such aspects as the development of sexual maturity and changes in allometric growth, which ultimately influence population dynamics by affecting reproductive output, demographics, and recruitment rates (Williams 1966, Stearns 1992). For many crabs, different patterns of relative growth of the carapace and/or abdomen result in discontinuities in growth curves and reflect the pubertal molt and the onset of sexual maturity (Barnes 1968, Hartnoll 1974, Gore and Scotto 1983, Huber 1985, Haefner 1985). Major

differences in allometric growth can also occur between the sexes and stages of maturity (Hartnoll 1963, Haefner 1985). These parameters were investigated for the sampled *C. japonica* population to determine changes in allometric growth that would indicate size at sexual maturity.

Fecundity is an important biological parameter in crustaceans and is used to determine reproductive potential. The aim of this particular section was to characterize the fecundity of *C. japonica* from the northeastern coast of New Zealand and describe its relationships to carapace size, body weight, brood weight and volume, and egg size and volume.

Another important factor that successful invasive organisms share is their ability to be generalist consumers (Vazquez 2006) and/or exhibit behavioral flexibility with respect to utilising food resources in a new environment (Lefebvre et al. 2004). As a large portunid crab, *C. japonica* has the capability of becoming a significant predator on important benthic invertebrates and may play a key role in structuring communities. To assess how *C. japonica* is interacting with the marine fauna of New Zealand, its natural diet was evaluated using two different methods of gut content analysis: the points method and frequency of occurrence. These data were then compared to similar diet analysis data from *C. japonica* in its range native, the similarly sized New Zealand native crab *Ovalipes catharus*, and various other portunid invaders.

Despite the recent invasion, broad distribution, and high densities of *Charybdis japonica* in northeastern New Zealand, there are only three papers concerning the biological or ecological status of this species in its invaded habitat (i.e. Gust and Inglis 2006, Miller et al. 2006, Fowler et al. 2011). This species is expected to expand its distribution and increase its numbers along the coast of New Zealand (Fowler et al. 2011). Therefore, this chapter aimed to characterize important biological parameters of *C. japonica* (population structure, spawning period, relative growth, sexual maturity, fecundity estimates and diet composition) as a baseline for the species' continued residency, reproduction and spread throughout New Zealand. This data will also provide a basis for subsequent management strategies for this species, and allow for comparisons with overall invasion theory concerning the attributes of successful invaders.

Methods

Trapping

Data on the abundance and population ecology of *Charybdis japonica* were obtained by trapping, with sampling methods and trap types standardized through time. *C. japonica* were collected from the Weiti River on the Whangaparaoa Peninsula of New Zealand (36° 38.4' S, 174° 43.6' E, Figure 2.1) in baited oval-shaped collapsible 'Opera house' traps (64 x 47 x 20 cm; 2 cm mesh). Two

rigid entrance funnels (diameter 9 cm) that opened into each trap from opposite sides were used to catch crabs from 28mm to 104mm carapace width (CW). Each trap was baited with one pilchard (*Sardinops sagax*) and allowed to fish for a 24 hour tidal cycle. Due to the obvious tidal schedule, the 24 hour cycle was not repeated at the same time every day during a particular month; it was offset by approximately 1 hour every subsequent day. However, month to month variability was kept at a minimum by choosing tidal cycles within one hour of the previous month. Day-to-day and seasonal variability in catch rates was quantified by repeated sampling of the Weiti River site, which was chosen due to the known presence of *C. japonica* and its accessibility (Figure 2.1). Between February 2008 and December 2009, traps were deployed and checked over five consecutive days each month except for June 2008, May 2009, August 2009, October 2009, and November 2009. Three lines of five traps each were set at the site, parallel to the shoreline, approximately 20 m apart and at a depth of about 1.5 m below mean low water. This produced a total trapping effort of 15 traps / day and 75 traps / month. Catches were processed at the trap site, removing crabs from the trap and individually placing them into 10 litre buckets containing seawater from the Weiti River for transport. For each trap, the sex and CW (between the tips of their lateral spines, Figure 2.2) to the nearest 0.1mm of each crab and the presence of other bycatch was recorded. Native crabs and other bycatch were released from the traps, but *C. japonica* individuals were then transported ca. 50 km to the Leigh Marine Laboratory for further analysis. Abundances of gravid females was also noted to identify the primary spawning period, and the size of the smallest gravid female was used to differentiate between juveniles and adults. Data on oceanographic conditions were obtained from the coastal monitoring station maintained by the Leigh Marine Laboratory (northeast coast of New Zealand, see Figure 2.1). Statistical analyses comparing day-to-day and seasonal catch rates were calculated with SigmaPlot V. 11.0.

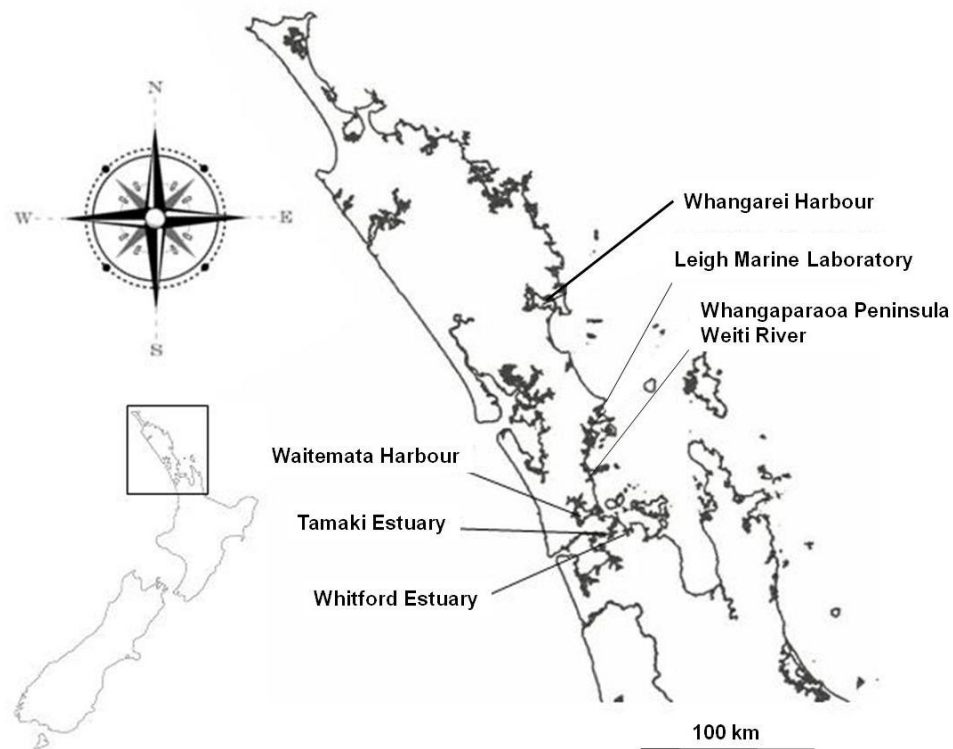


Figure 2.1 Known locations of *Charybdis japonica* in northeastern New Zealand, with the inclusion of the Leigh Marine Laboratory. All *C. japonica* used in the analyses throughout this thesis were collected from the Weiti River on the Whangaparaoa Peninsula of New Zealand ($36^{\circ} 38.4' \text{ S}$, $174^{\circ} 43.6' \text{ E}$).

Morphometrics

As part of the monthly trapping outlined in the trapping section, a subsample of 138 male and 71 female *C. japonica* were collected from the Weiti River (Figure 2.1) from November 2007 to September 2009 and were preserved in 70% isopropyl alcohol in the field. At the laboratory, individuals were blotted dry, weighed, and measured for carapace width (CW = measured at the widest part, between the two lateral spines), carapace length (CL = from the anterior median notch to the posterior carapace margin), abdomen width (AW = across the broadest part of the fourth abdominal segment), and abdomen length (AL = total length of abdomen and telson) (Figure 2.2). Only those crabs with all appendages intact were weighed. In addition to the morphometric measurements, the presence of external parasites and/or ectosymbiont fauna was recorded. Chelae were designated major or minor by the presence or absence of molariform teeth on the prodopus, and a note was made of whether the right or left chela was the major, or crusher, claw. The propodus height (PH = from the base of the large dorsal spine down to the base of the chelae) and propodus length (PL = greatest length of each chelae) of both chelae were determined (Figure 2.2). In addition, the interocular width (IW = distance between the preorbital spines), the diagonal distance (DD = the distance between the first and last anterior lateral spines), and the length of the male gonopod (MG) (first pleopod) was measured

(Figure 2.2). All measurements were made to the nearest 0.1 mm with vernier calipers or, in the case of wet weight, to the nearest 0.1g.

Bivariate scatter plots were made of all measurements against CW for each sex separately. CW was used as the independent variable because it is commonly used as a reference dimension for relative growth measurements, provides significant correlation coefficients, and is used to indicate size for many brachyuran crabs (Mantelatto and Garcia 2001). Linear relationships were expressed by the least squares regression $Y = aX + b$. The power function $Y = aX^b$ was used to describe morphological associations and the logarithmic transformation, $\log Y = \log a + b \cdot \log X$ was applied to non-linear relationships and to all the data to obtain the slope and therefore the constant of relative growth (Lewis 1977). For each regression, the obtained slope values were tested against the slope standard of 1 (for all size dimensions) or 3 (for weight) by Student t-test to determine the relative growth status of each body dimension for both sexes. A slope significantly less than 1 indicates negative relative growth (the dependent variable grows slower than the CW); a slope significantly greater than 1 indicates positive relative growth (the dependent variable grows faster than CW). A slope that was not significantly different from 1 shows that the dependent variable and CW grow at the same rate (Finney and Abele 1981).

Size at physical maturity, defined as the size at which crabs become sexually mature based on changes in morphometric parameters, was estimated from observed breaks in relative growth of particular body dimensions. An index of gonadal maturity was not possible due to the deterioration of some tissue samples before they could be analyzed. Using piece-wise regression analysis from a least-squares estimate, separate linear regression lines were fitted to the data on either side of the break or inflection of the growth pattern, and a t-test used to determine if the slopes of the 2 lines were significantly different (George and Morgan 1979, Mantelatto and Garcia 2001). All statistical analyses used SigmaPlot V. 11.0.

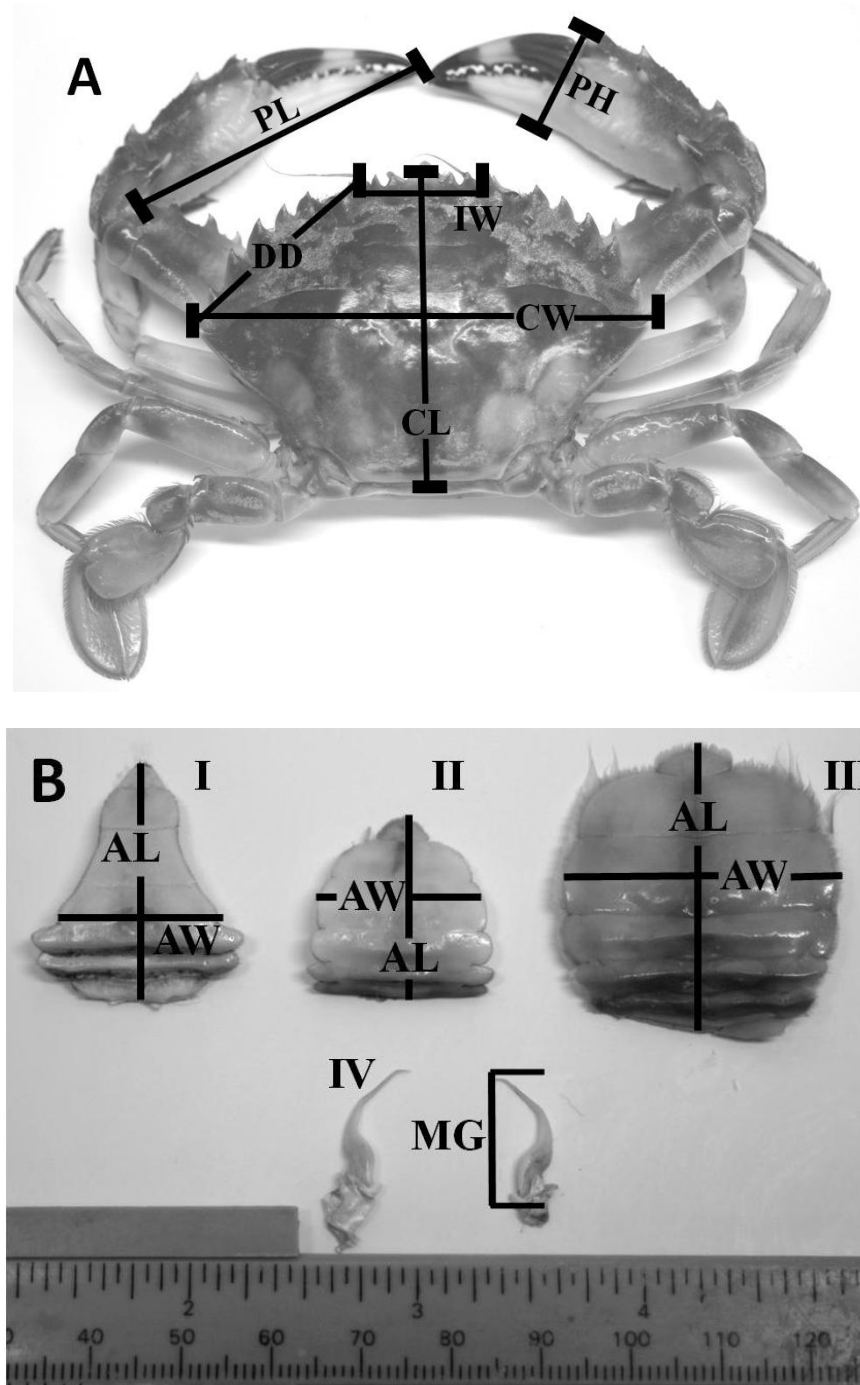


Figure 2.2 Morphometric measurements of *Charybdis japonica* for relative growth analysis (A). Abdomen and telson sections from a representative male (I), juvenile female (II) and mature female (III) and a male first pleopod (IV) are also shown (B). Abbreviations: carapace width (CW), carapace length (CL), interocular width (IW), diagonal distance (DD), propodus height (PH), propodus length (PL), abdomen width (AW), abdomen length (AL), and length of the male gonopod (MG).

Fecundity

Estimated fecundity

As part of the monthly trapping outlined in the trapping section, a subset of 27 gravid *C. japonica* were collected from the Weiti River (Figure 2.1) from November 2007 to November 2009. Upon collection, crabs were placed on ice and then into 70% isopropyl alcohol and brought back to the

Leigh Marine Laboratory for further analysis. Only crabs with embryos in the early stages of development (as determined by the lack of the formation of eyes) were considered because egg volume differs between developmental stages in brachyuran crabs (Hines 1982).

The carapace width (mm) and wet weight (g) of each gravid female (n=27), including their egg mass, was determined, after which the egg masses were detached from the pleopods and weighed separately. Four random subsamples of 1000 eggs each were counted from each egg mass and weighed. The body of the female, egg masses, and subsamples were then dried to a constant weight at 60°C (approximately one week for the body and four days for the eggs) and their values weighed to the nearest 0.001g.

Fecundity was calculated by determining the mean dry weight per egg and using this value to convert the dry weight of the egg mass to total egg number. Reproductive output per female was enumerated by expressing the egg mass dry weight as a percentage of the female body weight after the egg mass was removed (Hines 1982).

Due to a processing error, measurement of egg size was performed using only 25 gravid females from the pool of 27 individuals. Twenty eggs from each female were detached from the pleopods and measured under a binocular microscope with the aid of a micrometer. The mean egg diameter for each female was calculated as the average of the major and minor axis lengths from each of the 20 eggs. The average volume (cubic millimeters) of an egg was calculated according to Jones and Simons (1983) from the formula $1/6\pi I^3$, where I is the mean of the two diameters, including the chorionic membrane tightly adhering to the embryonic surface. The brood volume for each female was then calculated as the product of mean egg volume and number of eggs per egg mass (i.e. fecundity) (Hines 1982).

Realized fecundity

As part of the monthly trapping outlined in the trapping section, nine gravid *C. japonica* were collected from the Weiti River from January 14 to February 11 2009 and transported back to the Leigh Marine Laboratory alive. At the laboratory, the females were maintained in individual buckets containing 20 litres of UV-treated and 1 µl filtered seawater at ambient temperature, under a natural light regime, with air supplied by bubblers at a low pressure. Ambient seawater temperature during the experimental period was 21°C on average, with maximum and minimum values of 22°C and 19.3°C respectively. The crabs were fed daily a ration of 1 adult mussel (*Perna canaliculus*) or oyster (*Crassostrea gigas*), and any uneaten food was removed during exchange of 90% of the seawater. As *C. japonica* was observed to release all larvae over a period of approximately 2 hours during the early

morning hours (Fowler, *personal observation*), larval release was checked between 08:00 and 10:00 daily. *C. japonica* stage 1 zoeae are large enough to be seen with the naked eye; therefore, the water in the buckets was visually checked for any swimming larvae.

The number of stage 1 zoeae was estimated for each female by the volumetric method, which has been used for fecundity estimation in broodstocks of crab, prawn and fish species (Millamena and Quinitio 2000, Hoang et al. 2003, Mylonas et al. 2004). Ten 10mL aliquot samples were taken from the hatching bucket of each female after the female was removed and the water vigorously stirred to ensure a homogenous suspension of the larvae. The number of larvae was counted under a stereomicroscope. A mean concentration was determined for each female and related to the corresponding carapace widths using a linear regression after the data were log transformed.

Diet analysis

Coinciding with the morphometric measurements, a subsample of *C. japonica* were dissected and the gastric mill (proventriculus) removed. Due to the rapid clearing of food from the foregut of other portunid species, *C. japonica* individuals had been placed on ice and then in 70% isopropyl alcohol immediately after collection from traps (Hill 1976, Haddon and Wear 1987). After the gastric mill was removed, a subjective estimate was made of the fullness of the gastric mill: 0% (Class 0), 1 – 5% (Class 1), 6 – 35% (Class 2), 36 – 65% (Class 3), 66 – 99% (Class 4), and 100% (Class 5). Visual assessment of fullness was made possible due to the translucent quality of the thin-walled gastric mill. The contents were then emptied into 70% isopropyl alcohol in a Petri dish and examined under a binocular microscope.

Before identifying particular prey items, the stage of digestion was scored according to the following scale: (1) identifiable soft and hard parts not separated, (2) flesh partially digested or fine carapace present, (3) traces of unidentifiable soft material and/or fine carapace present but in poor condition, (4) unidentifiable or no soft material and/or hard parts, and (5) empty, or non-organic material or containing only fluid. The gastric mill contents were often shredded, making identification difficult. However, identification to family, genus and sometimes species was possible by comparing characteristic body parts with preserved whole animals. Prey items were recorded at specific or generic rank where possible. In the analysis of results, prey species or genera were grouped into coarser taxonomic categories (e.g. gastropods, bivalves, brachyurans). Due to the fact that these *C. japonica* specimens were caught in traps baited with pilchard (*Sardinops sagax*), the presence of *S. sagax* bones and/or scales in the gastric mill was recorded but not included in any analysis, including the fullness assessment.

In portunid crabs, mastication of food by mouth parts and the gastric mill and the rejection by the mouthparts of some hard parts of prey prior to ingestion precluded counts of prey in most cases. Therefore, the points method (PM) and the frequency of occurrence (FO) methods were chosen as quantitative scoring methods for the contents of gastric mills. Following the methods of Wear and Haddon (1987) to determine the relative contribution of the prey categories to the total content of each gastric mill using the PM, the percentage volume of each food item occurring in each gastric mill was first estimated based on visual observations and placed into categories. A prey item accounting for 95 – 100% of the gastric mill contents was given 100 points; 66 – 94%, 75 points; 36 – 65%, 50 points; 6 – 35%, 25 points; 5% or less, 2.5 points. The number of points allocated to each prey category was then weighted by the fullness of the gastric mill in which they were found by multiplying the number of points by a value dependent on the class of fullness (Class 5 = 1.0, Class 4 = 0.75, Class 3 = 0.5, Class 2 = 0.25, Class 1 = 0.02). Therefore, the maximum number of points a single prey category could receive in each gastric mill would be 100 (100 x 1.0, i.e. only one prey category in a completely full gastric mill); the minimum possible would be 0.05 (2.5 x 0.02, i.e. a prey category comprises <5% of the total gastric mill contents when the foregut is <5% full).

Because percentage volume estimates are biased against items which digest rapidly, such as polychaetes, and can be influenced by the presence of a few large items, another method of diet analysis was used (Kennedy 1969, Hyslop 1980). The FO of each prey category was calculated as the percentage of crabs that had consumed each prey category (Ropes 1968, Elner 1981, Wear and Haddon 1987). Problems with FO arise from biases in favour of recognisable hard parts (e.g. carapace, shell, and bone) and small items (e.g. ostracods, cumaceans, and algae) which may be of little food value. Regardless of which method is used, however, the important food items are always distinguished from rare or less important prey items (Elner 1981, Williams 1981).

Results

Trapping

A total of 286 *Charybdis japonica* males (mean (\pm 1 SE) carapace width (CW) and CW range: 68.9mm \pm 0.8, 28 – 103.7mm), 133 non-gravid females (56.2mm \pm 1.0, 28 – 79.6mm), and 44 gravid females (62mm \pm 1.3, 43.7 – 79mm) were collected from the Weiti River. Size frequency histograms from the entire sampling period show a unimodal size distribution for both males and females, with a majority of the specimens measuring 45 – 80mm CW (Figure 2.3). The size-frequency distribution of *C. japonica* in the Weiti River changed throughout the sampling period, hinting at the possibility of recruitment of small individuals into the river (Figure 2.4). Smaller individuals (>40mm) of both sexes appeared in samples from April to November (Figure 2.4). The graphs from February to April 2008

and from November 2008 to March 2009 show a slight trend of increased growth of the cohort, which is masked in May 2008 and April 2009, respectively, and further months due to the appearance of smaller individuals (Figure 2.4). Unfortunately, although there were indications that cohorts existed in the population, they were not sufficiently distinct to be tracked through time. This made it impossible to use them to generate growth curves for the species.

The overall average percentage of males collected each month was $61.5 \pm 3.1\%$ (range 41.2 – 90.5 %), with a higher proportion of males found most months (Table 2.1). Out of the total crabs caught, the proportion of those caught that were male increased with larger sizes in *C. japonica*, and culminated with all crabs over 80mm CW being male (Figure 2.3).

Gravid females were present from February to April 2008 (summer and autumn) and then again from November 2008 to March 2009 (spring, summer and autumn), with the highest frequency between November 2008 and February 2009 (spring and summer) (Figure 2.5 A). The smallest gravid female collected was 43.7mm CW in December 2009. Recruitment of juveniles (≤ 43.7 mm CW) was observed sporadically throughout the sampling period (Table 2.1).

Over the entirety of the trapping survey, an average of 0.34 ± 0.02 crabs were caught per trap, with a maximum of six crabs caught in one trap. The average number (± 1 SE) of crabs caught per day was 5.1 ± 0.3 , with a maximum of 12 individuals per day. Catch rates varied widely seasonally but seemed to parallel sea surface temperature fluctuations; catches tended to be highest in spring (September - November) and lowest in winter (June – August) (Figure 2.5 A). Overall seasonal differences in daily abundance were significant (ANOVA $F_{3,86} = 6.206$, $P < 0.001$), with significant differences between spring and winter (Tukey's test $P < 0.001$) and between spring and autumn (Tukey's test $P = 0.030$). All other seasonal comparisons showed no significant difference in the numbers of crabs caught per day. There was no obvious annual cycle of average CW for non-gravid females, gravid females or males throughout the year (Figure 2.5 B).

Male and female *C. japonica* were found mating in traps on three separate occasions: once in September 2008 and twice in January 2009. Although the males were relatively large (65, 66, and 72mm CW), the female size range was much larger (47, 58, and 68mm CW) and included a small female (47mm CW) that was mating with the 66mm CW male. The moult status of the females was not noted. In a separate instance in January 2009, a 85mm CW male was found consuming a 48mm CW conspecific male in a trap, validating observed cannibalism in the laboratory (Fowler, *personal observation*).

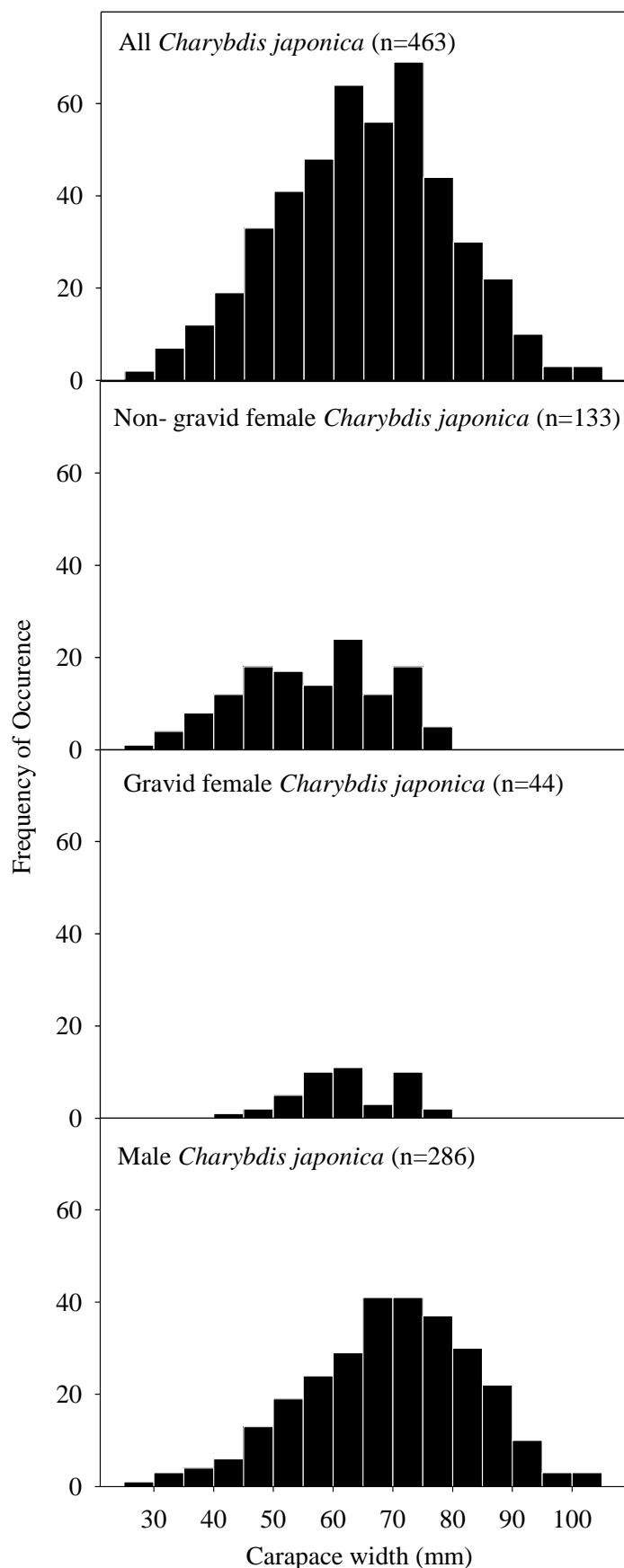


Figure 2.3 Carapace width (CW) frequencies of non-gravid female, gravid female and male *Charybdis japonica* (n = 463) collected monthly from the Weiti River, New Zealand from February 2008 to December 2009.

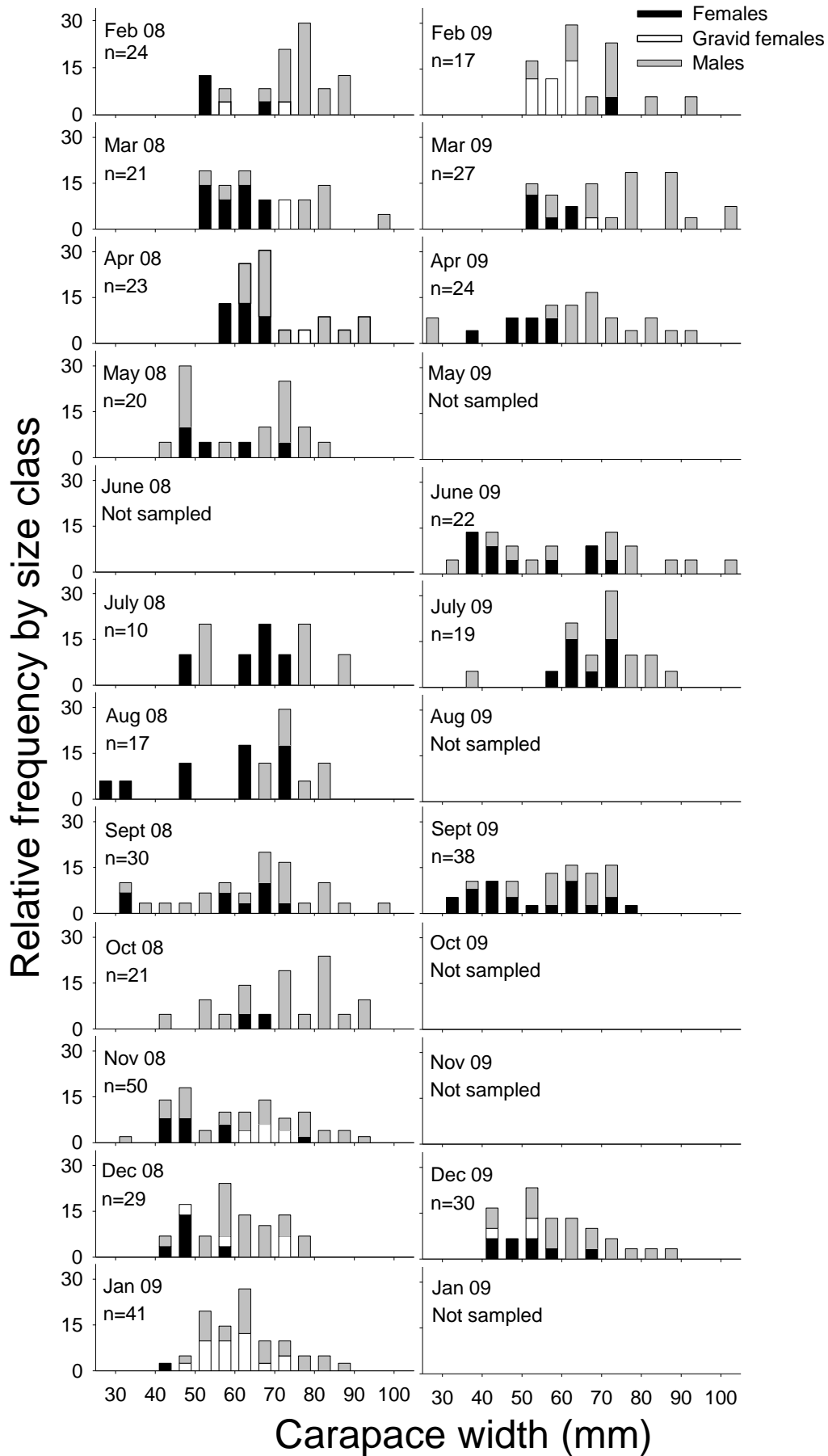


Figure 2.4 Monthly changes in size-frequency distribution of *Charybdis japonica* in the Weiti River, New Zealand from February 2008 to December 2009. Color key: Black, females; Light grey, gravid females; Dark grey, males.

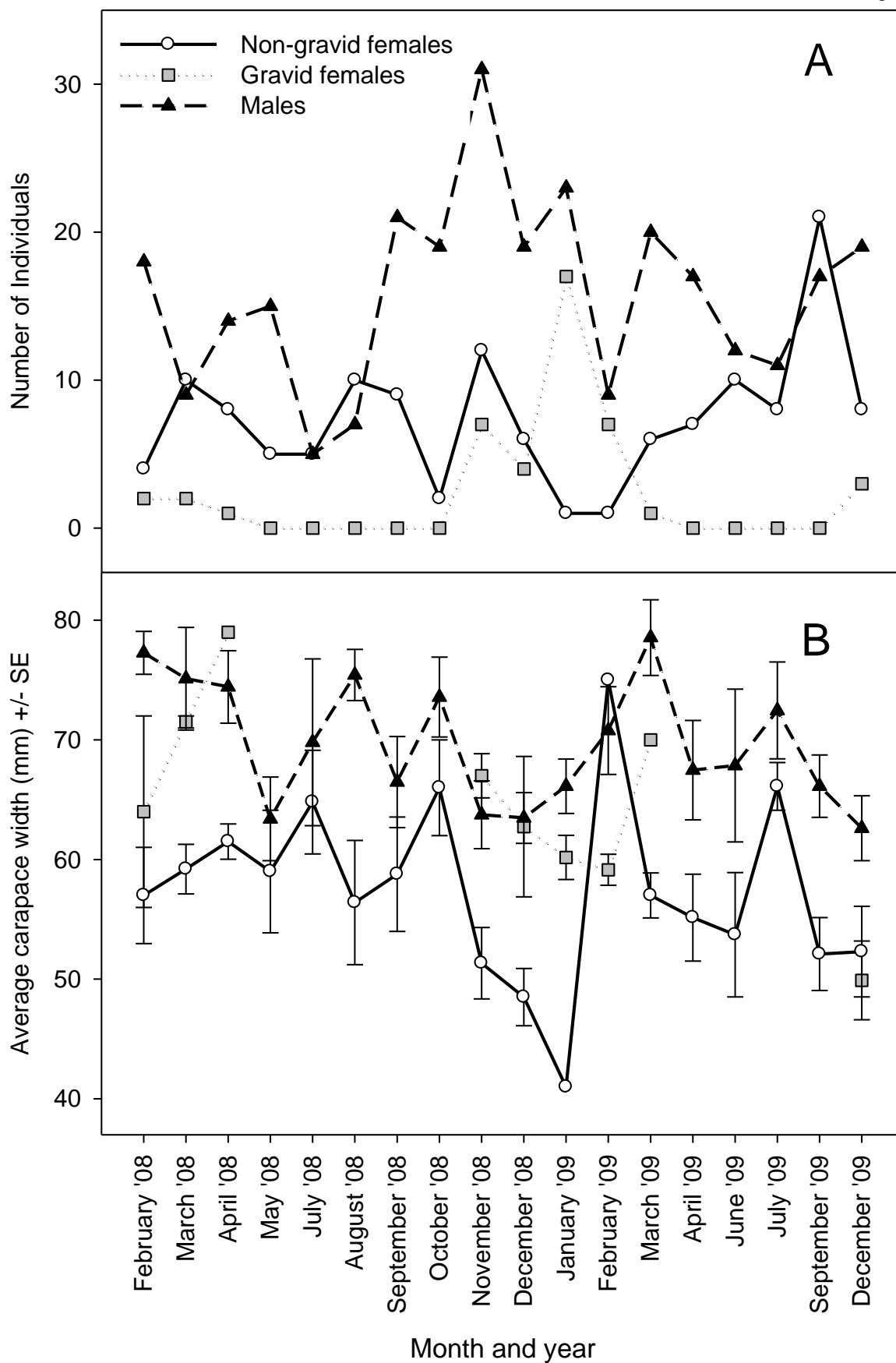


Figure 2.5 Monthly abundances of *Charybdis japonica* (mean (\pm SE)) (A) and average carapace widths (\pm SE) (B) of non-gravid females, gravid females and males collected from Weiti River, New Zealand from February 2008 to December 2009. Color and symbol key: White circles, non-gravid females; Light grey squares, gravid females; Black triangles, males.

Table 2.1 Number of *Charybdis japonica* collected from the Weiti River, New Zealand, February 2008 – December 2009. As the smallest gravid female collected was 43.7mm carapace width, all individuals, both male and female, smaller than this size were considered juveniles. As juveniles were sexed, their abundance is included in the sex ratios and male proportion data. Catch per unit effort (CPUE) is defined as the average number of crabs caught per trap for each month.

Month	Non-gravid Females	Gravid Females	Males	Juveniles	Total	Sex ratio (M : F)	CPUE
February 2008	4	2	18	0	24	3 : 1	0.31
March 2008	10	2	9	0	21	0.75 : 1	0.28
April 2008	8	1	14	0	23	1.56 : 1	0.31
May 2008	5	0	15	0	20	3 : 1	0.27
June 2008	-	-	-	-	-	-	-
July 2008	5	0	5	0	10	1 : 1	0.13
August 2008	8	0	7	2	17	0.7 : 1	0.23
September 2008	7	0	19	4	30	2.33 : 1	0.40
October 2008	2	0	19	0	21	9.5 : 1	0.28
November 2008	9	7	29	5	50	1.63 : 1	0.67
December 2008	5	4	18	2	29	1.9 : 1	0.39
January 2009	0	17	23	1	41	1.28 : 1	0.55
February 2009	1	7	9	0	17	1.13 : 1	0.23
March 2009	6	1	20	0	27	2.86 : 1	0.36
April 2009	6	0	15	3	24	2.43 : 1	0.32
May 2009	-	-	-	-	-	-	-
June 2009	7	0	10	5	22	1.2 : 1	0.29
July 2009	8	0	10	1	19	1.38 : 1	-
August 2009	-	-	-	-	-	-	-
September 2009	13	0	16	9	38	0.81 : 1	0.51
October 2009	-	-	-	-	-	-	-
November 2009	-	-	-	-	-	-	-
December 2009	6	3	18	3	30	1.73 : 1	0.40
Total	110	44	274	35	463	1.6 : 1	0.34

Morphometrics

In all comparisons except for the width and length of the abdominal segment, female *Charybdis japonica* exhibited smaller average measurements than males (Table 2.2). There were significant differences in all measurements between the sexes (Table 2.2.). There was no difference in the

relationships between male and female wet body weight and carapace width (CW) (Figure 2.6). The only example of sexual dimorphism was the length and width of the abdominal segment. For both sexes, the major, or crusher claw, was most often on the right side of the body, with only 19.2% of females and 14.1% of males exhibiting a left-handed crusher claw. In some cases, neither claw was deemed the crusher claw due to the lack of molariiform teeth (2.9% of females and 5.9% of males); these data were removed from the relative growth analysis for the respective measurements.

There were no morphological measurements that related to the onset of sexual maturity in males, but 2-segment linear piece-wise regressions showed that there were significant changes in the width and length of the abdominal segment associated with sexual maturity in females. Using the growth of the abdominal segment as a proxy for female sexual maturity reveals a large range of overlap of 45.5 to 54mm CW for the transition from juvenile to adult (Figure 2.7). Juvenile female *C. japonica* exhibit faster growth of the abdominal segment relative to CW before maturity (Figure 2.6 Table 2.3, t-test, $p < 0.0001$). Therefore, those morphological data related to the females deemed as juveniles from the regression analysis were treated as such for the rest of the analysis.

While juvenile females show significantly faster relative growth rates to CW for major prodopus length, minor prodopus length, the length of the abdomen and telson, the width of the abdominal segment, and wet body weight, adult females only show a faster growth rate of two secondary characteristics not associated with reproductive potential (i.e. minor prodopus length and diagonal distance) (Table 2.3). Males, on the other hand, show significantly faster relative growth rates of all chelae measurements and wet body weight to CW (Table 2.3). There was no relationship between the length of the male gonopod and any other morphological measurement, and there were no instances of negative relative growth recorded for either sex or maturity (Table 2.3).

Four species of ectosymbiont fauna were found on the carapace of the *C. japonica* individuals examined. The most prominent was spirorbid polychaete tubes, which were found covering sections of the carapace, walking legs and chelae of both males and females. There were 18 *C. japonica* specimens with ectosymbionts (15 males and 3 females from 71.2 to 94.2mm CW); no *C. japonica* smaller than 71.2mm were found to harbour ectosymbionts. Of all the individuals between 71.2 and 94.2mm CW, 25% had at least one ectosymbiont (30% of males and 25% of females). Live barnacles (*Balanus* sp.) were also found covering the carapaces of 8 *C. japonica* (6 males and 2 females) between 69.4 and 94.2mm CW, comprising 10% of the total population between that size range (9.5% of the male population between 69.4 and 94.2mm CW and 12.5% of the female population). A single unidentified parasitic barnacle was found buried into the carapace of two male *C. japonica* with carapace widths of 71.8 and 82.7mm, comprising 6% of the male population and 4% of both males and

females between those carapace widths. Slipper shells (*Crepidula costata*, n=2, maximum length 18.2mm) and a juvenile green mussel (*Perna canaliculus*, n=1, 12.7mm shell length) were also found on one male and two female specimens 72.5 – 76.7mm CW.

Out of the total of 138 males observed, 25.4% (42.3 - 92.7mm CW) were missing either one or several appendages, including chelae. 8.7% (12/138) of males had lost at least one chela, and 19.6% (27/138) had lost at least one walking or paddle leg. Out of the 71 females measured, 22.5% (40.9 – 73.9mm CW) were missing one or more appendages, including chelae. 14.1% (10/71) had lost at least one chela, and 18.3% (13/71) had lost at least one walking or paddle leg.

Table 2.2 Summary of morphological measurements of *Charybdis japonica* collected from the Weiti River, New Zealand, February 2008 – December 2009. Mean and standard error (\pm SE) as well as maximum and minimum measurements are reported for both males and females. As juveniles were sexed, their measurements are included in the appropriate sex category. The results of t-tests between the sexes for each morphometric measurement are reported, and in cases where the data failed the normality or equal variance test, a Mann-Whitney Rank Sum Test was completed.

	MALES					FEMALES					t-test or Mann Whitney U statistic	df or T value	P
	n	mean	\pm SE	max	min	n	mean	\pm SE	max	min			
Carapace width (mm)	138	68.4	1.1	94.8	35.4	71	59.1	1.3	78.8	36.0	-5.073	207	< 0.001
Carapace length (mm)	138	47.6	0.8	66.1	23.8	71	40.9	0.9	54.7	23.6	-5.203	207	< 0.001
Major Prodopus length (mm)	127	47.8	1.1	78.3	19.0	64	33.9	0.8	46.6	19.9	1310	3390	< 0.001
Major Prodopus width (mm)	128	17.6	0.4	28.3	7.8	66	13.7	0.4	21.0	7.4	2056	4267	< 0.001
Minor Prodopus length (mm)	127	47.3	1.1	78.4	19.1	59	33.2	0.9	45.7	18.2	1165	2935	< 0.001
Minor Prodopus width (mm)	130	15.2	0.3	25.8	6.5	62	11.5	0.4	16.7	6.2	1822	3775	< 0.001
Male Gonopod length (mm)	137	14.3	0.2	19.0	7.0	-	-	-	-	-	-	-	-
Length of abdomen and telson (mm)	138	25.7	0.5	36.7	12.5	71	28.4	0.9	40.8	12.5	3631.5	8722.5	= 0.002
Interocular width (mm)	138	20.2	0.3	27.4	11.0	71	17.3	0.4	23.2	10.4	2793	5349	< 0.001
Diagonal distance (mm)	138	32.6	0.6	45.5	16.5	71	28.1	0.6	38.8	16.6	-4.915	207	< 0.001
Width of abdominal segment (mm)	138	17.4	0.3	23.3	8.8	71	26.2	0.9	39.1	10.0	1904.5	10449.5	< 0.001
Wet body weight (g)	101	64.5	3.7	184.2	6.5	54	38.1	3.2	93.0	6.9	2745	5301	< 0.001

Table 2.3 Summary of relative growth of *Charybdis japonica* collected from the Weiti River, New Zealand, February 2008 – December 2009. Juvenile females were identified from the piece-wise regression analysis using a least-squares estimate. No juvenile males were isolated using the piece-wise regression analysis; therefore, the values for all males are presented. Abbreviations: CW = carapace width (mm); r^2 = determination coefficient; relative growth: (0) equal relative growth, (+) positive relative growth, (-) negative relative growth.

Juvenile Females

	n	$Y = aX^b$	r^2	t-statistic	P	Relative growth
CW v Carapace length (mm)	19	$Y = 0.4723X^{1.0958}$	0.9858	2.0558	NS	0
CW v Major Prodopus length (mm)	18	$Y = 0.1539X^{1.3389}$	0.9610	3.4095	<0.005	+
CW v Major Prodopus width (mm)	18	$Y = 0.0832X^{1.2514}$	0.9197	1.8112	NS	0
CW v Minor Prodopus length (mm)	16	$Y = 0.0752X^{1.5154}$	0.8828	2.3353	<0.05	+
CW v Minor Prodopus width (mm)	17	$Y = 0.0505X^{1.3306}$	0.8397	1.4399	NS	0
CW v Length of abdomen and telson (mm)	19	$Y = 0.1048X^{1.3409}$	0.9895	6.9430	<0.001	+
CW v Interocular width (mm)	19	$Y = 0.2708X^{1.0210}$	0.9580	0.2745	NS	0
CW v Diagonal distance (mm)	19	$Y = 0.3835X^{1.0522}$	0.9832	1.0763	NS	0
CW v Width of abdominal segment (mm)	19	$Y = 0.0703X^{1.4012}$	0.9678	4.3656	<0.001	+
CW v Wet body weight (g)	18	$Y = 1.7643e^{-5}X^{3.5587}$	0.9747	2.5372	<0.05	+

Adult Females

	n	$Y = aX^b$	r^2	t-statistic	P	Relative growth
CW v Carapace length (mm)	52	$Y = 0.6730X^{1.0074}$	0.9837	0.3895	NS	0
CW v Major Prodopus length (mm)	46	$Y = 0.5118X^{1.0303}$	0.9515	0.5816	NS	0
CW v Major Prodopus width (mm)	48	$Y = 0.1674X^{1.0831}$	0.9052	1.0736	NS	0
CW v Minor Prodopus length (mm)	43	$Y = 0.4834X^{1.0394}$	0.8816	0.4354	NS	0
CW v Minor Prodopus width (mm)	45	$Y = 0.0862X^{1.2017}$	0.8872	2.0477	<0.05	+

CW v Length of abdomen and telson (mm)	52	$Y = 0.3632X^{1.0787}$	0.9583	1.6709	NS	0
CW v Interocular width (mm)	52	$Y = 0.3041X^{0.9908}$	0.9802	- 0.3162	NS	0
CW v Diagonal distance (mm)	52	$Y = 0.3827X^{1.0535}$	0.9906	2.5236	<0.02	+
CW v Width of abdominal segment (mm)	52	$Y = 0.3942X^{1.0441}$	0.9632	1.0352	NS	0
CW v Wet body weight (g)	37	$Y = 7.7128e^{-5}X^{3.2015}$	0.9674	1.2377	NS	0

All Males

	n	$Y = aX^b$	r^2	t-statistic	P	Relative growth
CW v Carapace length (mm)	138	$Y = 0.6995X^{0.9988}$	0.9970	-0.1690	NS	0
CW v Major Prodopus length (mm)	127	$Y = 0.2232X^{1.2688}$	0.9814	11.1535	<0.0001	+
CW v Major Prodopus width (mm)	128	$Y = 0.0788X^{1.2792}$	0.9641	8.2604	<0.0001	+
CW v Minor Prodopus length (mm)	127	$Y = 0.2387X^{1.2516}$	0.9323	5.3532	<0.0001	+
CW v Minor Prodopus width (mm)	130	$Y = 0.0639X^{1.2940}$	0.9432	6.7431	<0.0001	+
CW v Length of abdomen and telson (mm)	138	$Y = 0.3456X^{1.0198}$	0.9590	0.7148	NS	0
CW v Interocular width (mm)	138	$Y = 0.3576X^{0.9544}$	0.9838	-2.8679	NS	0
CW v Diagonal distance (mm)	138	$Y = 0.4467X^{1.0150}$	0.9922	1.2821	NS	0
CW v Width of abdominal segment (mm)	138	$Y = 0.3353X^{0.9351}$	0.9758	-3.3802	NS	0
CW v Wet body weight (g)	101	$Y = 0.0001X^{3.1413}$	0.9877	2.4660	<0.02	+
CW v Male Gonopod length (mm)	137	$Y = 0.4173X^{0.8375}$	0.9287	-5.2760	NS	0

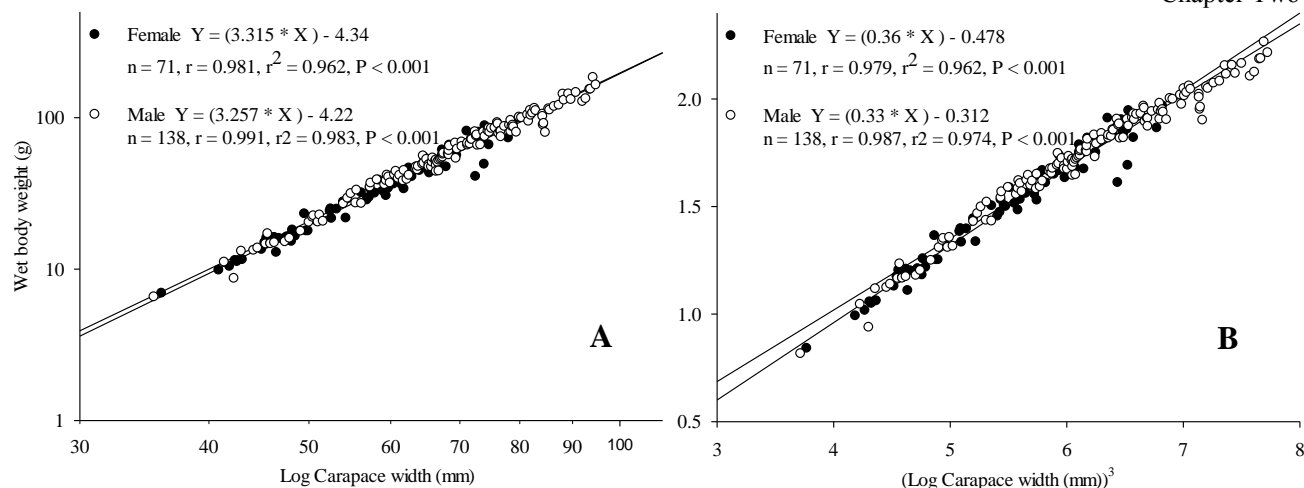


Figure 2.6 Relative growth of common log scale (A) and cubed log (B) carapace width in relation to common log scale wet body weight of male and female *Charybdis japonica* collected from Weiti River, New Zealand from February 2008 to December 2009.

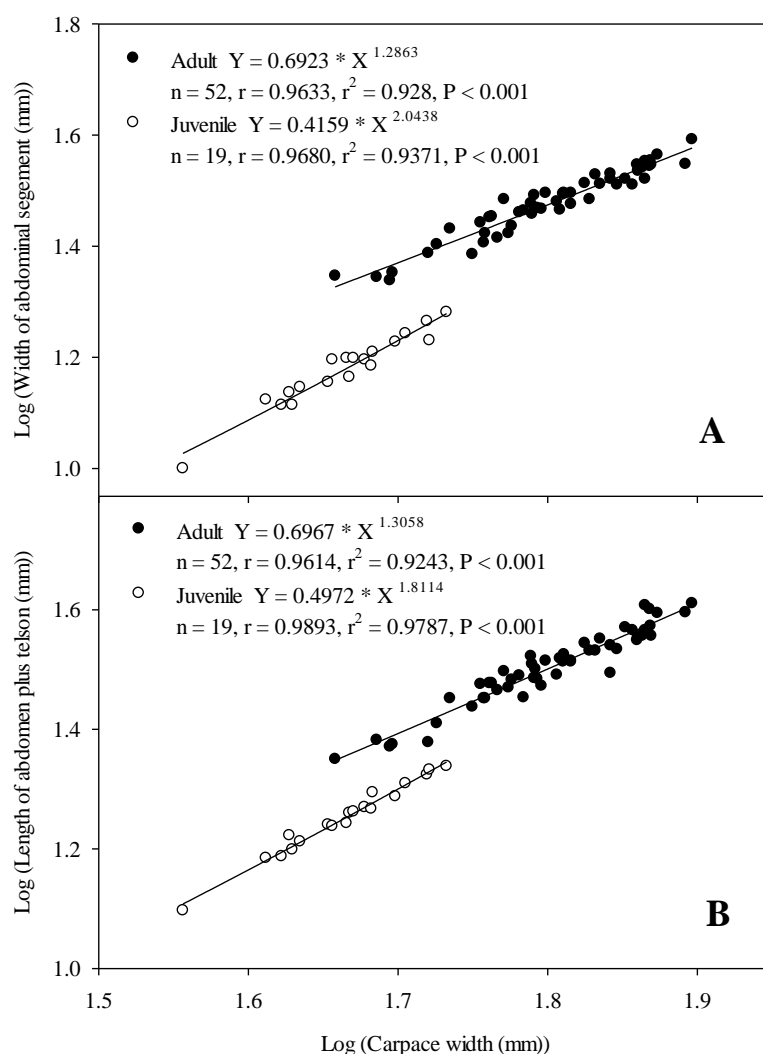


Figure 2.7 Relative growth of log carapace width in relation to width of the log abdominal segment (A) and the length of the log abdomen and telson (B) of adult and juvenile female *Charybdis japonica* collected from Weiti River, New Zealand from February 2008 to December 2009. Females were separated into adults and juveniles based on the observed breaks between the two lines and the differing slopes.

Fecundity

Estimated fecundity

The carapace widths (CW) of the 27 gravid females used to quantify and describe eggs and egg masses were an average of 64.9 ± 1.4 mm (range 49.5 to 78.8 mm). The average total number of dried eggs was $197,896 \pm 21,233$ per individual (range 26,285 to 414,461 eggs). There was a significant trend of higher numbers of dried eggs with larger carapace widths ($n=27$, $r^2 = 0.1444$, $P = 0.05$, Figure 2.8(A)) and an increase in dried egg masses with heavier dried body weight ($r^2 = 0.2923$, $P = 0.004$, Figure 2.9 (A)).

The reproductive output (RO) was enumerated by expressing the dry weight of the egg mass as a percentage of the female body weight after the egg mass was removed (Hines 1982) and averaged $5.2 \pm 0.52\%$ (range 0.7 to 12.2%). There was no correlation found between RO and CW or dried body weight (Figure 2.8 (B), Figure 2.9 (B)). The average RO during the first half of the reproductive season (November to January) was two to four times higher than the RO during February to April (Figure 2.10). 56% of the females tested exhibited RO values below 5%, indicating that the egg mass accounted for less than 5% of their non-gravid body weight, which may indicate a prevalence of abnormal broods.

The general *C. japonica* egg shape was slightly oval with an average longest diameter of 0.31 ± 0.004 mm (range 0.25 to 0.34 mm); the average minor axis was 0.29 ± 0.005 mm (range 0.23 to 0.32 mm). The average egg diameter (the average of the major and minor axis) was 0.295 ± 0.005 mm (range 0.24 to 0.33 mm). The average volume was 0.0138 ± 0.0006 mm³ (range 0.0072 to 0.0185 mm³). Average egg diameter and volume were not significantly correlated with dried body weight ($n = 25$, diameter $r = 0.215$, $r^2 = 0.046$, volume $r = 0.198$, $r^2 = 0.039$, each $P > 0.3$, Figure 2.9 (C)). The brood volume for each female was positively correlated with dried body weight ($n = 25$, $r = 0.502$, $P = 0.011$, Figure 2.9 (D)).

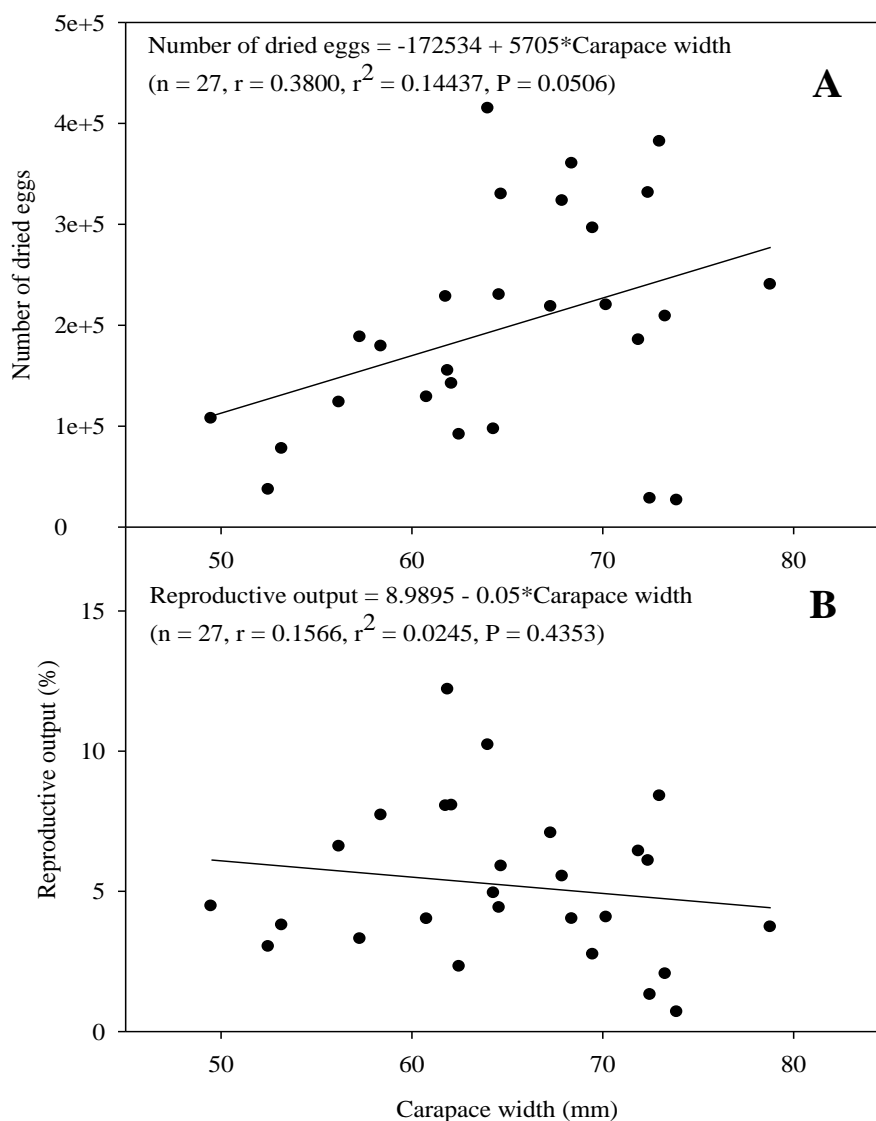


Figure 2.8 Linear regression analysis of carapace width and the number of dried eggs (A) and reproductive output (B) of 27 female *Charybdis japonica* collected from Weiti River, New Zealand from November 2007 to November 2009.

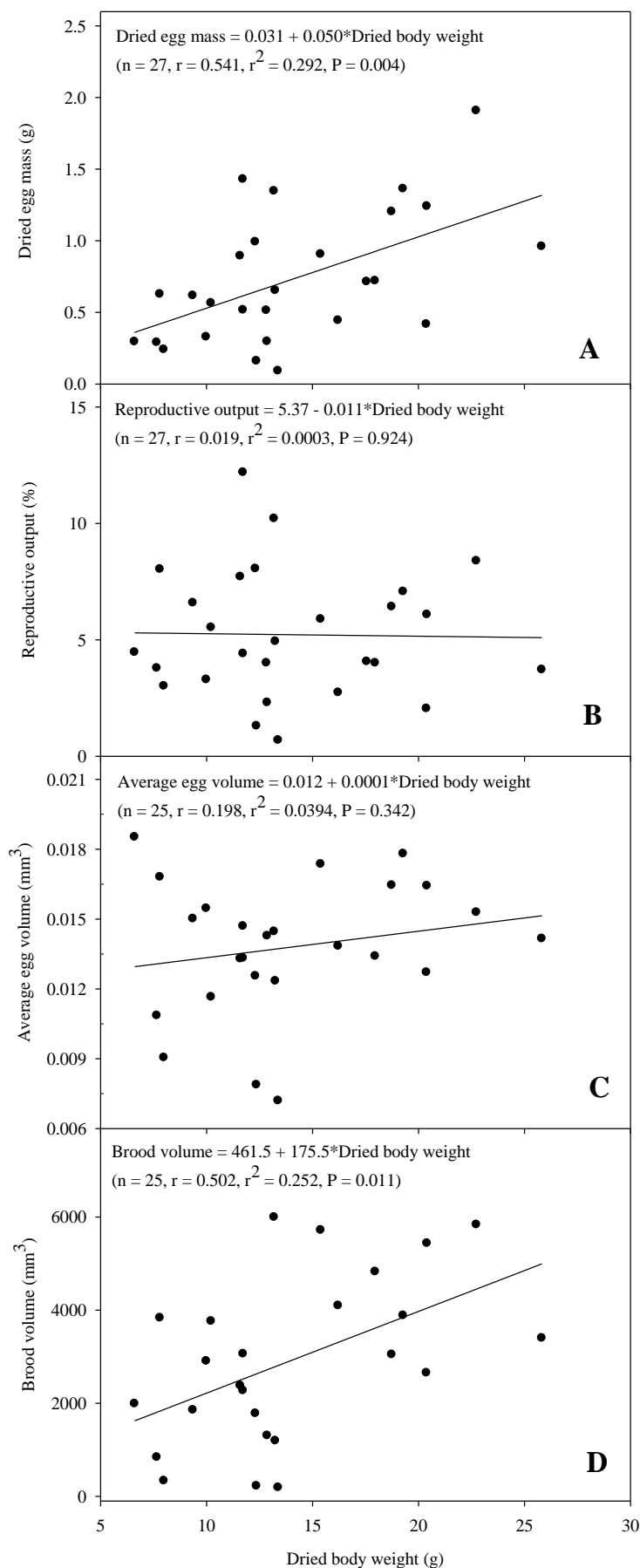


Figure 2.9 Linear regression analysis of dried body weight and dried egg mass weight (A), reproductive output (B), average egg volume (C), and brood volume (D) for *Charybdis japonica* collected from Weiti River, New Zealand from November 2007 to November 2009.

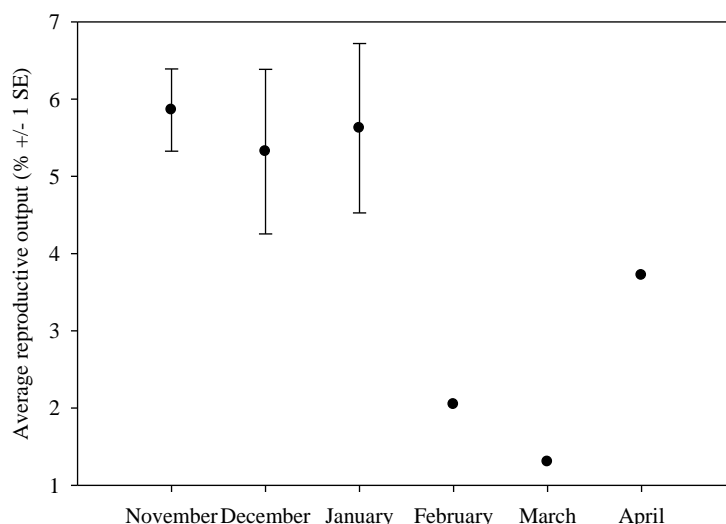


Figure 2.10 Average reproductive output (± 1 SE), defined as the egg mass dry weight as a percentage of the female body weight after the egg mass was removed, enumerated by each month of the reproductive season of *Charybdis japonica* from the Weiti River, New Zealand. Only one specimen was used for each month of February, March, and April, which explains the lack of standard deviation bars.

Realized fecundity

The holding period of gravid females until hatching was between 1 and 11 days (mean 8 days), depending on egg developmental stages at the time of capture. The estimated numbers of stage 1 zoeae from the nine females (CW range: 47 – 75mm; mean \pm SE: 61.9 ± 2.8 mm) ranged from 20,200 to 160,400 (mean \pm SE: $87,311 \pm 16,497$), which were lower than the estimated fecundity values for other similarly sized *C. japonica* females (Figure 2.11). There was no significant relationship between the number of stage 1 zoeae and CW ($n = 9$, $r = 0.1182$, $P = 0.7620$). The ability of *C. japonica* females to lay subsequent broods was not investigated.

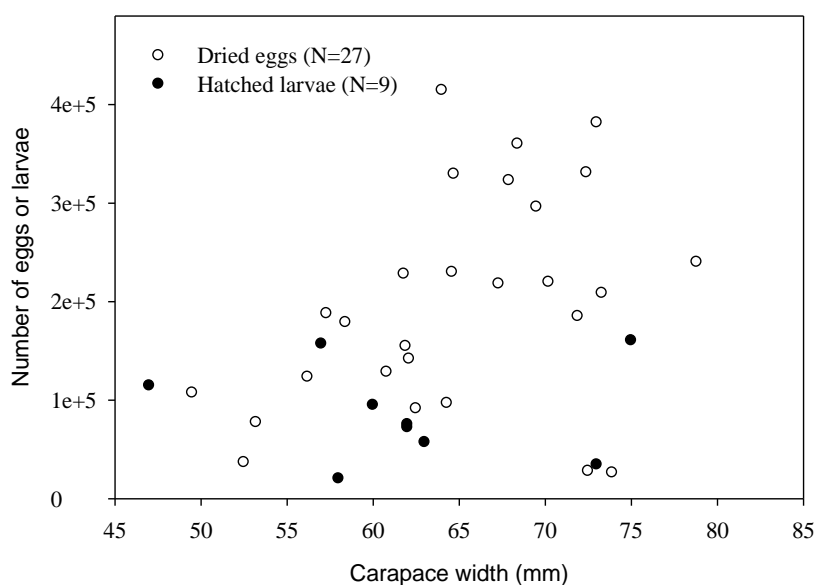


Figure 2.11 Differences in the estimated fecundity and realized fecundity rates as represented by the numbers of dried eggs and hatched larvae from female *Charybdis japonica* collected from the Weiti River.

Diet Analysis

From the 173 gastric mills examined, two (1.2%) were empty and seven (4.1%) were 100% full. Of the 171 gastric mills with contents, 89 (52%) contained 100% fish bones and/or scales from the pilchard bait (*Sardinops sagax*) along with bits of coloured plastic and were eliminated from the subsequent analysis.

Most food ingested by the crabs was finely fragmented and thoroughly digested, although the extent of mastication varied with the type of prey and the way in which it was consumed. The remains of small animals with hard parts were identified with relatively high assurance. These included Polychaeta, Crustacea (Anomura, Brachyura, Cirripedia, Alpheidae, and Isopoda), and Mollusca taxa (Gastropoda, Bivalvia, and Polyplacophora) (see Table 2.4 for a complete list of consumed prey). Other matter found in the gastric mill included sand grains, bird feathers, and organic debris including unrecognizable tissue or undefined particles of apparently organic origin.

In terms of points, the most important generalized prey category was Bivalvia, with *Perna canaliculus* contributing the largest amount (65 points, 25% of all Bivalvia eaten were *P. canaliculus*). Following Bivalvia, the other top 4 most important prey categories included, in order, Brachyura, plant material, Gastropoda, and Cirripedia. When comparing the frequency of occurrence (FO), Bivalvia was again the most important generalized prey category, but it was *Nucula hartvigiana* and not *P. canaliculus* that contributed the highest FO. Following Bivalvia, the other top 4 most important prey categories ranked differently according to FO and included, in order, Gastropoda, Brachyura, plant material and Cirripedia.

Of the remaining generalized prey categories, Foraminifera, Amphipoda, Isopoda, Alpheidae, and Anomura were only found in one gastric mill of separate *C. japonica*. Polychaeta and Polyplacophora were each only found in two gastric mills of separate *C. japonica*.

Considering rankings according to total points outside of the generalized categories, the highest ranking prey category was the Gastropoda family Buccinidae followed by the green-lipped mussel *P. canaliculus*, unidentified Brachyura, the camouflage crab *Notomithrax* sp., and unidentified members of the Bivalvia family Mytilidae. Contrasting with the rankings of total points, the FO rankings show the Gastropoda family Buccinidae sitting at the top, followed by the barnacle *Balanus* sp., the bivalve *N. hartvigiana*, the Gastropoda family Trochidae, and the green-lipped mussel *P. canaliculus*.

Due to a processing error, not all gastric mills were able to be identified with their designated crab sex, carapace width, or date of trapping. However, separating the gastric mills by known sex (male n = 45, female n = 13), males were found to have consumed mostly Bivalvia in terms of both

points and FO and prey species was dominated by *Macomona liliana* in points and *N. hartvigiana* in FO (Table 2.5). Females, however, consumed mostly Brachyura and gastric mills were dominated by *Notomithrax* sp. in terms of both points and FO (Table 2.5).

Keeping the number of replicates standard for each size, a range of carapace widths was determined for comparing the dietary components of small (40.9 – 65.7mm CW) and large *C. japonica* (65.8 – 93.5mm CW). While the three most important dietary categories for large crabs were plant material, Bivalvia and Gastropoda for both points and FO (although the rankings differed between points and FO), the top 3 categories for small crabs, in order for both points and FO, were Bivalvia, Brachyura and Cirripedia.

Using the female sexual maturity classification found in Section 2.2.2 of this chapter in which certain individuals 45.5 to 54mm CW were found to be juvenile according to the growth of their abdomen in relation to carapace width, females were separated into juvenile (n = 4) or adult (n = 9) and their diet composition compared. For juvenile females, in terms of points and FO, the most important generalized prey category was plant material, followed by Gastropoda (dominated by the Buccinidae family) and Polychaeta. The diet of the adult females was very different, with both points and FO dominated by Brachyura (dominated by *Notomithrax* sp.), followed by Bivalvia (dominated by *P. canaliculus* in points and *N. hartvigiana* in FO).

Diet contents were also separated by known dates of trapping (spring: September – November, n = 23; summer: December – February, n = 19; autumn: March – May, n = 16). Due to the low numbers of *C. japonica* trapped during the winter and the need for live specimens for laboratory experiments, no diet analysis was completed during June – August. However, during both autumn and spring, the most important generalized prey category in terms of points was Bivalvia, although the dominate species varied; this changed to Gastropoda, followed closely behind by Brachyura, during the summer.

Table 2.4 Summary of prey found in gastric mills of *Charybdis japonica* collected from the Weiti River, New Zealand, February 2008 – December 2009.

Prey Type	Types of fragments found in gastric mills
Foraminifera	Small pieces (rare)
Polychaeta	Jaws, chaetae and pieces of body wall (rare)
Spionidae	
Nereidae	
Crustacea	
Decapoda: Brachyura	Pieces of carapace, appendages and setae
Majidae	
<i>Notomithrax</i> sp.	
Alpheidae	Cephalothorax, telson, uropods, and various appendages
<i>Alpheus</i> sp.	
Cirripedia	Whole or separated plates
<i>Balanus</i> sp.	
<i>Austrominius modestus</i>	
Anomura, Amphipoda, Isopoda	Cephalothorax, telson, uropods, and various appendages
Mollusca	
Gastropoda	Opercula (whole or partial) and shell (pieces)
Trochidae	
<i>Cominella quoyana</i>	
<i>Cominella adspersa</i>	
Eationiellidae	
Buccinidae	
Bivalvia	Crushed pieces of shell and attached tissue
<i>Dosinia</i> sp.	
<i>Nucula hartvigiana</i>	
<i>Limnoperna pulex</i>	
<i>Musculista senhousia</i>	
<i>Perna canaliculus</i>	
<i>Crassostrea gigas</i>	
<i>Macomona liliana</i>	
<i>Anomia trigonopsis</i>	
Polyplacophora	Plates and girdle scales
Plants	Small pieces

Table 2.5 Frequency of occurrence (FO) and points (see Materials and Methods) for the 13 gastric mill prey content categories of *Charybdis japonica* collected from the Weiti River, New Zealand, February 2008 – December 2009. Due to a processing error, not all gastric mills were able to be identified with their designated crab sex, hence the discrepancies between the total number of individuals sampled and the numbers of separated males and females.

Prey Category	Total FO (n = 84)	Total Pts.	Male FO (n = 45)	Total Pts.	Female FO (n = 13)	Total Pts.
Foraminifera	1	1.3	1	1.3	0	0
Polychaeta	2	2.6	0	0	1	0.1
Crustacea						
Brachyura	13	151.8	6	29.9	5	90.6
Amphipoda	1	0.5	1	0.5	0	0
Isopoda	1	12.5	1	12.5	0	0
Alpheidae	1	37.5	0	0	1	37.5
Anomura	1	1.9	0	0	0	0
Cirripedia	10	93.8	6	66.3	3	15.0
Mollusca						
Gastropoda	17	123.6	10	81.3	4	28.6
Bivalvia	27	258.8	16	130.0	3	75.0
Polyplacophora						
	2	43.8	1	25.0	0	0
Plants	13	125.9	9	85.2	2	26.3

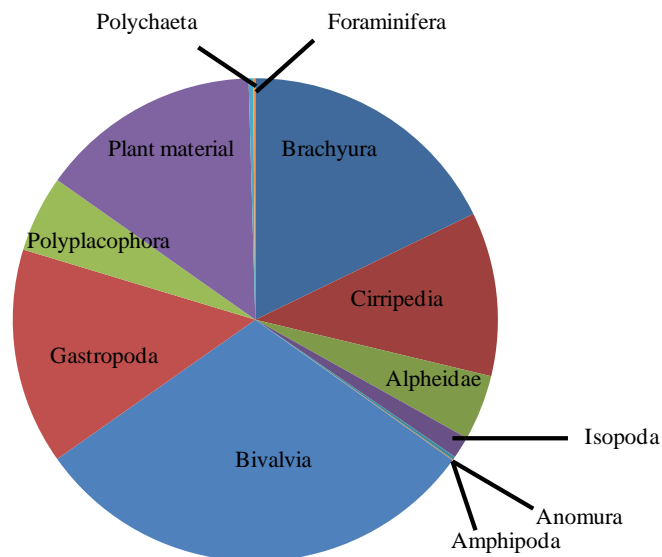


Figure 2.12 Percent points of the 13 dietary categories from the gastric mills of combined male and female *Charybdis japonica* (n = 84) collected from the Weiti River, New Zealand, February 2008 – December 2009.

Discussion

Trapping

Population structure

The size distribution of an invading population may be an important determinant of the potential for impact on native biota. Especially for a predator such as *Charybdis japonica*, the size of the crab may determine the outcome of interactions with other species as well as determining the depth to which the crab may forage in soft substrate environments (Jensen and Jensen 1985, see Chapter 3). Based on multi-year trapping in the Weiti River, a large size range of both sexes of *C. japonica*, including small juveniles, is established in this location. Trapping numbers indicate the presence of multiple age classes and possible self-recruitment and/or outside recruitment into the Weiti River. Size-frequency data suggest that there are at least two age classes in the Weiti River; one is the new juvenile class that appears in April or May, and the other is the class of juveniles and adults from previous year(s). It is possible that other age classes exist of the older, larger individuals that do not moult as frequently. The appearance of gravid females in November suggests that mating starts at the end of winter and continues throughout summer. Juvenile crabs ($\leq 43\text{mm}$) were found throughout the sampling period, but the largest proportions occurred during the winter, between June and September, and are thought to be recruits from the same year. This is consistent with the presence of gravid females between November and April and the time it is thought to take for *C. japonica* larvae to settle out of the plankton and grow to a size that will be trapped.

While a 2002-2003 initial survey of the population in the Waitemata Harbour found no juveniles and only large adult crabs (Gust and Inglis 2006), Jones and Browne (2006), in a more comprehensive survey in 2005-2006, found *C. japonica* to be a stable population with juveniles. This later population structure found by Jones and Browne (2006) in the Whitford, Upper Waitemata, and Weiti locations is comparable to this study; both studies found *C. japonica* specimens to be of a smaller average CW than those reported by Gust and Inglis (2006). The discrepancy between the population structures of the three different surveys of *C. japonica* in northeastern New Zealand could be explained by a couple different hypotheses. First, some invasive species exhibit significant lag periods between the first and secondary invasion that can last years or decades (Crooks and Soule 1999). Therefore, the smaller size range of large adults seen in the survey by Gust and Inglis (2006) may represent an initial founding population that had not been able to recruit back into that population. An alternate explanation is the temporal difference of the previous trapping surveys as compared to the one in this chapter. The other studies only surveyed areas during the late summer, and as catches within the Weiti

River were found to increase during the spring and summer months, the chosen time frame may have biased the catch rates of *C. japonica* and may explain why no juveniles were captured.

Possible movement patterns

The presence of gravid females only in the late spring, summer, and early autumn months (November to April) and the temporal variability with overall catches of both sexes and all size ranges related to sea surface temperatures (i.e. seasons) may imply ontogenetic changes in habitat use or migrations related to reproductive behaviour. In its native range of Taiwan, Korea and China, *C. japonica* also exhibit a reproductive season from late spring to early autumn (Wang et al. 1996, Kim 2001, Hsueh and Hung 2009). Huh and An (1998) and Oikawa et al. (2004) also reported an increase in trapped *C. japonica* with increasing temperature in Korea and Japan, respectively, which suggests a low level of activity during winter or a change of habitat. This seasonality in crab trappings has been shown in several other marine crustacean species (Bennett 1974, Hill 1975, Brown and Bennett 1980, Carroll 1982, Williams and Hill 1982, Armstrong 1985, Doi et al. 2008, Narita et al. 2008), as some species bury into the sediment and remain dormant for the winter period (van Engel 1962, Shiota and Kitada 1992). Although it is possible that the low abundance levels of *C. japonica* during colder months may be a result of inactivity, surveys from its native range suggest *C. japonica* may migrate due to habitat shifts or to avoid non-optimal environmental conditions.

Differences in the abundance of crabs present during summer and winter may indicate a change in habitat by *C. japonica* individuals. While Gust and Inglis (2006) found no habitat association for *C. japonica*, it may be due to the limited time frame of their study, the lack of a seasonal component, and the exclusion of juveniles. Kim (2001) reported that Korean *C. japonica* juveniles are found in tidepools in the rocky intertidal zone, after which they migrate to deeper subtidal sites as adults. Other species have shown differential migratory responses due to sex (Saski and Kawasaki 1980) or season (Panning 1939, van Engel 1962, Shiota and Kitada 1992) and are very common for brachyuran crabs (Broekhuysen 1936, Arriola 1940, Ong 1966, Crothers 1967, Muus 1967, Rasmussen 1973, Hill 1975, Dries and Adelung 1982, McDermott 1998, Attrill et al. 1999).

As a species that spends a significant amount of time in the estuarine and brackish environment and whose larvae are known to be affected by salinity (Fowler et al. 2011), *C. japonica* may migrate to avoid non-optimal salinity levels both for adults and larvae. Like most portunids, *C. japonica* females must moult before they can copulate (Hartnoll 1969). However, once they moult, it can take several days for them to complete the process of building a new shell. During this time, females are particularly vulnerable prey items, and individuals may enter the heterogeneous habitat found in

brackish estuaries and harbours like the Weiti River for safety. However, it may not be advantageous for the female to release her larvae in lower salinity waters due to their decreased survival rate, and she may migrate offshore to spawn like other portunid species (van Engel 1958, Kung 1973, Sumpton et al. 1989, Kailola et al. 1993). Further investigation into the movement patterns of *C. japonica* during different seasons is needed to determine whether this species exhibits seasonal and/or reproductive migrations related to habitat or other environmental factors in northeastern New Zealand.

Sex and size ratios of trapped *C. japonica*

Comparisons between male and female *C. japonica* abundance showed males to dominate the overall catches and to grow to a greater size than females. Heavily male-biased catches of *C. japonica* of over 77% have been reported by other studies from northeastern New Zealand (Gust and Inglis 2006, Jones and Browne 2006, Miller et al. 2006). While the ratio in this study indicates more females in the population (62% male) than reported before, other portunid trapping surveys also report male-biased catches (Armstrong 1985, Sumpton 1990, Kawamura et al. 1995, Bellchambers and de Lestang 2005). While the relatively higher trappings of males may be related to the antagonistic social interactions between the sexes (Holmes 2001, Bellchambers and de Lestang 2005), with large, dominant males aggressively discouraging smaller males and/or females from entering the trap, it may also be related to seasonal reproductive behavior. During the reproductive season (November to April), when female *C. japonica* molt before they become sexually receptive and when they are carrying eggs, they may seek shelter in traps. A confined female in a trap would be an easy sexual partner for a roving male. Male *C. japonica* were collected from the same trap in 36% of the cases when gravid females were captured and were observed mating in the traps in three separate instances. The reproductive behavior of males to seek out sexually receptive females can also be reciprocated, as with mature female blue crabs, *Callinectes sapidus*, seeking out males (Jivoff and Hines 1998).

The dominance of males in crabs above 80mm CW may be due to differential mortality or changes in behaviour between the sexes such as reduced feeding or movement out of the study area, resulting in reduced numbers of females above 80mm CW (Werner 1972). Fielding and Haley (1976) related the low numbers of female *Ranina ranina* caught to differential growth rates between the sexes, with the possibility of males reaching larger sizes if they had shorter intermoult periods or larger growth increments than females. However, due to a number of factors, of which sex and reproductive behavior are included, it is important to note that the sex ratio of trapped crabs may not accurately reflect the overall sex ratio of the population.

Morphometrics

Female relative growth

Understanding the life history of *C. japonica* in New Zealand involves describing biological aspects of this species such as size at maturity and changes in growth, both of which influence population dynamics by affecting reproductive output, demographics, and recruitment rates (Williams 1966, Stearns 1992). Juvenile females tend to have a faster growth rate of several morphological measurements relative to carapace width in order to reach reproductive size (i.e. wet body weight and abdominal length and width), at which point the growth rate of these measurements in relation to carapace width slows down and energy is diverted to egg production. Kim (2001) also noted this for *C. japonica* in Korea. This may also help explain why no female crabs over 80mm were caught over the course of the study. The decline in female brachyuran growth rate after maturity is not unusual and has been noted in other species (MacKay 1943, Prasad and Tampi 1954, Finney and Abele 1981, Hartnoll 1982, Davidson 1984, Cobb and Caddy 1989, Lee and Hsu 2003). As these measurements relate to fecundity (i.e. larger females with larger abdominal surface areas can hold more eggs), fast juvenile growth may be an advantage.

Growth in portunid crabs is extremely variable, with some species exhibiting indeterminate growth (succession of molts until mortality by external causes) and others exhibiting determinate growth (rigidly defined number of instars and no molting once the final instar is reached) (Hartnoll 1982). Although the smallest gravid female caught from the trapping survey was 43.7mm CW, data from the morphometric measurements indicate that *C. japonica* females exhibit a post-puberty size range of sizes 45.5 to 54mm CW. The molt increment of portunids is species specific and relates to the increase in carapace size between one instar and the next as the integument expands immediately after molting (Hartnoll 1982). Although the molt increment of *C. japonica* is unknown, Rice (1968) reported a mean increment of 22.3% for decapods. Using this molt increment, the pre-puberty size range (and molt to maturity) would be 35.5 – 42.0mm CW, and it could be estimated that *C. japonica* has six mature instars after the molt to maturity. Because the largest juvenile cannot molt to the largest adult size over a single instar, *C. japonica* growth appears to be indeterminate and individuals continue to molt after they attain puberty. There is probably no single “moult to puberty” (Hartnoll 1969) for *C. japonica* at a rigidly defined size. This large size range could be an adaptive advantage to diversity resource utilization of mature populations (Hartnoll 1982), and is not unusual as such large variation in female body size at puberty has been reported for other species of *Charybdis* (Sumpton 1990, Ogawa 1997, van Couwelaar et al. 1997, Balasubramanian and Suseelan 1998, Chu 1999, Kim 2001, Mantelatto and Garcia 2001, Doi et al. 2008).

In Korea, Kim (2001) reported the smallest gravid *C. japonica* female as 34.4mm CW. In Korea, the size at which 50% of the female population reached morphological maturity was 38.71mm CW; the size at which 50% of the females were physiologically mature was 52.63mm CW (Kim 2001). Therefore, the range of sizes for mature *C. japonica* females found in this study may be more ecologically relevant, incorporating both those females that have reached morphological maturity as well as those of physiological maturity. Based on the data from this study, it can be said that although a small proportion of female *C. japonica* can reproduce at 40mm CW, most attain functional maturity in size class 50mm CW, and all females are mature in size classes above 60mm CW in northeastern New Zealand. It should also be noted that although smaller females in size class 40-50mm CW may not be carrying eggs, this alone does not certify that they cannot produce eggs at these body sizes. Male *C. japonica* may prefer larger females and not mate with smaller conspecifics. Although the reasons driving the variation in when *C. japonica* reaches sexual maturity are unknown, it could be related to the long spawning season of the females, the differences in environmental conditions, and/or the genetic differences (Doi et al. 2008).

Difference in growth allocation between *C. japonica* males and females

Although there is no obvious sexual dimorphism between *C. japonica* females and males except for the shape of the abdominal segment, the difference in growth allocation may be related to the interactions between the sexes. Based on the relative growth studied in this chapter, females place more emphasis on growing secondary characteristics related to reproduction and producing a larger brood, while males put more energy into growing characteristics related to winning aggressive attacks and becoming a dominant male (i.e. chelae). There were no morphological measurements that related to the onset of sexual maturity in males, as males continue to gain weight and grow larger chelae in comparison to carapace width throughout their lives. Kim (2001) also found that male chelae length and width had positive growth relative to carapace width. As both immature and mature males may have to use their chelae in intra- and interspecific combat, the data from this study supports the hypothesis that growth of these appendages may be constant throughout their lives. This has been shown for several other male species of crab, including the native New Zealand portunid *O. catharus* (Armstrong 1985). As male *C. japonica* also use their chelae during mating to manipulate the female (Fowler, *personal observation*), increased chelae size may also aid this process. However, it is important to note that differences in sexual maturity in crustaceans are influenced by various environmental factors such as food availability and water temperature (Wenner et al. 1974, Annala et al. 1980). In New Zealand, it appears that the pubertal molt occurs over a range of sizes in female *C. japonica*, but that females have a higher relative growth rate of key reproductive features than males

until they reach puberty, after which males continue to grow and reach larger sizes than females. The indeterminate growth of *C. japonica* allows females to increase the number of spawns produced per intermolt period as they grow larger (Sainte-Marie 2007). Further work is needed to determine growth phases and reproductive development throughout the seasons (i.e. gonadal examination) and to establish the onset of maturity in *C. japonica* males.

Fouling organisms on *C. japonica*

External surfaces of *C. japonica* harbored few taxa, with only four species of fouling organisms recorded. As the abundance and species richness of fouling organisms is related to the moult cycle of the crab, more epibionts were expected on large crabs that have a longer intermolt period (Gili et al. 1993). Although *C. japonica* growth appears to be indeterminate, the occurrence of ectosymbionts on larger individuals (CW > 71.2mm) suggests that there may be a fixed number of post-pubertal molts (McLay, *personal communication*). However, the overall lack of epibionts on *C. japonica* specimens caught from the Weiti River was not surprising. Miller et al. (2006) found similar occurrences of serpulid polychaete worms and balanomorph barnacles littering the carapace of *C. japonica*, but they did not report finding any other external parasites. Overall, *C. japonica* exhibits low numbers of parasites in New Zealand and its native range compared to other species worldwide (Kim 2001, Miller et al. 2006). Therefore, at this time, the success of *C. japonica* in New Zealand cannot be attributed to its escape from native parasites.

Limb loss

As a crude measure of predation pressure on natural populations, 25.4% of all male *C. japonica* and 22.5% of all females were missing at least one limb in this survey. Miller et al. (2006) also reported similar proportions of limb loss (23.7%) in populations of *C. japonica* captured from the Waitemata Harbour. It is interesting to note that populations of the native portunid, *O. catharus*, caught by Miller et al. (2006) showed a higher overall rate of limb loss than *C. japonica*. As a less aggressive species (see Chapter 5), possibilities for the elevated limb loss in *O. catharus* may have to do with how this species responds to predation pressure, interspecific interactions with other crabs, and/or intraspecific interactions. While portunids are known to be highly aggressive (Huntingford et al. 1995) both towards each other and their predators (Smith and Hines 1991, Smith 1995), the loss of a limb(s) can impose energetic costs on the crab (i.e. reduced foraging efficiency) (Smith 1990, 1995). However, because it is unknown what species consume *C. japonica* in the wild, questions as to how and in what capacity *C. japonica* interacts with native predators remain unanswered although *C. japonica* seems to avoid limb loss better than the only similar native portunid.

Fecundity

Estimated and realized fecundity

In gravid *C. japonica* females, egg mass weight increased with increasing body weight, and the number of dried eggs was positively correlated with CW. The brood volume was positively correlated with dried body weight. Hines (1982) showed that the brood volume is primarily determined by the body cavity volume; as the brood is attached to the abdominal flap and therefore must be a function of the size of abdominal flap, the brood volume itself may also be under the control of relative growth (Fukui 1988). In their native range, female *C. japonica* have an average of 85,000 eggs per brood (Wang et al. 1996), which is lower than the average found in this study. Kim (2001) found that similarly sized *C. japonica* females in Korea had an average of 255,054 eggs per brood, with a range of 94,226 – 473,151. However, *C. japonica* in New Zealand can carry more than 400,000 eggs per brood, but this is not exceptionally high as fecundity estimates for similarly sized portunids range from 363,660 to over a million eggs in each brood (Arriola 1940, Ong 1966, Kung 1973, Batoy et al. 1987, Haddon 1994, Costa 1995). Knowing that *C. japonica* females with a lifespan of 4 years can produce up to three broods a season in their native range with similar sea surface temperatures (Kim 2001), it can be surmised that a single *C. japonica* in New Zealand could produce up to 4 million eggs during her lifetime and 1.3 million during a single breeding season. The relatively high fecundity rates of *C. japonica* may have aided the success of this species in newly invaded environments by sheer numbers of recruits (i.e. propagule pressure).

What is interesting, however, is the discrepancy between the total number of eggs attached to the pleopods and the estimated numbers of hatched stage 1 zoeae of similarly sized females. Although one female released all of her larvae successfully, up to 80% of other brood masses either did not hatch or were dislodged from the egg mass prior to hatching. No eggs were observed still attached to the pleopods of the females after the release event but unhatched eggs were found during the larval counts. As has been shown with multiple portunid species, fecundity is highly variable for females of similar sizes (Sumpton 1990, Haddon 1994) and may be attributed to multiple or fragmented broods (Mantelatto and Fransozo 1997). Similar to this study, Kim (2001) also found that brood loss in *C. japonica* averaged 13.57% in number and 34.57% in dried weight. Therefore, based on these data, I do not believe that the numbers of eggs of the *C. japonica* captured from the Weiti River were underestimated. Up to 71% of the brood could be lost at any stage due to the retention of oocytes in the ovaries, egg loss, egg predation and parasitism, and/or hatching failures (Kuris 1991).

Reproductive output

Reproductive output (RO) is the egg mass dry weight as a percentage of the female dried body weight after the egg mass was removed (Hines 1982), and it estimates the reproductive energetic investments of the female. In most brachyuran crabs, the RO is usually restricted to approximately 10% of the total body weight (Leme 2006), but the RO of female *C. japonica* from the Weiti River ranged from 0.7 to 12.2% with a mean value of 5.2%. 56% of the Weiti River females exhibited RO values below 5%, which may indicate a prevalence of abnormal broods. However, Kim (2001) found *C. japonica* females in Korea to have an average RO of 11%. Low RO values are not uncommon in studies of crab reproduction and most studies cite variations in environmental conditions as being the cause for such values (e.g. Leme 2006). The average RO during the first half of the reproductive season in the Weiti River was two to four times higher than the RO during the second half of the reproductive period. Although this may be a function of low replicate numbers in this study, brood numbers in other species have been shown to decrease over the course of the reproductive season with each sequential brood as mature oocytes may be reabsorbed or non-fertile clutches may be laid (McMullen and Yoshihara 1971, Fukui 1990, Oh and Hartnoll 1999). As Kim (2001) has reported that *C. japonica* in Korea can produce up to three broods a season, those individuals collected in the second half of the reproductive season in the Weiti River may have produced their second or third sequential brood that season, which may explain the lower RO values for those broods.

Egg diameter

The average egg diameter of *C. japonica* in the Weiti River was $0.295\text{mm} \pm 0.005\text{ SE}$, and, as expected neither the average egg diameter and volume was positively correlated with dried body weight. As the measurements of these variables are species, and not individually, specific, they were not expected to change over the range of CW tested. The variation in intraspecific egg size seen in this study may occur as a response to environmental factors acting on a local scale (Simons and Jones 1981). There are no other reported values for *C. japonica* egg diameter in either its invaded or native range, but these characteristics are also common among other species of *Charybdis* (Kurata and Matsuda 1980, Ogawa 1997, Balasubramanian and Suseelan 1998, Dineen et al. 2001, Doi et al. 2008). Larger eggs are able to produce larger larvae with more energy reserves available to them after hatching, allowing them partial independence from external food sources (i.e. lecithotrophic potential) (Rabalais and Gore 1985). This facultative lecithotrophy may allow *C. japonica* larvae to positively respond to temporal and spatial changes in the environment and may have influenced their ability to become successful.

Diet analysis

Although this study examined only a snapshot of *C. japonica*'s diet in northeastern New Zealand, the data show *C. japonica* as an opportunistic, generalist omnivore whose diet is comprised of mainly Bivalvia and to a lesser extent mobile epibenthic Gastropoda and Brachyura. Prey included gastropods, bivalves, decapods, shrimps, amphipods, isopods, polychaetes, foraminifera, plants, and barnacles. Several other species of portunids have a diet dominated by bivalves (Ropes 1968, Gotshall 1977, Hill 1979, Feder and Paul 1980, Elner 1981, Paul 1981, Williams 1981, Haefner 1985, Grosholz and Ruiz 1996). Even the native New Zealand portunid, *Ovalipes catharus*, is an opportunistic and generalist predator whose diet is dominated by either Bivalvia (*Paphies* sp.) or Crustacea (Amphipoda and Decapoda), depending on location (Davidson 1987, Wear and Haddon 1987). This diverse species composition of their diet shows that *C. japonica* is extremely versatile in its feeding behavior. This is not unusual for *C. japonica* as in their native range in China they also exhibit a generalist omnivorous diet consuming mainly Bivalvia, Polychaeta, benthic Crustacea, fish and Cephalopoda (Weimin et al. 1989, Kimura 2005, Quan et al. 2010). Many other successful invasive crabs have also been shown to have opportunistic, generalist feeding approaches which may increase their success at surviving in new habitats (Cohen et al. 1995, Dineen et al. 2001, Ledesma and O'Connor 2001, Rudnick and Resh 2005).

Feeding habits in the Weiti River

As the diet of a predator is based on both the predator's preference and the availability of a prey item in the natural environment, an unselective generalist predator, such as *C. japonica*, would be expected to display prey proportions equivalent to prey availability. Although the fauna of northeastern New Zealand coasts is documented in general terms (Morton and Miller 1973), the details of prey species presently available at the Weiti River are not known. From observation, several of the species that appear to be dominant or common appeared in the gastric mills of *C. japonica*. In the Weiti River, there are stable populations of gastropods (*Cominella* sp.), bivalves (*Crassostrea gigas*, *Macomona liliana*, *Perna canaliculus*, *Nucula hartvigiana*), and several species of barnacles, polychaetes, chitons, hermit crabs (*Pagurus* sp.), and decorator crabs (*Notomithrax* sp.). However, although they were common at the sampling site, fast moving, small epibenthic organisms were rare in *C. japonica*'s diet. As reports from China state that *C. japonica* is able to catch and consume both fish and benthic crustaceans (Weimin et al. 1989), one can only assume that *C. japonica* may not need to spend time or energy catching mobile organisms when benthic, immobile species are present in the Weiti River in such abundance. Although cannibalism was observed both in the laboratory and the field, there was no evidence of cannibalism from the gastric mills of sampled *C. japonica*, which is in

contrast to the diet composition of many other portunids, whose diets almost always include conspecifics (Wear and Haddon 1987, Cohen et al. 1995, Baeta et al. 2006). This could be due to the low population numbers of this species within the Weiti River and the possibility that individuals do not run into each other outside of the reproductive season. The large proportion of sand in their diet may be due to the scooping nature of portunids when feeding on small buried bivalves (Wear and Haddon 1987) and not from any want or need to consume sand. *C. japonica* has been observed feeding in this manner during laboratory experiments (Fowler, *personal observation*).

Age-specific feeding approaches

Changes in prey type between different size-age groups have been shown in several species of crabs (Ropes 1968, Paul 1981, Jewett and Feder 1982, Stevens et al. 1982, Abbas 1985, Davidson 1987) and may be a function of the mechanical properties of their feeding appendages (i.e. chelipeds and mouth parts). The chelipeds of *C. japonica* are heteromorphic, heterodontic (i.e. different sizes and shapes of “teeth” on the chelipeds), polyfunctional limbs, each specialized for various prey handling functions and are capable of handling a wide range of prey types and sizes by all sizes of crabs. While large crabs consumed a large proportion of plant material, small crabs consumed bivalves, brachyurans and barnacles. The ability of larger crabs to consume gastropods while smaller crabs prey on easily consumed species may also be a reflection of their cheliped strength (Schaefer 1970, Elner 1981, Brown et al. 1979). In other species, diet differences based on sex have also been explained by differences in chelae shape (Scherer and Reise 1981) or chelae size (Elner 1980). Comparisons of chelae length and width between similarly sized males and females showed males to have consistently longer and wider chelae. These increased chelae dimensions may help explain why males consumed more bivalves than females. Bivalve consumption would require more chelae strength to break the shell and dexterity to pull the muscle apart. Different stages of maturity may also show differences in diet (Ropes 1968, 1988, Elner 1977, Stevens et al. 1982, Abbas 1985), as seen with juvenile and adult female *C. japonica* in this study, and may be due to differences in energy requirements, ability to consume certain prey items, or prey species abundance due to habitat differences (Elner 1980). For instance, the preponderance of plant material in the gastric mills of juvenile female *C. japonica* may be related to their habitat choice of hiding among seaweed to escape predators. Juveniles of other species of grapsid, xanthid, majid, potamid and portunid crabs have also been shown to consume large proportions of plant material (Ropes 1968, Hill 1976, Warner 1977, Paul 1981, Jewett and Feder 1982, Williams 1982, Wolcott and O’Connor 1992).

Although stable isotope studies in China have shown that *C. japonica* consumes plant material (Quan et al. 2010), it is thought that they may ingest algae as a by-product of consuming other

organisms living in or on the plant (i.e. hydroids, bryozoans, coelenterates, molluscs, and crustaceans) (Choy 1986). Most of these algae epiphytes are either too small or would not leave enough evidence behind in the gastric mill to be identified. As an opportunistic predator, it is possible that *C. japonica* consumes plant material when it is abundant, and, as it is a sessile prey item, it is always easily caught. Crabs may also consume plant material to supplement or substitute other prey items in times when food is scarce (Gonzalez Gurriaran 1978), to satisfy the demands for carotenoids that the crab cannot synthesize itself (Adelung and Ponat 1977), or to gain sustenance in the form of laminarin (a polysaccharide sugar) during periods of low organic food availability (Chapman and Chapman 1980).

Seasonal prey switching response

The mechanical properties of their chelipeds may also allow *C. japonica* to successfully take advantage of seasonally abundant prey items. Seasonal dominance of bivalves in their diet during spring and autumn and gastropods and brachyurans during the summer may reflect a prey switching response by *C. japonica* to higher numbers and increased catch rate of mobile benthic invertebrates during the warmer summer months. The increase in bivalves in the diet during autumn may reflect the maturation and high densities of bivalves that were recruited the same year (Choy 1986). Bivalves may also be important in the diets of crabs preparing to molt and/or recently molted crabs as the calcium from their shells is required for further hardening of the carapace (Davidson 1987). As both sexes, but especially females, molt at the beginning of the reproductive season (i.e. spring), this may explain the high abundance of bivalves in the diet at this time. This seasonal prey switching response has been reported for other portunid species (Elner 1981, Paul 1981, Le Calvez 1984, Abbas 1985, Choy 1986, Le Calvez 1987, Wear and Haddon 1987), which may be due to the micro-distribution and behaviour of prey species (Laughlin 1982, Choy 1986, Cohen et al. 1995). Although an opportunistic, generalist predator, *C. japonica* probably utilises whatever food items are locally available at any time but may tend to congregate in areas where preferred prey species are present.

Problems with using diet analysis from baited traps

While this diet analysis is the first for *C. japonica* in its invaded habitat and accurately describes the population in the Weiti River, it must be remembered that these individuals were collected from baited traps. This study assumes that the trapped *C. japonica* individuals are representative of the entire population; it is possible that crabs eating a certain diet are more attracted to the fish bait than others. Over 50% of individuals were eliminated from the survey based on the preponderance of fish scales and bones in their gastric mills, which were thought to be consumed by the crabs while they were in the trap. However, several other species of portunids are known to keep

previously consumed prey items in their gastric mills for 12-36 hours after ingestion (Hill 1976, Abbas 1985, Choy 1986) and hard parts of their prey items for up to 8 days after ingestion (Hill 1979). As the baited traps fished for less than 24 hours, the data from this study accurately reflects recently consumed prey items that trapped *C. japonica* ate either in the Weiti River or while on the move. A more comprehensive survey over several known areas of *C. japonica*'s range using trawling nets and/or hand collection would be a more accurate way to describe their diet composition.

Conclusions

This study is the first on the growth, reproduction, and diet of *C. japonica* in its invaded range in northeastern New Zealand. While this study was based on 18 months of observations on a single *C. japonica* population from the Weiti River, the data show seasonal patterns of abundance and occurrence of gravid females, information on fecundity, and the first known prey items from diet analysis. While it can be postulated that similar populations of this species in other areas (i.e. Waitemata Harbour, Tamaki and Whitford estuaries, Whangarei Harbour) will parallel the results of this study, further investigation into those populations are needed to confirm that. Based on the information from this study and comparisons with other *Charybdis* species, the life history of *C. japonica* in northeastern New Zealand can be summarized as follows. Based on the first appearance of gravid females in November, it can be surmised that mating begins at the end of winter and continues throughout the summer months. After attaining reproductive size between 40 and 50mm carapace width, females hatch at least one brood of up to 400,000 eggs between spring and autumn (November to April) with a peak in summer. The young crabs that hatch early in the reproductive season (i.e. November, December) attain recruitment size in autumn and settle into estuaries. Individuals that are hatched later in the reproductive season continue to be recruited into the population during the winter and early spring. Throughout its benthic life, *C. japonica* is an opportunistic omnivore in northeastern New Zealand with a preference for invertebrate prey and exhibits active predatory behaviour on sessile and slow moving macroinvertebrates. Predation rates on individual prey species may change with season, location, and sex and size of *C. japonica*. *C. japonica* has the potential to influence the structure of these marine ecosystems. With a long larval life that facilitates dispersal, rapid growth to maturity, high fecundity, and a broad diet, it appears that *C. japonica* has biological and ecological attributes that have aided their integration into their novel New Zealand habitat.

Chapter Three

Laboratory and field experiments test the impacts of *Charybdis japonica* on native New Zealand marine benthic bivalves

Introduction

Crabs, whether native or non-native, can be an important structuring force in marine benthic communities (e.g. native: Eggleston et al. 1992, Ebersole and Kennedy 1995, Dudas et al. 2005; non-native: Brousseau et al. 2001). The introduction of a novel crab predator frequently results in changes in species abundances across many trophic levels, due to both direct and indirect effects (e.g. Lubchenco 1978, Grosholz et al. 2000, Walton et al. 2002, Lohrer and Whitlatch 2002, Floyd and Williams 2004, Dittel and Epifanio 2009).

Although predictions concerning the impact of a new invader on a native ecosystem can theoretically be deduced by examining its native range and ecological interactions, the actual outcome of this interaction is likely to be very different than the prediction. For instance, the physical properties of the invaded habitat may influence prey encounter probabilities and therefore might alter the predator's preferences (Mascaro and Seed 2000a). Native prey may find refuge in size, morphology, low or inflated population densities, and/or because they inhabit inaccessible environments (Seitz et al. 2001). Selective foraging can also have impacts on prey abundance and distribution (Mascaro and Seed 2000a), which can influence the invader's ecosystem effects.

As a large and abundant portunid crab with generalist feeding approaches, *Charybdis japonica* has the capacity to become a significant predator on important benthic invertebrates and may thus play a key role in structuring communities. *C. japonica* consumes a taxonomically diverse range of organisms in its native range (Dai and Yang 1991, Weimin et al. 1998, Kimura 2005) and invasive range (Chapter 2).

Early studies on crab predation in estuaries provided strong evidence that crabs are important predators on juvenile bivalves (e.g. Landers 1954, Carriker 1967, Ropes 1968, Jensen and Jensen 1985, Hines et al. 1990), supporting the hypothesis that crabs tend to choose relatively small prey relative to what is available (Seed and Hughes 1995). High juvenile mortality has important implications for prey population maintenance and is a serious threat to the successful management of commercial bivalve resources (Belding 1930, Davies 1966, Hanks 1963, Galstoff 1964). In New Zealand, important commercial and recreational endemic species such as the epibenthic and shallow-burrowing cockle (*Austrovenus stutchburyi*), pipi (*Paphies australis*), and the epibenthic green-lipped mussel (*Perna canaliculus*) are particularly vulnerable.

Given the broad diet of *C. japonica* in its native and invasive range (Chapter 2), the invasion by this species may have significant effects upon New Zealand's marine benthic invertebrate populations and subsequent effects on fisheries. Therefore, I conducted a number of laboratory and field experiments to evaluate the effects of the invader upon several common benthic marine bivalve species. Laboratory investigations determined what prey species *C. japonica* would consume, what prey sizes they target, and how sediment influences the number of prey items eaten within each size class. Field caging experiments examined the impacts of *C. japonica* on a community of benthic soft sediment invertebrates in an assumed non-invaded estuary. Surveys completed in the Waitemata Harbour, Auckland (36°50'S, 174°45'E) before the invasion of *C. japonica* in 1993 and 1994 (Hayward et al. 1997) provided a baseline of macroinvertebrate abundance, diversity and distribution. Following the methods and collecting from the same sites as Hayward et al. (1997), a survey was completed in 2008 to uncover any changes in benthic macroinvertebrate community structure that could be attributed to the arrival of *C. japonica*. The results of this study will provide a clearer understanding of *C. japonica*'s ability as a predator and attempts to assess the potential impact of this invader on infaunal populations of marine invertebrates, with particular reference to native bivalves.

Methods

Laboratory experiments

Intermoult *C. japonica* were collected from the Weiti River on the Whangaparaoa Peninsula of New Zealand (36° 38'24 S, 174° 43'38 E) in oval-shaped collapsible 'Opera house' traps baited with a single pilchard (*Sardinops sagax*) at approximately 2m depth. The dimensions of the traps were 640 x 470 x 200mm (l x w x h) with a diagonal mesh size of 20mm and an entrance funnel opening into the trap with a diameter of 90 mm. After a 24 hr soak, any trapped crabs were removed, individually placed in 10 litre buckets containing seawater from the Weiti River, and transported ca. 50 km to the Leigh Marine Laboratory. At the laboratory, the crabs were maintained in individual aquaria (40 x 50 x 30cm) each containing approximately 60 liters of sea water of unfiltered natural seawater at ambient temperature, under a light regime of 12L:12D, with air supplied by bubblers at a low pressure. Aquariums lacked sediment unless otherwise stated. Crabs, which were individually isolated to prevent aggressive interactions and injury, were fed chopped pilchard (*S. sagax*) until satiation every other day but were starved for a standard length of time (equal to the duration of the experimental days) prior to the experiments to standardize hunger levels and to ensure feeding during trials. Because the experiments ran for different periods of time, starvation times also varied; see methods for each experiment for starvation times. All experiments were conducted at the University of Auckland's Leigh Marine Laboratory.

The carapace width (CW) of each test crab and the prey shell length were determined to the nearest 1mm using dial callipers. Only those crabs with both chelae and other appendages intact were used in the feeding trials, and all crabs were monitored for moulting for a week after the conclusion of the experiments. As pre- or post-moult crab do not feed, if crabs moulted within a week of the conclusion of an experiment, data for that replicate would have been discarded; there was no moulting observed. Individual prey species were allowed to acclimatize for at least seven days after collection.

Shell lengths of the native *Perna canaliculus* and non-native *Crassostrea gigas* were defined as the distance from the umbo to the farthest point on the shell, while the shell lengths of *Austrovenus stutchburyi*, *Macomona liliana*, *Nucula hartvigiana* and *Paphies australis* were the maximum length of shell parallel to the umbo. At the conclusion of each replicate, only prey with visible signs of crab predation (crushed or chipped shells) were included in the predation estimates; chipped shells that were not opened by the crab were not considered as consumed prey. The presence of dead bivalves with intact shells was considered an indication of non-predatory mortality.

Experiment 1: Vulnerability of common marine invertebrates to *Charybdis japonica*

Based on what prey species were found in the diet analysis in Chapter 2 and their prevalence in the ecosystems that *C. japonica* has invaded in New Zealand, six prey species were chosen as potential food items (Fowler, *personal observation*). The prey species included the native bivalves *Macomona liliana*, *Austrovenus stutchburyi*, *Paphies australis*, and *Nucula hartvigiana* (all collected from the Puhoi River estuary, 36° 31'52 S, 174° 42'28 E), *Perna canaliculus* (from Pakiri Beach, 36° 15'34 S, 174° 45'07 E), and the non-native bivalve *Crassostrea gigas* (from the Weiti River, Whangaparoa, 36° 38'24 S, 174° 43'38 E).

Experiment 1 was conducted from 18 – 26 July 2007 when the water temperature was, on average, 14.9°C but ranged between 13.1 – 15.6°C. *C. japonica* were collected from 25 – 29 June 2007 and each of the 18 *C. japonica* (eight females (CW 59 – 87mm) and ten males (CW 48 – 88mm)) was randomly separated into aquaria and given 48 hours to consume a single live, unopened prey item. Prey were divided into three size classes (small, medium, large) based on known sizes and those sizes available in the field. *A. stutchburyi* and *M. liliana* used in this experiment ranged in size from 9 – 43mm, *P. canaliculus* from 32 – 106mm, *N. hartvigiana* from 4 – 8mm, *P. australis* from 15 – 69mm, and *C. gigas* from 26 – 106mm. Each crab was given all prey species by the end of experiment (N=6) but only one size (small, medium or large) of each prey item at a time. Each crab was given every prey item once and the three size classes (small, medium, large) were replicated three times for each prey species. The sequence of prey species and size to individual crab was randomized for all prey items to allow for possible temporal disparities.

During the experiment, the aquariums were monitored every two hours from 08:00 – 18:00 and the debris of an eaten prey or the whole uneaten prey removed. If the prey item was consumed, crabs were starved for 48 hours before another prey item was presented to them. If the prey item was not eaten after 48 hours, they were immediately given another prey item.

Experiment 2: Prey size selection of three common marine invertebrates by *C. japonica*

In order to test whether *C. japonica* shows any preference for certain prey size classes, three bivalve species (*M. liliana*, *P. australis* and *P. canaliculus*) were offered to *C. japonica* and their predation rates measured.

Experiment 2 was conducted from 14 August 2007 – 19 September 2007. *C. japonica* were placed in a random design in the same aquaria with unfiltered natural seawater at ambient temperature (average 14.9°C (range 12.1 – 17.8°C)). 18 *C. japonica* (eight females (CW 59 – 71mm) and ten males (CW 48 – 88mm)) were used in this experiment, each in their own aquarium. Earlier trials revealed that the upper size limit for *C. japonica* to consume these three prey items was 40mm, so only prey items up to 40mm were offered to individual *C. japonica*. For each replicate, an array of prey sizes based on standard shell length to tissue ratios (<8mm: 25 prey; 9 – 16mm: 20 prey; 17 – 24mm: 10 prey; 25 – 32mm: 5 prey; 33 – 40mm: 3 prey) was presented to a crab and after five days the numbers of prey consumed in each size category was determined. In total, each crab was given 63 individuals of the live, unopened prey species, one species at a time. Crabs were starved for four days prior to the experiments and between trials. At the end of the experiment, each crab was removed and the bottom of the tank siphoned to remove all eaten and uneaten prey. The uneaten prey items were then measured and counted to determine sizes and numbers of prey items consumed.

Experiment 3: The influence of sediment on predation rates by *Charybdis japonica*

In order to determine whether the presence of sediment affected predation rates, the predation rates of *C. japonica* on two burrowing species (*M. liliana* and *P. australis*) and a non-burrowing species (*P. canaliculus*) were measured over 24 hours in the presence and absence of sediment.

Analyses of the effect of sediment on percent prey consumed were run using the software package PRIMER 6 (Clarke and Gorley 2006) with the PERMANOVA+ add-on (Anderson et al. 2008). The experimental design consisted of three factors: sediment (presence or absence of sediment), sex of crab (male or female) and size class of prey (10 – 15mm, 16 – 20mm, 21 – 25mm, and 26 – 30mm). Individual variables were analysed according to the full three-factor design using permutational analysis of variance (PERMANOVA; Anderson 2001, McArdle and Anderson 2001) based on Euclidean distances, with 4999 permutations of residuals under a reduced model.

PERMANOVA pair-wise comparisons followed the overall partitioning when significant differences were detected among the treatments.

Experiment 3a: Experiments performed without sediment

Experiments without sediment were conducted from 30 September – 7 October 2007. *C. japonica* were collected from 14 – 18 August 2007 and were individually placed in a random design in the same aquaria with unfiltered natural seawater at ambient temperature, which averaged 14.7°C (range 14.5 – 14.9°C)). 18 *C. japonica* (eight females (CW 59 – 87mm) and ten males (CW 48 – 88mm)) were used in this experiment, each in their own aquaria. Pairs of each prey species (*M. liliana*, *P. australis* and *P. canaliculus*) from 10 – 30mm were given to each crab for each 24 hour feeding trial for a total of 42 live, unopened prey items during one round of testing. All three prey species were concurrently tested among different crabs, and only one species of prey was given to a single crab during the 24 hour period. The sequence of prey items for an individual crab was randomized. Crabs were starved for 24 hours prior to the experiments and between trials. At the end of the experiment, each crab was removed, then all eaten and uneaten prey items were removed, measured and counted.

Experiment 3b: Experiments performed with sediment

Experiments with sediment were carried out from 18 April – 16 May 2008 with *M. liliana* and *P. australis* and from 27 November – 6 December 2008 for *P. canaliculus*. *C. japonica* were collected from 10 – 15 April 2008 and from 10 – 14 November 2008 and were individually placed in a random design in aquaria with unfiltered natural seawater at ambient temperature (average 18.6°C (range 18.1 – 19.2 °C) during April; average 17.4°C (range 16.4 – 17.9°C) during November – December).

For the experiments with *M. liliana* and *P. australis*, a total of 20 *C. japonica* (eight females (CW 51 – 67mm) and twelve males (CW 55 – 82mm)) were used, each in their own aquaria. For the experiments with *P. canaliculus*, a different set of 18 *C. japonica* (ten females (CW 35 – 73mm) and eight males (CW 36 – 96mm)) were used. Pairs of each prey item (*M. liliana*, *P. australis* and *P. canaliculus*) from 10 – 30mm were given to each crab for each 24 hour feeding trial for a total of 42 live, unopened prey items during one round of testing. Only one species of prey was given to a single crab during the 24 hour period. Crabs were starved for 24 hours prior to the experiments and between trials.

Based on earlier trials, the maximum burial depth of 30mm long *M. liliana* (the largest size used in this experiment) collected for this experiment was 100mm, and the maximum burial depth of 30mm *P. australis* was 50mm. Sediment (sandy mud for *M. liliana*; gravel for *P. australis*) was obtained from the estuaries where the bivalves were collected. The 42 prey items of *M. liliana* and *P.*

australis were placed on the surface of the sediment and allowed 24 hours to bury. Those that were still on the sediment surface at the end of the 24 hours were gently pushed into the sediment. *C. japonica* (n=20) were then added to the aquaria and allowed to feed for 24 hours.

As a control, *P. canaliculus*, which do not bury, were offered to *C. japonica* (n=18). Before the start of the experiment, 42 *P. canaliculus* were measured and placed in a bucket with a rock and allowed to attach to the flat top surface of the rock with byssal threads. Those that did not attach were replaced with equal sized individuals and allowed to grow byssal threads. Once all 42 *P. canaliculus* were attached to the rock, they were placed into the aquarium and the surface of the rock was made level with the surface of the sediment, which was 50mm deep. This allowed *P. canaliculus* to be at the surface level of the sediment. *C. japonica* were then added to the aquaria and allowed to feed for 24 hours. At the end of the experiment, each crab was removed and the sediment siphoned and sieved to remove all eaten and uneaten prey items. The uneaten prey items were then measured and counted to determine sizes and numbers of prey items consumed.

Field experiments

Exclusion experiment

In order to assess the impacts of *C. japonica* on benthic invertebrates in what was thought to be an uninvaded environment, individuals were caged and allowed to forage on natural soft sediment communities in the Mahurangi estuary (36°29'20 S, 174°43'39 E) from 20 – 28 November 2007.

Treatments were (1) open plots (uncaged) to measure natural predation rates, (2) partial cages (left open on two sides) to test for cage artifacts, (3) caged plots lacking *C. japonica* to test natural survival and the effectiveness of the retrieval method, and (4) caged plots with a single *C. japonica*. Like many other enclosure experiments, predator density (crabs m⁻²) was probably inflated although prey density approximated natural values in areas outside the range of *C. japonica*. I attempted to compensate for this by limiting the duration of the experiment to one week.

Cages were constructed out of metal poles 10mm in diameter, bent and welded into 1 x 1 x 0.3m (l x w x h) frames over which a PVC coated wire mesh of 20mm was securely attached. Mesh was applied to the outside of the entire frame (including the bottom surface) to minimize the possibility of *C. japonica* escaping. The mesh size of 20mm was chosen because it allowed *C. japonica* to forage for prey species under 20mm, which had previously been shown to be consumed by *C. japonica* in laboratory experiments. This size also allowed *C. japonica* to extend its chelae outside the cage to forage on invertebrates either on or in the sediment. When established at the field site, the mesh was placed on the sediment surface, and not buried, to minimize benthic disturbance.

All cage experiments were conducted on unvegetated, firm mud subtidal sites with existing natural macroinvertebrates present. Each cage treatment had seven replicates, which were placed at the site at low tide on 20 November 2007. Each cage was firmly stabilized using two tent poles, 10mm in diameter, which were bent at the top and placed over the frame of the cage and pushed down into the sediment to a depth of 0.5m. All cages and other experimental plots were placed one meter apart to minimize interactions. *C. japonica* were starved for 72 hours prior to the start of the experiment to standardize hunger levels, and only males were used to ensure that population establishment was impossible in the event of an escape.

After one week, each cage was removed during low tide and individual *C. japonica* were collected. Four sediment cores (diameter 15cm) to a depth of 10cm (representing approximately 50% of the total area underneath the cage) were taken from underneath each cage and from the uncaged treatments and washed over a 1mm sieve. Samples were preserved in 70% isopropyl alcohol and Rose-Bengal, and individual macroinvertebrates were later enumerated, identified, and measured by cage (e.g. all four sediment cores were enumerated as a single sample).

When examining the effect of *C. japonica* on the abundance and diversity of invertebrates, those in the open, half-meshed and no crab plots were combined into a single “no crab” category. ANOVA tests were conducted to determine if there was a significant effect of cage or crab on macroinvertebrate abundance or species richness. Analyses of the effect of *C. japonica* presence on overall benthic community structure were completed using the software package PRIMER 6 (Clarke and Gorley 2006). Prey items were enumerated by species and this data was $\log(x+1)$ transformed and resemblance was measured as Bray-Curtis similarity. Using the log transformed data, treatments were grouped by prey species similarity to show the effect of *C. japonica* on macroinvertebrate assemblages. Non-metric multidimensional scaling (MDS) was used to visualize the differences between cages with *C. japonica* and those without. One-way ANOSIM was conducted to determine if there were significant differences in species assemblages between plots with *C. japonica* and those without.

Field survey

Hayward et al. (1997)’s survey of the Waitemata Harbour (36°50’S, 174°45’E) in 1993 and 1994 provided a baseline of macroinvertebrate abundance, diversity and distribution that could be compared to a 2008 survey to detect any changes that could be attributed to the arrival of *C. japonica*. If *C. japonica* had a significant effect on the macroinvertebrates, we would expect to see reductions in preferred prey species. Unchanged or increased abundance of non-prey species would indicate that other environmental changes were responsible. Due to the multiple unavoidable issues surrounding the comparison between the two surveys (see below), only major impacts would be able to be detected.

Hayward et al. (1997) Waitemata Harbour study

Hayward et al. (1997) dredged bottom samples from 72 stations around the Waitemata Harbour during June and July 1993 and again in January and February 1994. Between November 1994 and January 1995, they sampled a further 78 stations in the upper Waitemata Harbour above the harbor bridge. Samples were hand-hauled using a naturalist's dredge (10L capacity) from a 4m dinghy powered by a small outboard motor. Hayward et al. (1997) estimated that the dredge sampled 6 – 10cm into the sediment, and they report that it returned to the surface 90 – 110% full. The samples were washed over a 1mm sieve and the remaining contents fixed with preservative. All live organisms were hand-picked, identified and counted.

Effect of *Charybdis japonica* on the Waitemata Harbour benthic macroinvertebrate communities

To quantify the effect of *C. japonica* predation in the field, bottom samples were dredged from 17 stations in the Waitemata Harbour, Auckland on March 27 and 28, 2008 (Figure 3.1). Station locations were selected to give a broad coverage of the whole subtidal area of the harbour and to coincide with known locations of *C. japonica* trappings (Gust and Inglis 2006) and stations chosen by Hayward et al. (1997) from their reported GPS coordinates.

Due to the high unlikelihood that *C. japonica* consumed species under 4mm, samples were motor-hauled off the back of a 15m long research vessel using a naturalist's dredge, (56.5 x 24 x 28.5mm (l x w x h)) covered in 4mm mesh with an approximate capacity of 28L due to its pyramidal shape. Three replicate tows were completed at each station, and the contents of the dredge were sieved over 4mm mesh to remove mud and silt, placed into a 1L container and preserved in 70% isopropyl alcohol and Rose-Bengal. As I was most interested in mobile benthic macroinvertebrates, stones and other debris harbouring sedentary organisms were discarded. If the dredge removed more samples than could be put into a 1L container, a representative sample was randomly selected to fill the container. At some stations, the bottom substrate was a thick mat of the invasive Asian mussel *Musculista senhousia*; at these sites, the contents of the dredge could not be sieved and a sample was placed into a 1L container for later sieving. At the Leigh Marine Laboratory, samples were again sieved over a 4mm sieve, and all of the preserved organisms were hand-picked, identified and counted.

Differences in infaunal assemblages between surveys were investigated with PRIMER 6 (Clarke and Gorley 2006). Due to the high unlikelihood that *C. japonica* consumed species under 4mm, Hayward et al.'s (1997) data was restricted to those organisms that would be above this size. Macroinvertebrates were enumerated by species and this data was square-root transformed and

resemblance measured as Bray-Curtis similarity. Non-metric multidimensional scaling (MDS) was used to visualize the differences between sites and surveys and one-way ANOSIM was conducted to determine if there were significant differences in species assemblages between surveys. SIMPER analysis was also conducted on the square-root transformed data to determine which species were driving the differences between the surveys.

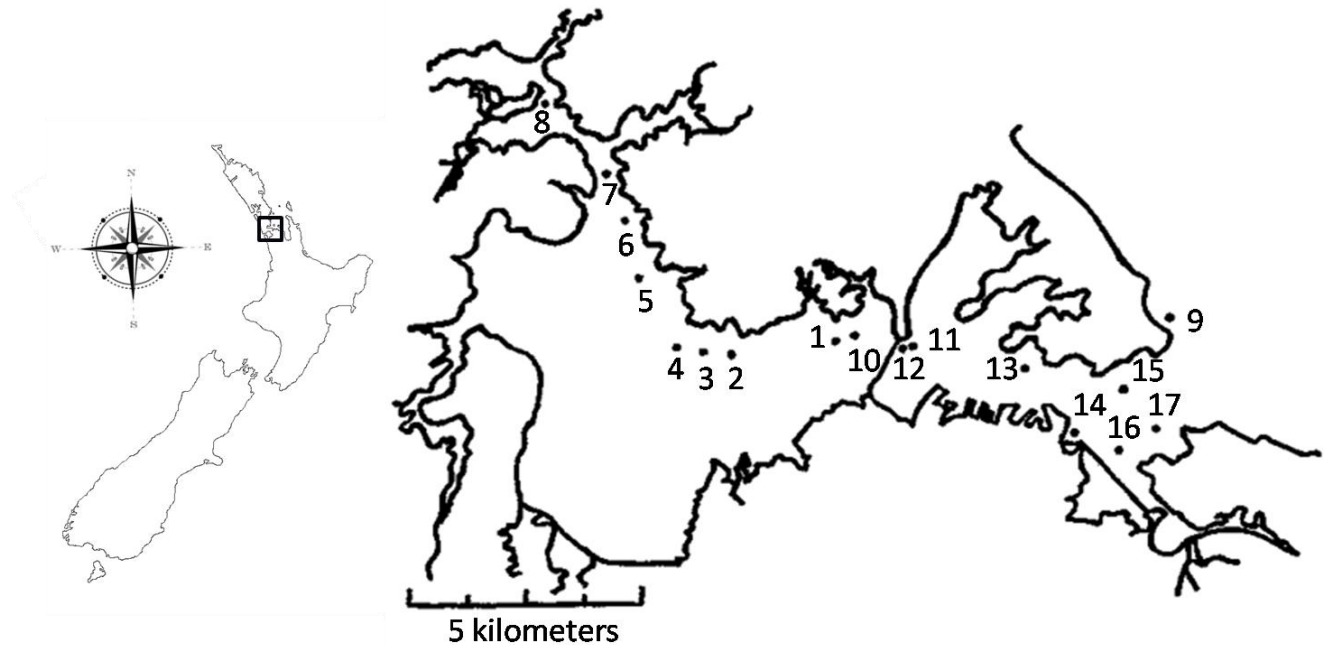


Figure 3.1 Location of the Waitemata Harbour study area, Auckland, New Zealand. Sampling stations were selected to give a broad coverage of the whole subtidal area of the harbor and to coincide with known locations of *Charybdis japonica* trappings (Gust and Inglis 2006) and stations chosen by Hayward et al. (1997) from their GPS coordinates.

Results

Experiment 1: Vulnerability of common marine invertebrates to *Charybdis japonica*

All six prey species offered to *C. japonica* were consumed irrespective of prey or predator size (Figure 3.2). *C. japonica* ate more *M. liliana* than any other prey species (Table 3.1). Only one *A. stutchburyi* (9mm) was consumed out of 18 offered, and it was eaten by a male *C. japonica* (CW 51mm). Prey items above 35mm were largely ignored by *C. japonica* (Figure 3.2, Table 3.1); however, the largest prey species consumed was a 40mm *C. gigas* (Table 3.1). As the carapace width of *C. japonica* increased, the prey size consumed also increased ($n=40$, $r_{(38)}=0.319$, $r^2=0.102$, $P=0.045$, Figure 3.2). There were no differences found between males and females of *C. japonica* in terms of percentage of prey consumed or of prey species consumed. However, even small *C. japonica* were able to eat all sizes of prey up to the 40mm maximum (Figure 3.2).

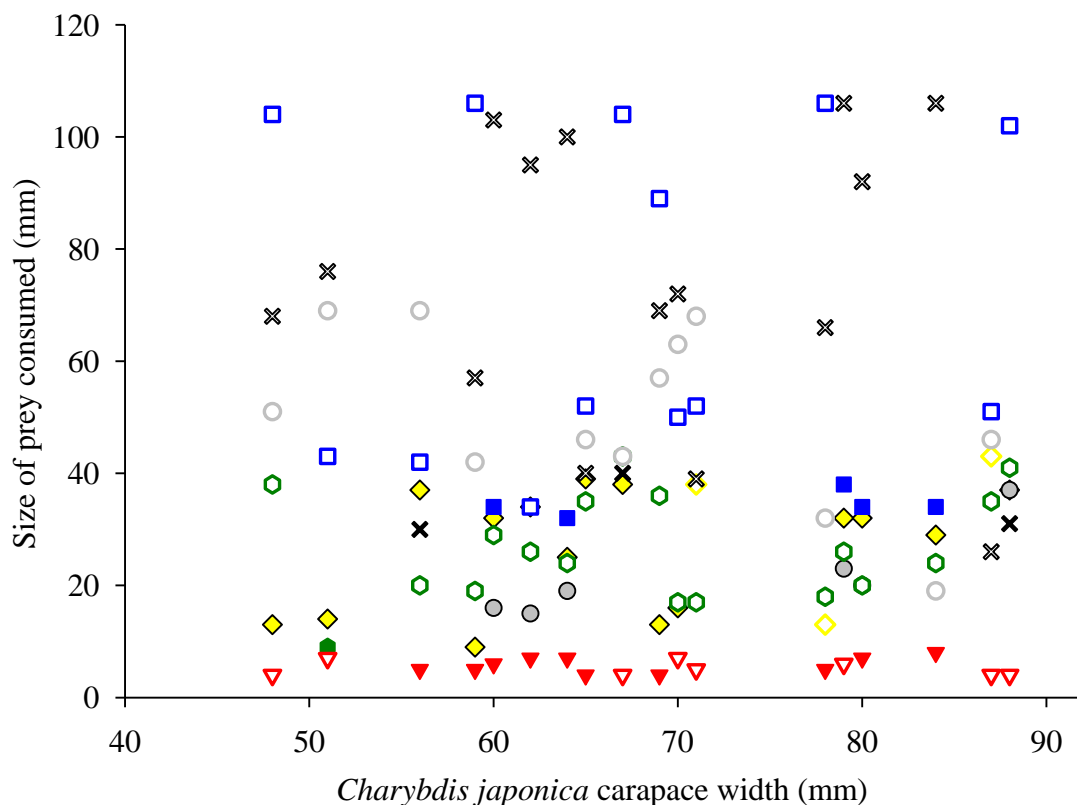


Figure 3.2 Sizes of all prey (mm) offered to *Charybdis japonica* in a 48 hour period as a function of crab carapace width (mm). Consumed prey items are represented as solid shapes, while uneaten prey items are open shapes. Color and shape key: *Austrovenus stutchburyi*, green hexagon; *Macomona liliana*, yellow diamond; *Perna canaliculus*, blue square; *Nucula hartvigiana*, red triangle; *Crassostrea gigas*, black x; *Paphies australis*, grey circle.

Table 3.1 Comparisons of prey size ranges offered to *Charybdis japonica*, percentage of prey items consumed and largest size consumed for each of the seven prey species. Each prey species was offered to 18 different *C. japonica*.

Prey species	Size range	Percent prey items consumed	Largest size consumed
<i>Austrovenus stutchburyi</i>	9 – 43 mm	6 %	9 mm
<i>Crassostrea gigas</i>	26 – 106 mm	17 %	40 mm
<i>Macomona liliana</i>	9 – 43 mm	83 %	39 mm
<i>Nucula hartvigiana</i>	4 – 8 mm	56 %	8 mm
<i>Paphies australis</i>	15 – 69 mm	33%	37 mm
<i>Perna canaliculus</i>	32 – 106 mm	28%	38 mm

Experiment 2: Prey size selection of three common marine invertebrates by *C. japonica*

There was a strong positive correlation between *C. japonica* carapace size and average prey size consumed for all three prey species, in which larger crabs were able to consume larger prey items (*P. canaliculus* (n=18, $r_{(16)}=0.812$, $r^2=0.660$, $P<0.001$), *P. australis* (n=18, $r_{(16)}=0.778$, $r^2=0.605$, $P<0.001$) and *M. liliana* (n=18, $r_{(16)}=0.774$, $r^2=0.599$, $P<0.001$); Figure 3.3). *C. japonica* favoured *P. australis*

and *P. canaliculus* in the 9 – 24mm size range and *M. liliana* in the 17 – 32mm size range (Figure 3.4, Table 3.2). For all three prey species, the 0 – 8mm size class was largely ignored (Figure 3.4, Table 3.2).

Female *C. japonica* preferred both *P. australis* and *P. canaliculus* in the 9 – 24mm size range and *M. liliana* in the 17 – 32mm size range (Table 3.2, Figure 3.4). Male *C. japonica*, however, showed a much broader prey size range preference (Figure 3.4, Table 3.2). For all three prey species, males ate more than females in the largest size range (33 – 40mm), while females ate more than males in the 9 – 16mm size range.

Nearly all *C. japonica* individuals (78%) examined were able to consume large *M. liliana* between 33 – 40mm, while only 39% and 33% of the same *C. japonica* individuals could consume large (33 – 40mm) *P. canaliculus* and *P. australis*, respectively. Overall, *C. japonica* consumed more *M. liliana* than either *P. australis* or *P. canaliculus* (Table 3.2). Small *C. japonica* (CW > 60mm, n=5) were unable to consume *P. australis* or *P. canaliculus* above 24mm. The largest number of individual prey eaten during the 4 day experiment by a single *C. japonica* was 47 *P. canaliculus* (Table 3.2). The largest *P. canaliculus* and *P. australis* consumed was 40mm, and the largest *M. liliana* eaten was a 38mm individual (Table 3.2).

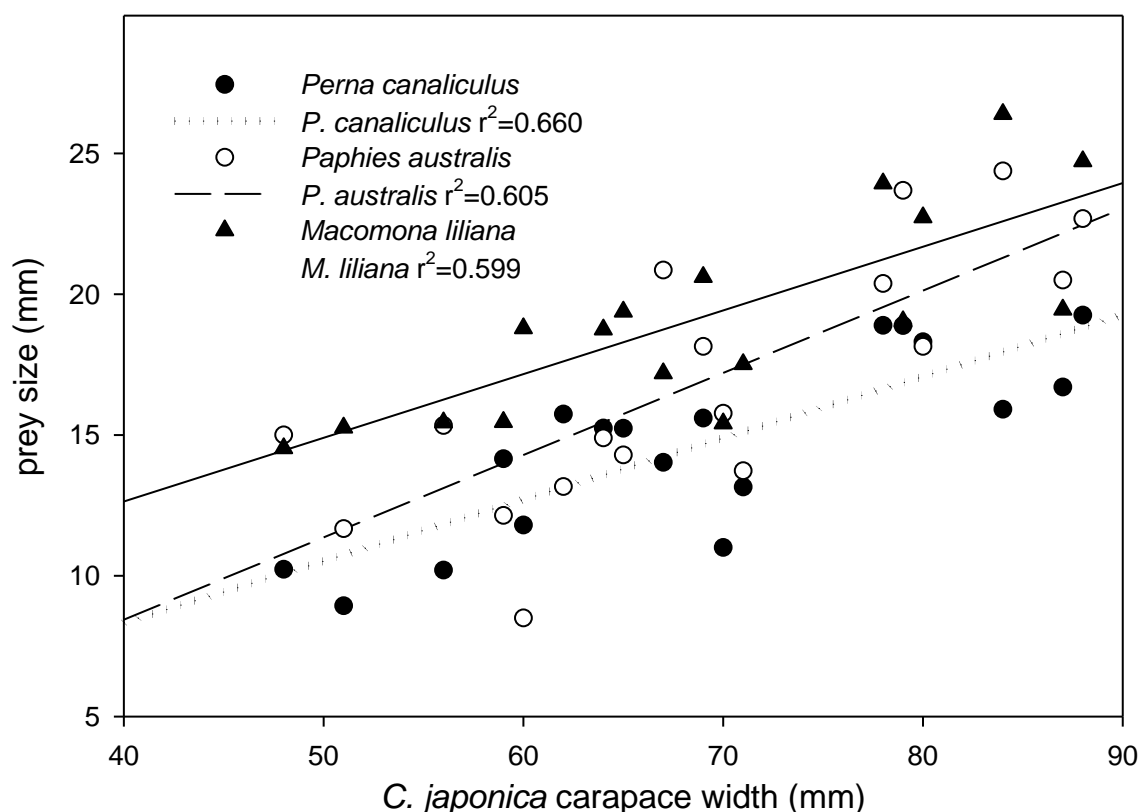


Figure 3.3 Average prey sizes consumed over a 4 day period for each of the three prey species as a function of *Charybdis japonica* carapace width. 18 *C. japonica* (8 females (CW 59 – 71mm) and 10 males (CW 48 – 88mm)) were used in this experiment.

Table 3.2 Average percent of prey species consumed of total prey items presented to *Charybdis japonica*, largest size consumed, largest number of individuals consumed and total number of individuals consumed over a 4 day period according to prey size class and separated into both males and females, only females (n=8) and only males (n=10).

Total Charybdis japonica

<i>Prey Species</i>	<i>0 – 8mm</i>	<i>9 – 16mm</i>	<i>17 – 24mm</i>	<i>25 – 32mm</i>	<i>33 – 40mm</i>	<i>Largest size consumed</i>	<i>Largest number of individuals consumed</i>	<i>Total number of individuals consumed</i>
<i>P. australis</i>	6.7 %	36.1 %	50.0 %	34.4 %	20.3 %	40 mm	22	292
<i>P. canaliculus</i>	19.3 %	48.6 %	50.0 %	38.9 %	20.3 %	40 mm	47	398
<i>M. liliana</i>	12.7 %	38.8 %	70.6 %	73.3 %	49.9 %	38 mm	37	416

Female Charybdis japonica

<i>Prey Species</i>	<i>0 – 8mm</i>	<i>9 – 16mm</i>	<i>17 – 24mm</i>	<i>25 – 32mm</i>	<i>33 – 40mm</i>	<i>Largest size consumed</i>	<i>Largest number of individuals consumed</i>	<i>Total number of individuals consumed</i>
<i>P. australis</i>	12.0 %	40.6 %	45.0 %	20.0 %	8.3 %	37 mm	22	135
<i>P. canaliculus</i>	17.5 %	52.5 %	55.0 %	32.5 %	4.1 %	33 mm	34	177
<i>M. liliana</i>	10.5 %	43.1 %	78.8 %	80.0 %	41.5 %	38 mm	37	195

Male Charybdis japonica

<i>Prey Species</i>	<i>0 – 8mm</i>	<i>9 – 16mm</i>	<i>17 – 24mm</i>	<i>25 – 32mm</i>	<i>33 – 40mm</i>	<i>Largest size consumed</i>	<i>Largest number of individuals consumed</i>	<i>Total number of individuals consumed</i>
<i>P. australis</i>	2.4 %	32.5 %	54.0 %	46.0 %	30.0 %	40 mm	22	157
<i>P. canaliculus</i>	20.8 %	45.5 %	46.0 %	44.0 %	33.2 %	40 mm	47	221
<i>M. liliana</i>	14.4 %	35.4 %	64.0 %	68.0 %	56.7 %	38 mm	37	221

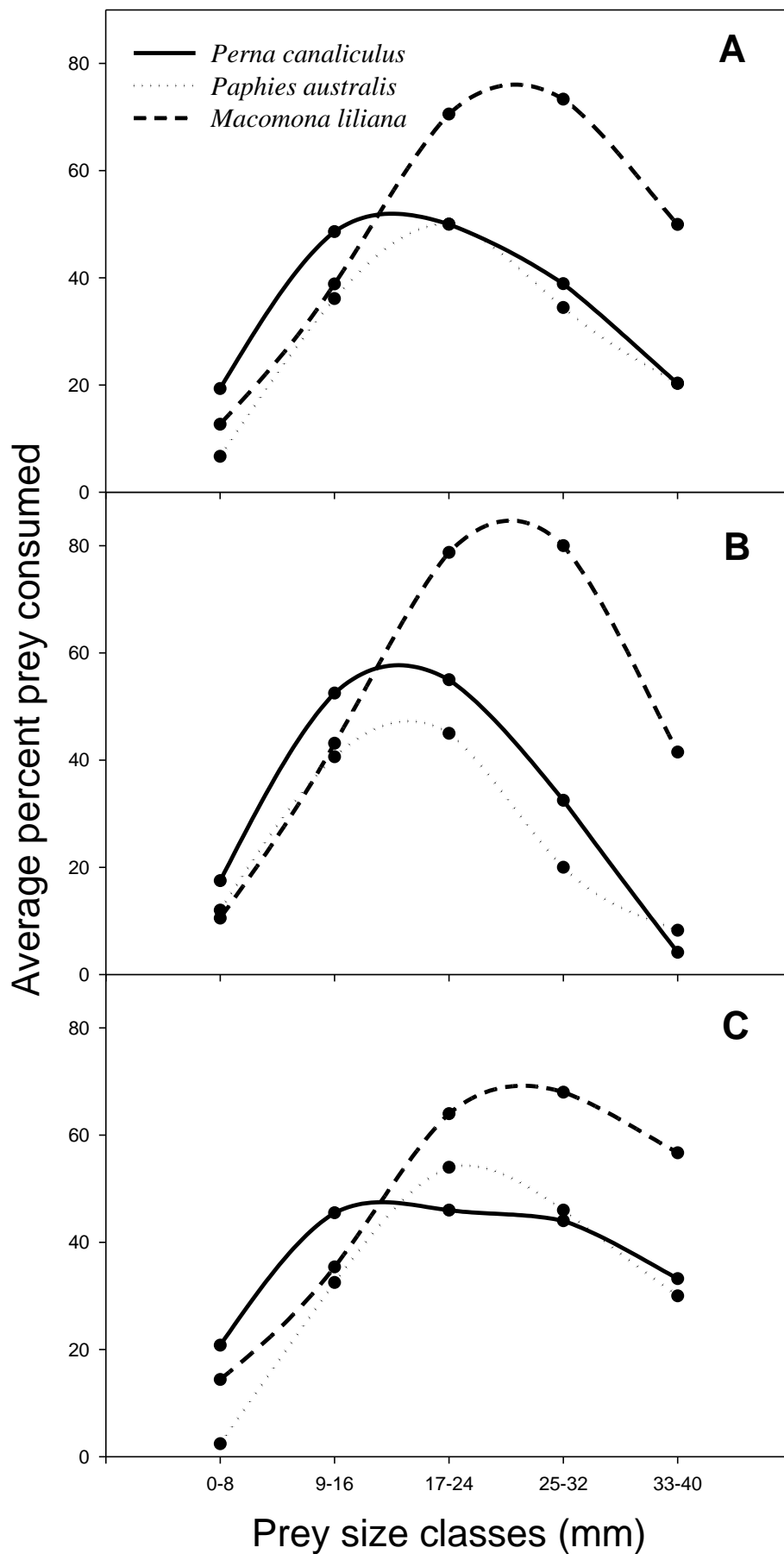


Figure 3.4 Average percent of all three prey species consumed by *Charybdis japonica* fit as a multiple spline curve and separated by the 5 prey size classes (mm) and by all individuals (A), only females (B) and only males (C).

Experiment 3: The influence of sediment on predation rates by *Charybdis japonica*

C. japonica ate less *P. australis* when sediment was present (PERMANOVA, $F_{(1, 104)}=5.8782$, $P=0.0164$, Table 3.4). The interaction of sediment and the sex of the crab impacted the average percent of *P. australis* that *C. japonica* consumed (PERMANOVA, $F_{(1, 104)}=9.7987$, $P=0.002$, Table 3.4), but this was driven by the decrease of the average percentage of *P. australis* consumed by males (pair-wise PERMANOVA, $t_{(64)}=4.3998$, $P<0.001$). Irrespective of sex, *C. japonica* preferred *P. australis* in the 16 – 25mm range without the added protection of sediment for prey burial; when experiments were conducted with sediment, *C. japonica* preferred *P. australis* in the largest size range of 26 – 30mm (Figure 3.5, Table 3.3). *P. australis* prey items of 30mm were consumed by seven different *C. japonica* (38.9% of the tested population) of both sexes (CW 67 – 87mm) in aquaria lacking sediment; in experiments with sediment four different *C. japonica* (33% of the tested population) of both sexes (CW 58 – 79mm) ate 30mm *P. australis*. Only one male (CW 79mm) consumed more than 30 individuals of the total of 42 prey items available in the no-sediment experiment (Table 3.3). Four of the six *C. japonica* equal to or over 67mm CW in the sediment treatment did not consume any *P. australis*.

C. japonica consumed less *M. liliana* when the bivalves were able to bury (PERMANOVA, $F_{(1, 104)}=25.009$, $P=0.0002$, Table 3.4). Without sediment, *C. japonica* preferred *M. liliana* in the 16 – 30mm range but in the presence of sediment this preference range decreased to include prey in the size range of 16 – 25mm (Figure 3.5, Table 3.3). The largest *M. liliana* (30mm) was consumed by eight different *C. japonica* (44.4% of the tested population) of both sexes (CW 59 – 87mm) in aquaria lacking sediment while five crabs in the sediment treatment (41.7% of the tested population) of both sexes (CW 56 – 68mm) ate 30mm *M. liliana*. In the absence of sediment, all crabs tested consumed at least one *M. liliana* above 25mm; however, only one male (CW 87mm) consumed more than 35 individuals of the total of 42 prey items available (Table 3.3). In the presence of sediment, only one female (CW 61mm) consumed more than 25 individuals of the total of 42 prey items available (Table 3.3).

Both sediment (PERMANOVA, $F_{(1, 128)}=12.436$, $P=0.0012$, Table 3.4) and the sex of *C. japonica* (PERMANOVA, $F_{(1, 128)}=8.3118$, $P=0.006$, Table 3.4) impacted the average percent of *P. canaliculus* eaten. Without sediment, *C. japonica* preferred *P. canaliculus* in the 16 – 25mm range; *C. japonica* preferred a much smaller prey size range in sediment treatments, preferring 10 – 20mm *P. canaliculus* (Figure 3.5, Table 3.3). Male *C. japonica* consistently consumed more *P. canaliculus* than females irrespective of whether sediment was available or not. The largest *P. canaliculus* (30mm) were consumed by seven different *C. japonica* (38.9% of the tested population) of both sexes (CW 64 – 88mm) in the absence of sediment, while nine different *C. japonica* of both sexes (50% of the tested

population) and CW of 63 – 96mm were able to consume 30mm *P. canaliculus* when sediment was available. While two male crabs (CW 96 and 95mm) consumed all 42 *P. canaliculus* offered to them in the presence of sediment, only two males (CW 79 and 88mm) consumed more than 35 individuals of the total of 42 prey items available in the absence of sediment (Table 3.3).

C. japonica were able to consume the largest prey items available of all three prey species (30mm) no matter if sediment could be used as burial refuge (Table 3.3). *C. japonica* consumed a higher percentage of both *P. australis* and *M. liliana* when sediment was not available to the prey species as a burial refuge; crabs ate more *P. canaliculus* in the presence of sediment (Figure 3.5, Table 3.3).

Table 3.3 Average percent of prey species consumed of total prey items presented to *Charybdis japonica*, largest size consumed, largest number of individuals consumed and total number of individuals consumed over a 4 day period according to prey size class. Two values are reported and indicate the result for the without sediment / with sediment experiment.

<i>Prey Species</i>	<i>10 – 15mm</i>	<i>16 – 20mm</i>	<i>21 – 25mm</i>	<i>26 – 30mm</i>	<i>Largest size consumed</i>	<i>Largest number of individuals consumed</i>	<i>Total percent of individuals consumed</i>
<i>P. australis</i>	27.7% / 9.6%	46.4% / 19.5%	39.9% / 19.2%	28.3% / 26.7%	30 / 30	37 / 22	35.2% / 18.3%
<i>M. lilana</i>	27.8% / 21.8%	55.7% / 26.0%	60.5% / 25.7%	56.8% / 15.0%	30 / 30	36 / 25	47.9% / 21.2%
<i>P. canaliculus</i>	32.9% / 62.9%	45% / 65.6	40.6% / 52.2%	33.9% / 38.9%	30 / 30	37 / 42	37.8% / 55.2%

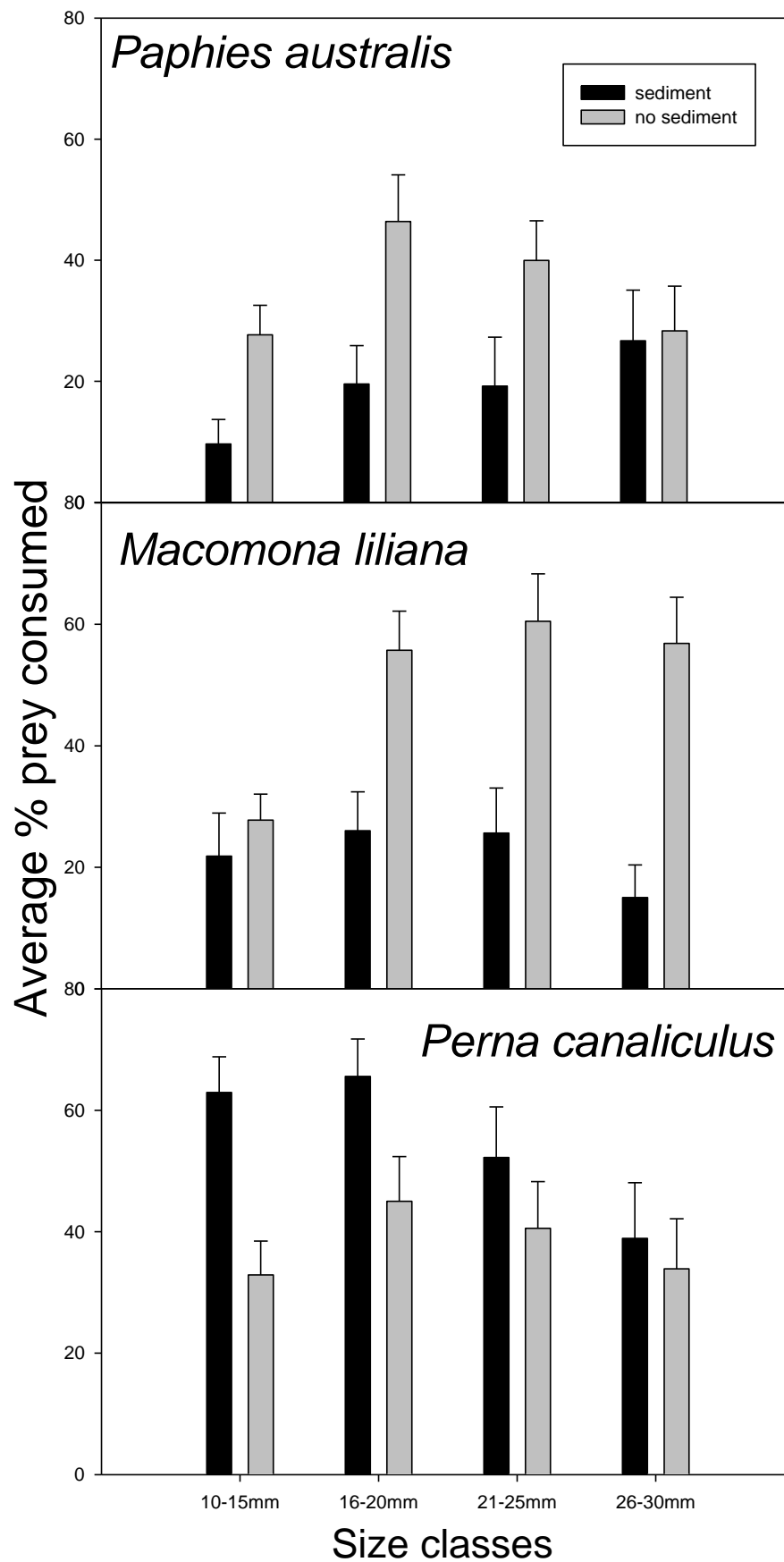


Figure 3.5 Average percentage of prey items (\pm SE) consumed of total prey items in each size class presented to *Charybdis japonica* over a 24 hour period as a function of sediment availability.

Table 3.4 Summary of permanova tests used to describe the proportion of *Paphies australis*, *Macomona liliana* or *Perna canaliculus* that *Charybdis japonica* consumed of the total prey available. Asterisks indicate a significant effect.

<i>Prey species</i>	<i>Factor(s)</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>
<i>Paphies australis</i>	Sediment	1	4060.4	5.8782	0.0164 *
	Sex	1	1974.5	2.8585	0.0974
	Size class	3	1038.3	1.5031	0.2248
	Sediment x sex	1	6768.5	9.7987	0.002 *
	Sediment x size class	3	827.56	1.198	0.3242
	Sex x size class	3	127.88	0.1851	0.9092
	Sediment x sex x size class	3	294.42	0.4262	0.7232
<i>Macomona liliana</i>	Sediment	1	17569	25.009	0.0002 *
	Sex	1	269.79	0.3840	0.5352
	Size class	3	1461.5	2.0804	0.1104
	Sediment x sex	1	2281.3	3.2473	0.0754
	Sediment x size class	3	1570.4	2.2355	0.0944
	Sex x size class	3	299.82	0.4268	0.7362
	Sediment x sex x size class	3	357.6	0.5090	0.6734
<i>Perna canaliculus</i>	Sediment	1	12167	12.436	0.0012 *
	Sex	1	8132.4	8.3118	0.006 *
	Size class	3	2044.8	2.0899	0.098
	Sediment x sex	1	72.267	7.39E-2	0.7728
	Sediment x size class	3	887.93	0.9075	0.4416
	Sex x size class	3	835.6	0.8540	0.4658
	Sediment x sex x size class	3	203.78	0.2083	0.8938

Field Experiments

Exclusion experiment

One male *C. japonica* escaped from the caged treatment; sediment cores from underneath that replicate were disregarded in all subsequent analyses.

Species present underneath the plots, irrespective of cage treatment, included those from 15 different Polychaeta families, one Sipuncula taxa, nine Bivalvia species, four Anomura species, two Gastropoda species, three Decapoda species, one Isopoda species and one Echinodermata species. Combining the abundance of all nine bivalve species for each cage, there was no difference in their abundance due to cage treatment (ANOVA, $F_{(3, 23)}=0.856$, $P=0.478$) or the presence of *C. japonica* (t-test, $t_{(25)}=-1.573$, $P=0.128$). Three of the six bivalve species used to test the vulnerability of common marine invertebrates to predation by *C. japonica* in laboratory experiments were found underneath the cages from the field experiment (*Paphies australis*, *Macomona liliana*, and *Nucula hartvigiana*). However, there were no discernable changes in *P. australis*, *M. liliana*, or *N. hartvigiana* abundances

between the cage treatments, nor were abundances of these prey species affected by the presence or absence of *C. japonica*.

When the four treatments were compared between groups, there was no effect of cage on total invertebrate taxa abundance (ANOVA, $F_{(3, 23)}=0.634$, $P=0.601$, Figure 3.6) or taxonomic richness (ANOVA, $F_{(3, 23)}=0.410$, $P=0.748$). The presence or absence of *C. japonica* had no impact on total taxa abundance (ANOVA, $F_{(1, 25)}=1.809$, $P=0.191$, Figure 3.6) or richness (ANOVA, $F_{(1, 25)}=1.220$, $P=0.280$, Figure 3.6). The benthic community structure was not affected by the presence of *C. japonica* ($R= -0.026$, $P=0.639$, Figure 3.7). Due to the short duration of the experiment, the apparent increase in the average number of total macroinvertebrates from sediment cores underneath those cages with *C. japonica* is assumed to be due to natural variability of the soft sediment populations, with the randomly allocated treatments apparently falling by chance on patches with systematically varying densities of prey.

The five most abundant prey species or family of species found underneath the cages in decreasing order of abundance were *Nucula hartvigiana*, *Purpuricardia purpurata*, Phoronidae, Maldanidae and Nephytidae. The presence or absence of *C. japonica* had no impact on the abundances of these five taxa (ANOVA, $F_{(1, 25)}=1.381$, $P=0.251$, Figure 3.8). When the four cage treatments were compared between groups, there was no effect of cage on the total numbers of the five most abundant prey species (ANOVA, $F_{(3, 23)}=0.561$, $P=0.646$, Figure 3.8).

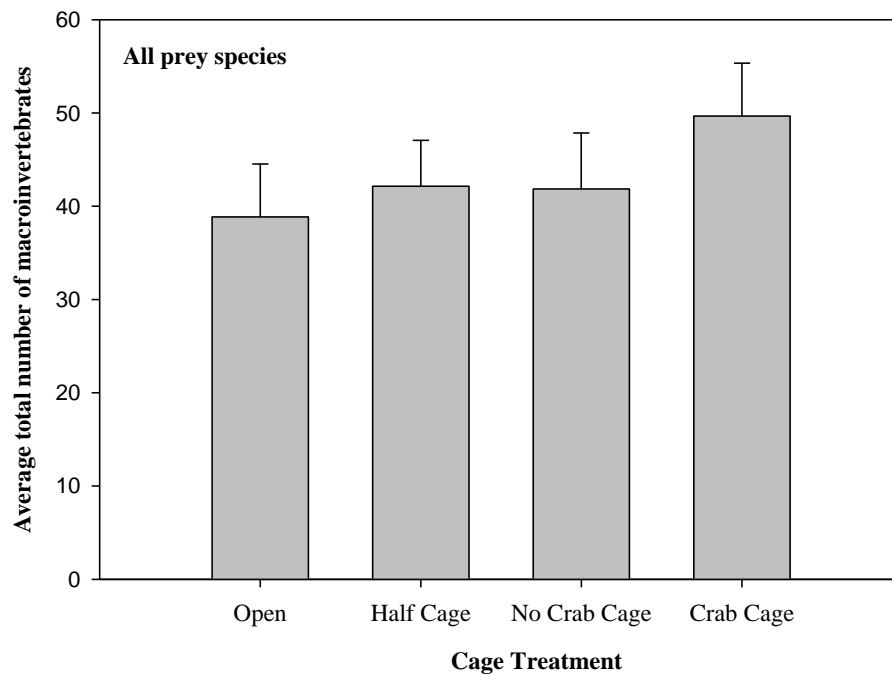


Figure 3.6 Average total abundance (\pm SE) of all prey species present in the sediment samples taken from underneath each of the four cage treatments. Combining all cages for each treatment, the approximate area of sediment sampled for each treatment was 0.5m^3 .

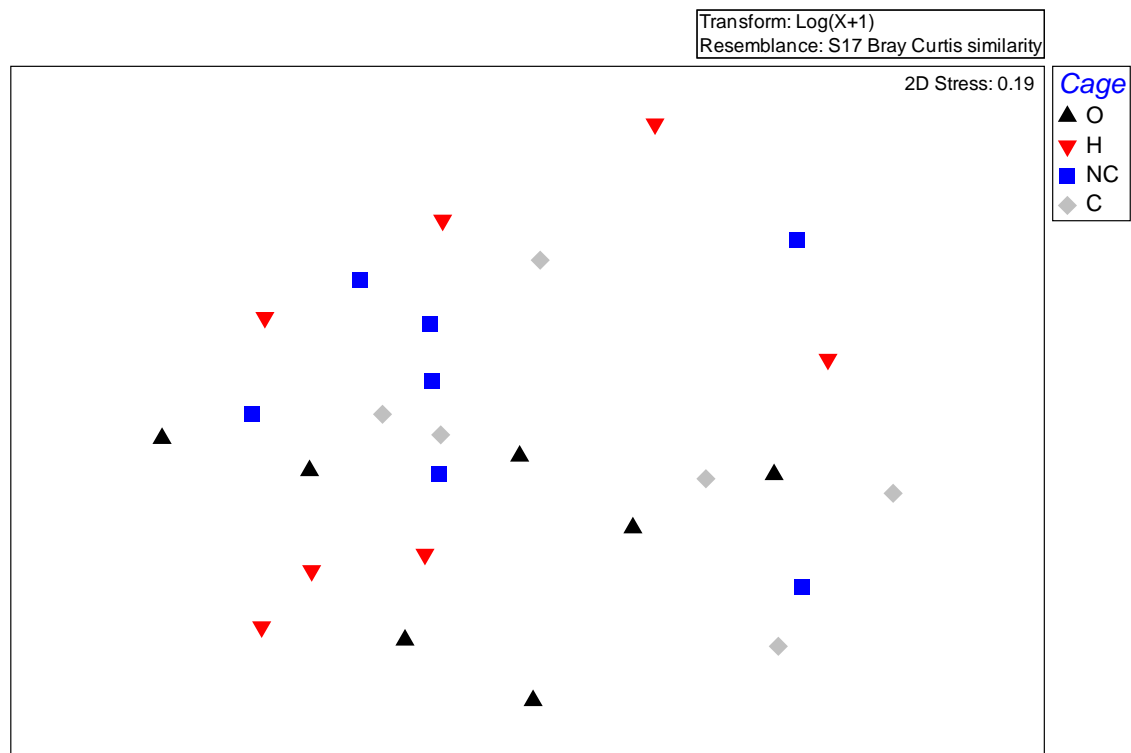


Figure 3.7 MDS plot using Bray-Curtis similarity based on log transformed abundances of 36 macroinvertebrate species from open plots (O), partial cage plots (H), whole caged plots lacking *Charybdis japonica* (NC) and whole caged plots with a single male *C. japonica* (C).

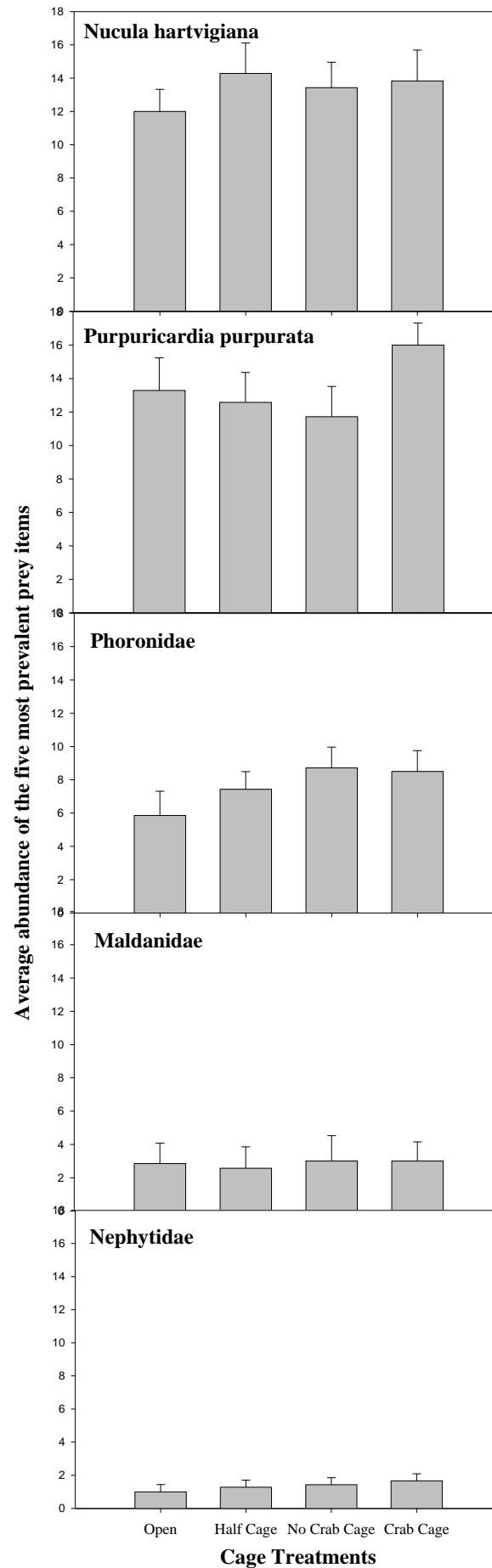


Figure 3.8 Average abundance (\pm SE) of each of the five most prevalent species found in the sediment from underneath the four cage treatments.

Effect of *Charybdis japonica* on the Waitemata Harbour benthic macroinvertebrate communities

Comparing infaunal assemblages of those species $\geq 4\text{mm}$, the average dissimilarity between Hayward et al. (1997)'s survey and this survey was 82%, showing the two surveys to be quite distinct from one another ($R=0.442$, $P=0.001$, Figure 3.9). This was characterized by a high abundance of the non-native bivalve species *Musculista senhousia* and *Theora lubrica*, brittle stars (Ophiuroidea), and the Spionidae polychaete family in the 2008 samples and a higher abundance of the Capitellidae polychaete family in the 1993/1994 samples (Table 3.5). Of the top 10 species that contributed to the overall dissimilarity between the two surveys, *C. japonica* most likely preys upon the four bivalve species, which are *M. senhousia*, *T. lubrica*, *Nucula* sp., and *Leptomya retiara*, as well as *Paguristes setosus* (Table 3.5).

Considering just the 34 bivalve species $\geq 4\text{mm}$ found in both surveys, the average dissimilarity between the groups was 86.8%, which was driven by *T. lubrica*, *M. senhousia*, *Nucula* sp., *L. retiara*, and *Arthritica bifurca*, in that order ($R=0.299$, $P=0.001$). *T. lubrica* and *M. senhousia* were more abundant in the 2008 survey while *Nucula* sp., *L. retiara*, and *A. bifurca* were more abundant during the 1990's. It is possible that *C. japonica* could consume these species, but this was not experimentally tested. Four of the six bivalve species used to test the vulnerability of common marine invertebrates to predation by *C. japonica* in laboratory experiments were found during the two surveys (*Macomona liliiana*, *Nucula* sp., *Crassostrea gigas*, and *Austrovenus stutchburyi*). These bivalve species also had a high average dissimilarity (82.4%) that contributed to the overall significant difference in these bivalve species communities between the two sampling periods ($R=0.143$, $P=0.008$). The dissimilarity between the surveys was mainly driven by the decrease in populations of *Nucula* sp. and the increase of the populations of *C. gigas* in the 2008 survey.

When I compared the same sites sampled in the 1990's to those sampled in 2008, overall, there were 20 invertebrate taxa present in the 1990's survey that were not found at any site in the 2008 sampling (Table 3.6). Conversely, 45 invertebrate taxa and one vertebrate from the Tripterygiidae family were identified in the 2008 survey but did not appear at any site from the 1990's sampling period (Table 3.6). Only the invasive Asian date mussel *M. senhousia* increased in large numbers (<50 individuals) between the two sampling periods. Although Hayward et al. (1997) did not identify *M. senhousia* in their summer sampling, almost 10,000 individuals were recorded in the 2008 survey.

Of those species found in the 1990's survey, 13 invertebrate taxa increased their range in the 2008 survey by appearing in at least two times as many sites than in Hayward et al. (1997). Six

invertebrate taxa have decreased their range in 2008 by appearing in at least half the number of sites that they were recorded at during the 1990's. Of these six invertebrate taxa, *C. japonica* could possibly consume the bivalves *A. bifurca* and *L. retiara* as well as the crabs *Halicarcinus* sp. and *Macrophthalmus hirtipes*.

Species present in both surveys but with an apparent significant increase in abundance (>50 individuals) since the 1990's include members of the Spionidae and Syllidae families, the order Ophiuroidea, the phylum Sipuncula, and the invasive bivalve *T. lubrica* (Table 3.6). Members of the Capitellidae, Opheliidae, and Terebellidae families, the class Holothuroidea, the gastropod *Maoricolpus roseus*, and the bivalves *L. retiara*, *A. bifurca* and *Nucula* sp. showed a significant decrease in abundance in 2008 (Table 3.6).

Another way to examine the differences in macrofaunal community structure is to show the proportional change in species abundance between the two survey periods. Using the formula (\log_{10} (Hayward et al. (1997) abundance) / \log_{10} (2008 survey abundance)) for each species, this method better illustrates the magnitude of change in the community. Those species that were found to show the largest degree of proportional change were *L. retiara*, Hesionidae, *Halicarcinus cookii*, and *M. hirtipes*; all of these taxa showed dramatic decreases in abundance from 1993/1994 to 2008 (Table 3.7). Of these, *C. japonica* is thought to possibly consume *L. retiara*, *H. cookii*, and *M. hirtipes*.

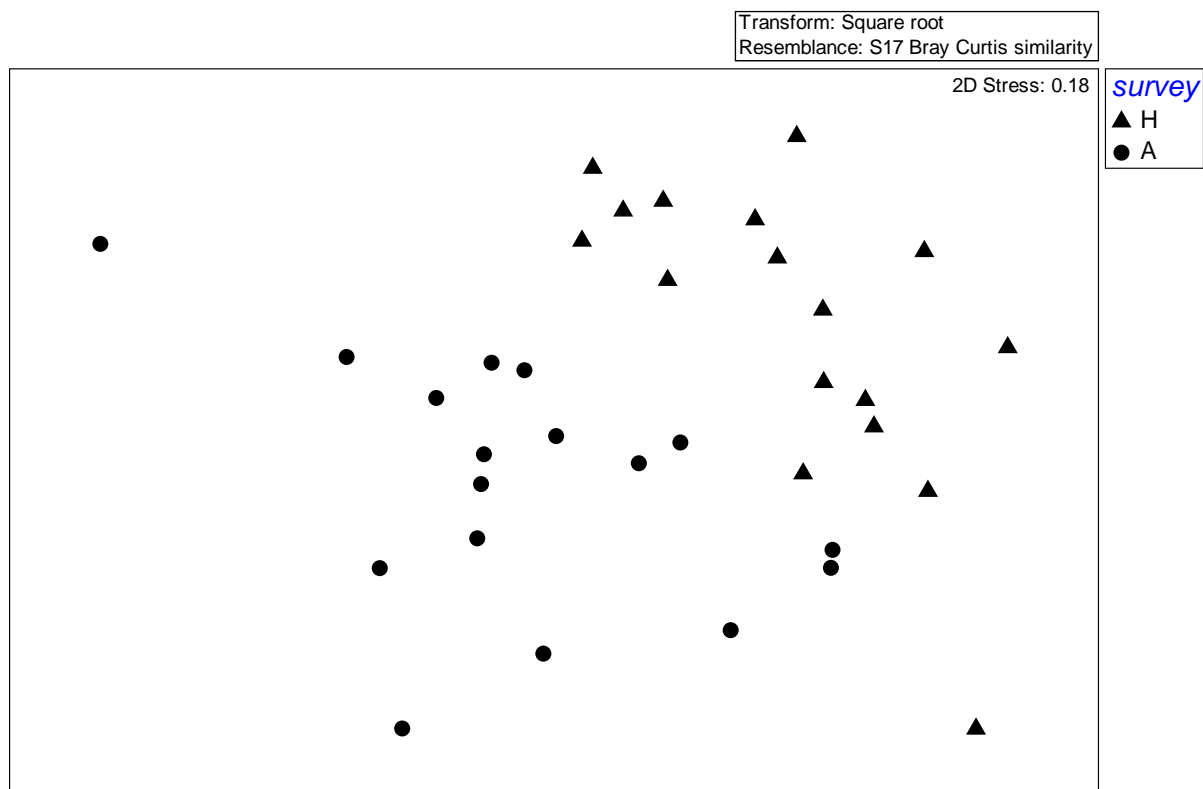


Figure 3.9 MDS plot using Bray-Curtis similarity based on square-root transformed abundances of macroinvertebrate species ≥ 4 mm from the Hayward et al. (1997) survey (H) and the 2008 survey (A).

Table 3.5 Top 10 species $\geq 4\text{mm}$ driving the differences between the Hayward et al. (1997) survey and the 2008 survey determined by SIMPER analysis from the square-root transformed data.

<i>Species</i>	<i>1990's Average Abundance</i>	<i>2008 Average Abundance</i>	<i>Average Dissimilarity</i>	<i>Dissimilarity Standard Deviation</i>
<i>Musculista senhousia</i>	0.00	4.39	4.66	0.39
Ophiuroidea	2.07	3.72	3.92	1.11
Spionidae	2.04	2.26	3.68	0.81
<i>Theora lubrica</i>	1.20	2.11	3.56	0.75
Capitellidae	3.26	0.27	3.55	1.42
Cirratulidae	2.29	0.48	2.59	1.12
<i>Paguristes setosus</i>	0.00	2.17	2.50	1.00
<i>Nucula</i> sp.	2.11	0.91	2.38	1.12
<i>Leptomya retiara</i>	1.66	0.10	1.98	0.75
Syllidae	0.46	1.56	1.79	1.05

Table 3.6 Total abundance and the difference between surveys of all invertebrates and vertebrates $\geq 4\text{mm}$ listed by the degree of change (Hayward et al. 1997). Positive degrees of change indicate higher abundances in the 2008 survey; negative values indicate higher abundances in 1993/1994. Prevalence, as denoted by number of sites in which the species was found, is also compared between the two surveys. Those prey items thought to be consumed by *Charybdis japonica* are highlighted in bold.

Taxa	1990's Total	2008 Total	Degree of change	1990's Prevalence	2008 Prevalence
<i>Musculista senhousia</i>	0	2287.33	2287.33	0	11
Spionidae	119	400.67	281.67	15	10
Ophiuroidea	146	381.33	235.33	12	15
Sipuncula	3	205	202	2	9
<i>Paguristes setosus</i>	0	167.33	167.33	0	12
<i>Theora lubrica</i>	112	231	119	7	10
Syllidae	18	79.67	61.67	4	12
Micro-Gastropoda	3	41	38	1	6
Thalassinidea	3	28	25	3	8
Spirobus	0	22.33	22.33	0	8
Serpulidae	2	20.67	18.67	1	9
Ostracoda	7	22.33	15.33	5	10
<i>Crassostrea</i> sp.	0	12.67	12.67	0	4
<i>Limaria orientalis</i>	17	29	12	4	10
<i>Anthopleura aureolata</i>	2	12.67	10.67	1	6
Nematoda	0	9.67	9.67	0	11
Platyhelminths	0	8.67	8.67	0	9
<i>Fellaster zelandiae</i>	0	8	8	0	2
Alpheidae	13	20	7	5	12
<i>Venercardia purpurata</i>	9	13	4	6	9
<i>Amalda australis</i>	0	4	4	0	1
Cirripedia	0	3.67	3.67	0	5
<i>Coscinasterias calamaria</i>	0	3.67	3.67	0	5
Pycnogonida	6	9.67	3.67	2	7
<i>Paguristes subpilosus</i>	0	2.67	2.67	0	3
<i>Solemya parkinsonii</i>	0	2.33	2.33	0	4

Eunicidae	0	2	2	0	4
<i>Cominella adspersa</i>	0	2	2	0	4
<i>Anomia trigonopsis</i>	0	1.67	1.67	0	4
<i>Austrovenus stutchburyi</i>	0	1.67	1.67	0	3
<i>Macomona liliana</i>	0	1.67	1.67	0	2
<i>Pyromaia tuberculata</i>	0	1.67	1.67	0	4
<i>Patiriella regularis</i>	3	4.67	1.67	2	9
Anomiidae	0	1.33	1.33	0	3
Philinidae	0	1.33	1.33	0	3
Phoronidae	1	2	1	1	2
<i>Myadora striata</i>	0	1	1	0	1
Opisthobranchia	0	1	1	0	3
<i>Pellicaria vermis</i>	0	1	1	0	3
<i>Petrolisthes elongatus</i>	1	2	1	1	1
Majidae	0	1	1	0	1
Chaetopteridae	0	0.67	0.67	0	2
<i>Soletellina nitida</i>	0	0.67	0.67	0	2
<i>Amalda macronata</i>	0	0.67	0.67	0	1
<i>Eationella limbata</i>	0	0.67	0.67	0	1
<i>Zeacolpus</i> sp.	0	0.67	0.67	0	2
Decapoda	0	0.67	0.67	0	1
<i>Helice crassa</i>	0	0.67	0.67	0	1
Pilargidae	0	0.33	0.33	0	1
<i>Gari</i> sp.	0	0.33	0.33	0	1
Mactridae	0	0.33	0.33	0	1
<i>Myadora boltoni</i>	0	0.33	0.33	0	1
Tellinidae	0	0.33	0.33	0	1
<i>Austromitra rubiginosa</i>	0	0.33	0.33	0	1
<i>Bulla quoyi</i>	0	0.33	0.33	0	1
Calyptraeidae	0	0.33	0.33	0	1
Retusidae	0	0.33	0.33	0	1
Stiligeridae	0	0.33	0.33	0	1
<i>Zeacumantus lutulentus</i>	0	0.33	0.33	0	1
<i>Pilumnus novaezelandiae</i>	0	0.33	0.33	0	1
Pinnotheridae	0	0.33	0.33	0	1
Tripterygiidae	0	0.33	0.33	0	1
Anthozoa	0	0.33	0.33	0	1
<i>Sigapatella novaezelandiae</i>	3	3	0	3	3
Porifera	0.67	0.67	0	1	1
Polynoidae	15	14.67	-0.33	7	13
Sabellariidae	2	1.67	-0.33	2	3
Cumacea	3	2.67	-0.33	3	4
Magelonidae	1	0.67	-0.33	1	1
<i>Modiolarca impacta</i>	1	0.67	-0.33	1	2
<i>Corbula zelandica</i>	6	5.33	-0.67	4	5
<i>Chlamys zelandica</i>	1	0.33	-0.67	1	1
<i>Lithophaga truncata</i>	1	0	-1	1	0

<i>Zenatia acinaces</i>	1	0	-1	1	0
<i>Xymene gouldi</i>	1	0	-1	1	0
<i>Paguristes barbatus</i>	1	0	-1	1	0
<i>Echinocardium cordatum</i>	1	0	-1	1	0
<i>Ruditapes largillierti</i>	3	1.67	-1.33	3	2
Scablibregmatidae	2	0	-2	2	0
<i>Atrina zelandicus</i>	2	0	-2	1	0
Oweniidae	4	1.67	-2.33	3	2
<i>Halicarcinus cookii</i>	4	1.33	-2.67	3	3
<i>Pagurus</i> sp.	3	0.33	-2.67	1	1
Sigalionidae	3	0	-3	3	0
<i>Borneola reniformis</i>	3	0	-3	3	0
<i>Hiatella arctica</i>	3	0	-3	2	0
Phyllodocidae	6	1.67	-4.33	4	3
Micro-Bivalvia	7	2.67	-4.33	2	3
Glyceridae	12	7.33	-4.67	8	9
Maldanidae	9	4	-5	3	5
<i>Notomithrax minor</i>	6	1	-5	4	3
Tanaidacea	5	0	-5	3	0
<i>Zegalerus tenuis</i>	11	5.67	-5.33	4	5
Orbiniidae	10	4	-6	5	5
Mysida	6	0	-6	4	0
Pectinariidae	16	9.67	-6.33	8	13
Lumbrineridae	15	8.33	-6.67	6	10
<i>Pleuromeris zelandica</i>	7	0	-7	3	0
Nereididae	11	1.67	-9.33	4	4
<i>Dosina</i> sp.	13	2	-11	5	4
<i>Felaniella zelandica</i>	17	6	-11	6	8
Nephtyidacea	15	3.67	-11.33	7	6
<i>Halicarcinus</i> sp.	12	0.67	-11.33	4	2
Nemertea	23	8.33	-14.67	8	10
<i>Petrolisthes novaezelandiae</i>	17	0	-17	2	0
<i>Melliteryx parva</i>	18	0	-18	4	0
Paraonidae	24	5.67	-18.33	6	4
Dor	19	0	-19	6	0
<i>Tawera spissa</i>	20	0	-20	7	0
Cossuridae	21	0	-21	5	0
Ampharetidae	22	0	-22	6	0
<i>Macrophthalmus hirtipes</i>	28	2	-26	11	3
Flabelligeridae	30	3	-27	2	2
Goniadidae	37	4	-33	10	4
Hesionidae	36	2	-34	4	3
Chitonidae	50	10	-40	3	10
Sabellidae	57	10.67	-46.33	8	10
Opheliidae	61	8.33	-52.67	9	5
<i>Arthritica bifurca</i>	60	3.33	-56.67	10	2
Holothurians	77	14.33	-62.67	10	9

<i>Maoricolpus roseus</i>	153	57.67	-95.33	4	5
<i>Leptomya retiara</i>	104	1.33	-102.67	11	2
Terebellidae	144	3	-141	10	6
Cirratulidae	173	16.67	-156.33	12	7
<i>Nucula</i> sp.	188	24	-164	9	12
Capitellidae	273	3.67	-269.33	16	6

Table 3.7 Proportional change of infaunal macroinvertebrates and vertebrates ≥ 4 mm between surveys. Proportional change was calculated as \log_{10} (Hayward et al. (1997) abundance) / \log_{10} (2008 survey abundance). In the left column, positive proportional changes indicate those species that decreased in abundance from 1993/1994; negative proportional changes indicate species that have increased in abundance. Those with zero proportional changes have not changed in their abundance. In the right column are those species that were not present in one of the surveys, hence their extremely large proportional change. Those prey items thought to be consumed by *Charybdis japonica* are highlighted in bold.

Taxa	Proportional change	Taxa	Proportional change
<i>Leptomya retiara</i>	16.14	<i>Musculista senhousia</i>	∞
Hesionidae	5.17	<i>Paguristes setosus</i>	∞
<i>Halicarcinus cookii</i>	4.82	Spirobus	∞
<i>Macrophthalmus hirtipes</i>	4.81	Ampharetidae	∞
Nereididae	4.69	Cossuridae	∞
Terebellidae	4.52	<i>Tawera spissa</i>	∞
Capitellidae	4.32	Dor	∞
<i>Dosina</i> sp.	3.70	<i>Melliteryx parva</i>	∞
Phyllodocidae	3.51	<i>Petrolisthes novaezelandiae</i>	∞
<i>Arthritica bifurca</i>	3.40	<i>Ostrea</i> sp.	∞
Flabelligeridae	3.10	Nematoda	∞
Oweniidae	2.71	Platyhelminths	∞
Goniadidae	2.60	<i>Fellaster zelandiae</i>	∞
<i>Ruditapes largillierti</i>	2.15	<i>Pleuromeris zelandica</i>	∞
Nephtyidacea	2.08	Mysida	∞
Micro-Bivalvia	1.98	Tanaidacea	∞
Opheliidae	1.94	<i>Amalda australis</i>	∞
Paraonidae	1.83	Cirripedia	∞
Cirratulidae	1.83	<i>Coscinasterias calamaria</i>	∞
Sabellidae	1.71	Sigalionidae	∞
Chitonidae	1.70	<i>Borneola reniformis</i>	∞
Orbiniidae	1.66	<i>Hiatella arctica</i>	∞
<i>Nucula</i> sp.	1.65	<i>Paguristes subpilosus</i>	∞
Holothurians	1.63	<i>Solemya parkinsonii</i>	∞
Maldanidae	1.58	Eunicidae	∞
<i>Felaniella zealandica</i>	1.58	<i>Cominella adspersa</i>	∞

Nemertea	1.48
<i>Zegalerus tenuis</i>	1.38
Sabellariidae	1.36
Lumbrineridae	1.28
Glyceridae	1.25
<i>Maoricolpus roseus</i>	1.24
Pectinariidae	1.22
Cumacea	1.12
<i>Corbula zelandica</i>	1.07
Polynoidae	1.01
<i>Sigapatella novaezelandiae</i>	1.00
Porifera	1.00
<i>Theora lubrica</i>	0.87
<i>Venercardia purpurata</i>	0.86
Alpheidae	0.86
<i>Limaria orientalis</i>	0.84
Ophiuroidea	0.84
Spionidae	0.80
Pycnogonida	0.79
Patiriella regularis	0.71
Syllidae	0.66
Ostracoda	0.63
Thalassinidea	0.33
Micro-Gastropoda	0.30
<i>Anthopleura aureolata</i>	0.27
Serpulidae	0.23
Sipuncula	0.21
Phoronidae	0.00
<i>Petrolisthes elongatus</i>	0.00
<i>Chlamys zelandica</i>	0.00
Magelonidae	0.00
<i>Modiolarca impacta</i>	0.00
<i>Pagurus</i> sp.	-1.00
<i>Halicarcinus</i> sp.	-6.13

Scablibregmatidae	∞
<i>Atrina zelandicus</i>	∞
<i>Anomia trigonopsis</i>	∞
<i>Austrovenus stutchburyi</i>	∞
<i>Macomona liliana</i>	∞
<i>Pyromaia tuberculata</i>	∞
Anomiidae	∞
Philinidae	∞
<i>Myadora striata</i>	∞
Opisthobranchia	∞
<i>Pellicaria vermis</i>	∞
Majidae	∞
<i>Lithophaga truncata</i>	∞
<i>Zenatia acinaces</i>	∞
<i>Xymene gouldi</i>	∞
<i>Paguristes barbatus</i>	∞
<i>Echinocardium cordatum</i>	∞
Chaetopteridae	∞
<i>Soletellina nitida</i>	∞
<i>Amalda macronata</i>	∞
<i>Eationella limbata</i>	∞
<i>Zeacolpus</i> sp.	∞
Decapoda	∞
<i>Helice crassa</i>	∞
Pilargidae	∞
<i>Gari</i> sp.	∞
Mactridae	∞
<i>Myadora boltoni</i>	∞
Tellinidae	∞
<i>Austromitra rubiginosa</i>	∞
<i>Bulla quoyi</i>	∞
Calyptraeidae	∞
Retusidae	∞
Stiligeridae	∞
<i>Zeacumantus lutulentus</i>	∞
<i>Pilumnus novaezelandiae</i>	∞
Pinnotheridae	∞
Tripterygiidae	∞
Anthozoa	∞
<i>Notomithrax minor</i>	∞

Discussion

Laboratory experiments

While starved *Charybdis japonica* consumed all species of bivalves offered irrespective of predator or prey size, they preferred small adult species like *Nucula* sp. and juveniles of other species between 8 and 35mm. There was a positive relationship between *C. japonica* carapace width and prey size consumed, but even the smallest *C. japonica* individuals were able to consume prey items up to 40mm. Although sediment reduced the overall ability of *C. japonica* to feed on *Paphies australis*, *Macomona liliana*, and *Perna canaliculus*, *C. japonica* was able to consume even the largest prey offered (30mm) irrespective of sediment availability. *C. japonica* ate fewer *P. australis* and *M. liliana* when the prey species were allowed to bury; while *C. japonica* preferred larger buried *P. australis*, they were unable to consume high numbers of large *M. liliana* that had buried deeper into the sediment. In the presence of sediment, *C. japonica* ate more *P. canaliculus* but preferred smaller sized individuals than in experiments devoid of sediment. When sediment was available for the bivalves to bury, a single starved *C. japonica* consumed up to 42 *P. canaliculus*, 25 *M. liliana*, or 22 *P. australis* in 24 hours; when the bivalves remained unburied, a single starved *C. japonica* could eat a maximum of 37 *P. canaliculus*, 36 *M. liliana*, or 37 *P. australis* in 24 hours. The ability of *C. japonica* to consume large numbers of buried and unburied juvenile bivalves may have important implications for the management of this invasive species and the ultimate ecosystem impacts of their invasion.

During this study, the densities of small prey items were higher than larger prey, which would increase the encounter rate of the crabs with smaller prey. However, previous experimental work has shown that predatory crabs prefer smaller prey items, down to a critical size, when there is a range of sizes available (Elner and Hughes 1978, Hill 1979, Jubb et al. 1983, Hughes and Seed 1981, Seed 1982, ap Rheinallt 1986, Brousseau et al. 2001, Walton et al. 2002, Floyd and Williams 2004). This may be due to larger sized prey having immunity related to their shell properties, including size, thickness, degree of inflation, and the presence or absence of a gap (Seed and Brown 1978, Whetstone and Eversole 1978, Dare et al. 1983, Mascaro and Seed 2000b, Brousseau et al. 2001). While small prey items may be actively chosen by the predator, the limitations of the predator's claw morphology and biomechanics may also influence their food choice. For example, bivalves with highly inflated and/or thicker shells require increased shell-breaking time and, thus, decrease the overall profitability of the prey (Boulding 1984). Chipped edges of many large, unopened oysters (*Crassostrea gigas*) and *P. australis* indicated that the crabs had handled and abandoned these prey; this rejection may be related to the bivalves' shape and the ineffectiveness of edge-chipping in opening them. *M. liliana* have an extremely thin shell and compressed shape, hence a greater proportion of flesh contributing to

the total weight of the individual, as compared to both other species; and while both *P. australis* and *P. canaliculus* are able to completely close their shells, *M. liliana* have a siphonal and pedal gap in their shell that may aid the crab in consuming it. Brousseau et al. (2001) suggested that the thin shell and siphonal and pedal gape of the soft-shelled clam aided *Carcinus maenas* in consuming more large individuals of this species than similar sized individuals of other, thicker shelled bivalves. Although the morphology (i.e. thin shell, compressed shape, siphonal and pedal gape) of *M. liliana* increases its vulnerability to predation, burial depth may provide a predation refuge. Deeper burial may enable them to sustain high densities by decreasing their encounter rate with crab predators. Burial depth becomes a refuge from predation as it increases the predator's energy requirements and therefore decreases the prey's total profitability.

It is well known that crabs choose their diet to maximize the net energy intake per unit foraging time (i.e. optimal foraging theory) (Emlen 1968, Pulliam 1974, Charnov 1976, Elner and Hughes 1978, Hughes 1980, Kaiser et al. 1993, Mascaro and Seed 2001), and that the energy uptake from particular sized prey changes with crab size and species (Elner and Hughes 1978, Hughes and Seed 1981, Jubb et al. 1983). The optimal foraging theory (Hughes 1980, Pyke et al. 1997) predicts that a predator like *C. japonica* would prey upon small bivalves, as they afford a high energy return per unit foraging time. Larger bivalves with thicker shells would require more energy to break into and may result in chelae damage to the crab (Floyd and Williams 2004), while thinner shells of same sized prey would have more flesh for the predator to consume and would be easier to open. However, although simple foraging behavior predictions assume that handling times and profitability remain constant over time, other studies have shown that these values are influenced by numerous factors including prey encounter rates, hunger, experience, and perception of prey items (Werner 1974, Calow 1975, Cornell 1976, Kislalioglu and Gibson 1976, Hughes 1979, Palmer 1981, McNair 1981, 1982, Cunningham and Hughes 1984, Pyke 1984). The influence of these factors can reduce the profitability of certain prey items, allowing them to be outranked by previously lower ranked prey (Hughes 1979). For example, for *Ovalipes catharus* feeding on blue mussels, *Mytilus edulis*, profitability curves would suggest they would prey on small mussels due to their thinner shells; but, because of the increase of encounter rates and decrease of handling times when consuming large mussels, the large mussels actually became more profitable for *O. catharus* to consume (Davidson 1986). This may be a factor driving *C. japonica* to continue to consume large *M. liliana* even when they are buried.

There was a strong negative effect of sediment on the total number of prey consumed for all three bivalve species. While the smaller *P. australis* size classes (10-25mm) are able to use sediment as a burial refuge, the shell morphology (thick shell, no pedal gape) of the largest size class is enough

to keep *C. japonica* from consuming large numbers of them irrespective of sediment availability. There was a negative effect of sediment on *C. japonica*'s foraging abilities on *M. liliana* between the sizes of 16 and 30mm. Without sediment present, it may not be advantageous for *C. japonica* to spend time eating the smaller *M. liliana* prey when they can collect the larger, more profitable prey items with the same thin shells; with sediment present, *C. japonica* may continue to forage on the larger *M. liliana* because it may be more profitable for them to consume the larger sized prey. In terms of *P. canaliculus*, sediment impeded the ability of *C. japonica* to consume the smallest two prey size categories, but the more interesting aspect is the overall increase in average percent of prey consumed in the presence of sediment. Apparently, the byssal strength of *P. canaliculus* attached to the rocks was no match for the strength of *C. japonica*. However, it appears as both shell morphology and burial depth contribute to the overall susceptibility of these bivalve species to predation by *C. japonica*.

Substratum type has been shown to be a limiting factor in determining where prey items can establish and can ultimately influence the success of predators on buried prey (Blundon and Kennedy 1982, Arnold 1984, Castagna and Krauter 1985, Sponaugle and Lawton 1990). For example, lower in the subtidal, some bivalve species like *P. australis* cannot bury deeply into the compact sediment and tend to be closer to the surface, making them more vulnerable to predation. Several previous studies on predatory crabs have shown reduced foraging abilities when their prey items were allowed to bury (Virstein 1977, Holland et al. 1980, Blundon and Kennedy 1982, Zaklan and Ydenberg 1997, Smith et al. 1999, Floyd and Williams 2004, Dudas et al. 2005). The only indigenous paddle crab of similar size to *C. japonica* in New Zealand, *O. catharus*, also exhibits reduced predation levels on buried *Paphies ventricosa* (30-40mm shell length) when compared to the same unburied prey (Haddon et al. 1987). Although the compressed shape of *M. liliana* may increase its vulnerability by decreasing predator handling time, it also allows these bivalves to easily bury deep into the sediment and thus sustain high densities in their depth refuge. However, both Dungeness and red rock crabs have been reported to bury down to 30cm deep in search of bivalve prey (Auster and Crockett 1984, McGaw 2004), and green crabs, *C. maenas*, in its invasive range, dig down to 15cm in search of bivalve prey (Ropes 1968, Lindsay and Savage 1978, Ropes 1988). As *C. japonica* can consume large *P. australis* and *M. liliana* that can bury down to 10cm in sediment, it is a testament to their foraging capabilities (Morton and Miller 1973, Pridmore et al. 1991). Although some predatory crabs will dig for buried bivalves, overall, bivalve burial depth may afford protection from predation because of the increased time required to obtain the prey and the overall decrease in the prey's profitability. Therefore, the interaction between substratum type and burial depth and shell morphology is influential in determining how these species interact with *C. japonica* and other potential predators. However, it is

important to note that if presented with an easier food option, *C. japonica* may abandon its original digging operation.

Prey species selection in the field is highly dependent on prey availability, density, and the probability of encountering a prey species. The small size of the experimental aquariums virtually eliminated the search time of these predatory crabs, and therefore these results represent idealized foraging conditions and possible satiation levels of *C. japonica* rather than the actual functional response of the species. However, in areas where the natural recruitment of bivalves is substantial (i.e. for *A. stutchburyi*, *M. liliana*, *N. hartvigiana* and *P. australis*) or where there are large populations of juvenile bivalves reared for aquaculture purposes (i.e. for *P. canaliculus* and *C. gigas*), these laboratory feeding rates provide a reasonable estimate of the predatory potential of *C. japonica*.

C. japonica co-occurs with all of the bivalve species tested in these laboratory experiments in intertidal and subtidal habitats characterized by the presence of hard substrates such as dock pilings, rocks, or concrete slabs (in the case of *P. canaliculus* and *C. gigas*) or by soft sediment or sand for burial (in the case of *A. stutchburyi*, *M. liliana*, *N. hartvigiana* and *P. australis*) (Fowler, *personal observation*). *A. stutchburyi*, *M. liliana*, *N. hartvigiana* and *P. australis* are consistently among the top five to ten most abundant macrofaunal species found in northeastern New Zealand's estuaries and harbours. In fact, due to the juvenile recruitment patterns of these species, they have been shown to dominate the macroinvertebrate fauna in the Waitemata Harbour (Halliday et al. 2006). Densities of *M. liliana* have been reported as up to 10 individuals per 130 cm², with *A. stutchburyi* reaching densities of 18 individuals per 130 cm² and *N. hartvigiana* attaining 45 individuals per 130 cm² in northeastern New Zealand (Cummings et al. 2006). Invasive populations of *C. gigas* occur at high densities (480 individuals per m²) on the intertidal rocky Meola Reef in the Waitemata Harbour and are the numerically dominant species at this site (Ford et al. 2006). *P. australis* populations can reach even higher densities in northeastern New Zealand, with some sites containing up to 4400 individuals per m² (Hooker 1995).

The green-lipped mussel, *P. canaliculus*, fishery is the largest aquaculture industry in New Zealand, with over 140,000 tons produced in 2002, amounting to \$200 million (Jeffs 2003). In northeastern New Zealand, 26.6 hectares are available for mussel farming, and about 500 tons are produced yearly (Jeffs 2003). Northland also is the site of all mussel spat (i.e. settled larvae) collected (over 200 tons) for various aquaculture facilities around New Zealand (Jeffs 2003). At aquaculture farms, spat are seeded on length of rope at high densities (i.e. 200 to 300 individuals per metre of rope); the rope is then hung from floating buoys in coastal areas and estuaries until the mussels reach about 80mm after 18 months (Jeffs 2003). As mussel aquaculture sites are normally in areas conducive to

harbouring populations of *C. japonica* (i.e. shallow harbours and estuaries sheltered from wind and waves with high water quality and tidal flow) (Jeffs 2003), the high stocking densities of this commercially important species may be at risk from high predation levels by *C. japonica*. While it is unknown if *C. japonica* could climb mussel ropes, they could certainly swim upward from the estuary floor to attack the mussels. Other similar crab species have been found living and preying upon mussels and the vast amount of epifauna in high densities on similar suspended mussel aquaculture rafts (Romero et al. 1982, Freire and Gonzalez-Gurriaran 1995, Clynick et al. 2008). As Jeffs (2003) reports that 80 to 90% of seeded spat is lost each season due to migration and/or predation already, results from this study suggest that green-lipped mussels (*P. canaliculus*) may be at further risk of predation by *C. japonica*.

If *C. japonica* can access high densities of any of these bivalve species, they could cause declines in abundances and may influence community dynamics. Because adult benthic bivalves appear to have a depth and/or size refuge from *C. japonica* predation, the effects of a decline in juvenile bivalve populations may not be apparent until well after the initial invasion, when the juvenile cohorts are effectively removed and the adult bivalves are not replaced. Recreational or commercial harvesters are only interested in the large, adult bivalves and may not immediately notice a decline in juvenile numbers. The predicted value of the loss of diversity due to the decrease in New Zealand's shellfish abundance by a similar invasive crab, *C. maenas*, is estimated to be \$4.8 million per annum (Bell et al. 2008); based on the results from this study, there is no reason why *C. japonica* would not be as much a threat. As *C. maenas* has not yet been found in New Zealand waters, current risk assessments should take into account the role of *C. japonica* on these fisheries. With the threat of a current expansion of *C. japonica* into areas of heavy bivalve aquaculture as well as recreational bivalve fisheries, more information on the effects of this species on these populations is needed to preserve harvested taxa.

As the sediment and non-sediment experiments were not interspersed in time (i.e. all of the non-sediment trials were completed before all of the sediment trials), it is possible that the results of these tests may be confounded by a temporal disparity due to differences in water temperature or some other factor. The subject of decreased feeding rates of crustaceans in cooler water temperatures is highly controversial, with some studies supporting it (Ropes 1968, Hill 1980, Sanchez-Salazar et al. 1987, Belair and Miron 2009) and others rejecting it (Ennis 1973, Mascaro and Seed 2001, Breen and Mataxas 2008), while others believe that feeding rates change with alterations in metabolism (Klein Breteler 1975) due to prey switching between seasons. However, crabs can adapt to seasonal changes in temperature within a week (Cuculescu et al. 1998, Hopkin et al. 2006), and some crabs are actually

more active at lower temperatures (Belair and Miron 2009). Trials without sediment were performed when sea surface temperatures (SST's) were 14.3 – 15.2°C (mean 14.8°C); trials with sediment were performed when SST's were 17.8 – 20.1°C (mean 18.8°C). In a similar experiment contrasting the feeding rates of invasive and native crabs, a 4°C temperature change between experiments was deemed not large enough to generate significant changes in predatory behaviour (Breen and Mataxas 2008). Although the 4°C difference seen in this study may have influenced the outcome of these experiments, the overall hypothesis that the burying behaviour of *P. australis* and *M. liliana* afford these species a predator defence was not called into question. During trials without sediment, when the SST's were cooler and the crab supposedly should have showed repressed feeding activities, *C. japonica* was able to consume a large number of prey items; when prey items were allowed to bury into the sediment during higher SST's, it could have been expected that *C. japonica*'s predatory activity would increase. If this was true, these results show the full potential of *C. japonica* predation on buried bivalve populations during the summer months, when they may be the most active. As *P. canaliculus* is a mussel and does not bury, *C. japonica*'s predation rate on this species should not differ between the sediment and no sediment trials. However, the temporal SST change may also explain why there was an increase in the number of *P. canaliculus* consumed by *C. japonica* during warmer trials with sediment; the higher SST's may have increased *C. japonica*'s appetite for this prey species. Thus while SST's may have influenced the total numbers of prey items consumed by *C. japonica*, the overall trends concerning the effect of sediment and the preference of certain prey sizes remain unchallenged.

The overall results from this study should be viewed cautiously as *C. japonica* is a highly mobile intertidal and subtidal predator. Standardizing hunger levels is necessary for experimental manipulations, but *C. japonica*'s hunger levels should be more variable in the wild. Giving crabs prey items at the beginning of the trial also eliminated the time it would take for crabs to search for food. As such, there are likely some qualitative and quantitative behavioral differences between the laboratory settings and natural conditions (e.g. Nelson 1981, Breen and Metaxas 2008). Further experimental and field manipulations are needed to examine the impacts of intra- and inter-specific multiple predators (Murdoch 1973, Griffin 2006, Griffin and Byers 2006), short and long term learning (Cunningham and Hughes 1984, Murdoch 1973, Roudez et al. 2008), polyphagy (Murdoch and Oaten 1975, Murdoch et al. 1985) and prey switching (Murdoch 1969, 1977, Murdoch et al. 1985) on *C. japonica*'s feeding responses.

Field experiments

Exclusion experiment

Although the laboratory feeding experiments seemed to suggest that *Charybdis japonica* could have substantial impacts on the community structure of benthic systems, the one week field caging experiment did not discover any negative impacts attributed to the presence of *C. japonica*. There was no discernable impact of *C. japonica* on total bivalve abundance, total invertebrate taxa abundance, or taxonomic richness, including those species used in laboratory trials. Therefore, there is little evidence from these field experiments that *C. japonica* is having any impact on the macrobenthic structure of the marine community in northeastern New Zealand at this point in time.

However, caging experiments have been instrumental in illustrating the effects of predators in other marine communities (see Peterson 1979, Thrush 1999) although they may confound results in several ways (e.g. Hulberg and Oliver 1980, Underwood 1986). To decrease any possibilities of cage artefacts in this study, experimental empty caged plots were contrasted with open plots at the chosen site just outside the known range of *C. japonica* in a similar but seemingly unimpacted area. Fouling of the cages was minimal, and there was no drift algae found attached to the cages due to the short time-scale of the experiment. Refuge and feeding by other macroinvertebrate species within cages is a possible confounding factor, but due to the small mesh size and the lack of observed species, these are deemed negligible effects. If predators had removed any prey species from the caged plots, it would be expected that they would remove similar numbers from all plots. It could be that other predators avoided cages with *C. japonica* and consumed prey items either in cages without *C. japonica* or in the open plots, thereby making it more difficult to detect any impacts of *C. japonica*. As the total abundance of macroinvertebrates was higher from underneath all caged treatments compared to open plots, there may be a slight influence of the cages on community structure (i.e. prey species using the cage as a predation refuge, lower light levels, reduced flow rates inside the cages). Overall, however, there was no effect of the cages on macroinvertebrate abundance or taxonomic richness; therefore, any changes could be attributed to the presence of *C. japonica*.

Due to the short nature of the experiment, it was hypothesized that there would be changes in species abundance but that species richness would remain constant; however, there were no changes in macroinvertebrate fauna due to the presence of *C. japonica*. In similar caging experiments, researchers found no impact of the invasive European green crab *C. maenas* on infaunal or epifaunal abundance or richness after either one week, one month, or two months (Gee et al. 1985, Walton et al. 2002, Ross et al. 2004). Nelson (1981) also found no impact of the blue crab, *Callinectes sapidus*, on macrofaunal

abundances after a three week cage experiment in Florida, USA. Another portunid crab, *Liocarcinus depurator*, did not alter the marine benthic community in Scotland after a month long caging experiment (Hall et al. 1990). However, a long term study (nine years) found that *C. maenas* exerts strong “top-down” control over native benthic populations and reduced abundances of several invertebrate species in a marine food web in central California (Grosholz et al. 2000). Therefore, the limited time of these field experiments (one week) may have not been sufficient enough time to elucidate any patterns or statistical anomalies due to low experimental predation intensity.

One of the confounding factors with this particular field experiment is that individual *C. japonica* have been sporadically caught in the Mahurangi Harbour since 2003 (Lohrer et al. 2008, Fowler *unpublished data*). It is generally thought there are no established populations of *C. japonica* in the Mahurangi Harbour based on a lack of trapped gravid females. However, it is possible that an undetected population had established and impacted the community before the start of the experiment, which would explain the lack of apparent effect of caged *C. japonica*. For example, while only a single *C. japonica* was trapped from the Weiti River during 2002 (Gust and Inglis 2006), 50 individuals were captured over the same time period in 2008 (Chapter 2). Based on the extensive trapping conducted by myself and the Ministry of Agriculture and Forestry Biosecurity New Zealand (MAFBNZ), however, I strongly doubt there was a cryptic population of *C. japonica* established in the Mahurangi Harbour during the course of this experiment.

Another reason there were no changes elicited in this study may be that the overall predation pressure in cages with *C. japonica* was similar to the predation pressure by other species in open cages and open plots. For example, other known predatory invertebrates and vertebrates such as shrimp, crabs (i.e. *Macrophthalmus hirtipes*), fish (i.e. *Pagurus auratus*), and whelks (i.e. *Cominella* sp.) are found in the experimental area and may consume some of the same species as *C. japonica*. Many infaunal crab prey items are themselves predators (i.e. macrofaunal polychaetes) that tend to increase in numbers in the absence of their predators; the prey species of these infaunal predators may be less abundant in areas where crabs are not found due to predation pressure by predators other than *C. japonica* (Ambrose 1984). It may be that the collective predation pressure exhibited by multiple predators in this system is not influenced by the addition or subtraction of a single predator (Raffaelli et al. 1989).

Also, the field site was extremely variable in its community structure, which may have precluded the appearance of any differences between treatments; the relatively high variation among plots could have led to a lack of statistical power. Surveys completed in the Waitemata Harbour from 2000 to 2006 found populations of *P. australis*, *M. liliana*, and *N. hartvigiana* to display highly

variable patterns of abundance with no periodicity or directional trends (Halliday et al. 2006). In future studies, it may be advantageous to seed field plots with known numbers of possible prey items to generate a more accurate representation of the effects of this predator.

The cages used in this study were completely enclosed in mesh on all sides, including the bottom, to limit the burial escape of this invasive species into a new area. Although *C. japonica* were found to effectively feed on buried prey while inside cages in laboratory trials (Fowler, *unpublished data*), their predatory behavior may have been altered in the field experiments due to factors associated with the mesh barrier on the bottom of the cages, interference with *C. japonica*'s possible tidal migration due to being caged, or changes in feeding rhythms and/or foraging behavior. It is also possible that crabs exclusively foraged at the edges of the cage, which were not sampled. While it is possible that *C. japonica* did not eat at all during their confinement in the cages, analysis of the gut contents of confined crabs showed that individuals consumed crustaceans, polychaetes, echinoderms, and molluscs.

A further explanation of the lack of decreased species abundance and diversity is the broad diet of *C. japonica* (see Chapter 2). Given the broad taxonomic span of their prey, direct effects on a single prey species may not be observed. However, this study found a greater total macrobenthos abundance from underneath cages with *C. japonica* than from either control cages or controls; a study completed by Nelson (1981) found similar results from caged field experiments using *C. sapidus*. It is possible that *C. japonica* effectively reduced the density of a particular keystone species inside the cages only to have other species' abundances increase (e.g. Virnstein 1977).

Some adult bivalve populations in the wild are somewhat protected from crab predation by long periods of exposure due to habitation of the intertidal zone, high aggregation numbers, and/or the ability to bury deep into the sediment (Haddon et al. 1987). Although juvenile bivalves, such as *P. australis*, may be found high in the intertidal, portunid crabs are highly mobile predators that often move large distances over a short period of time (Hill 1978, Boulding and Hay 1984, Hines and Wolcott 1990) while foraging at high tide and may come inshore to prey upon these susceptible populations. This high level of movement also influences how and where crabs deem areas of high or low prey density, how long they spend in a particular area, and their efficiency of obtaining prey items (Pyke et al. 1977, Kacelnik and Krebs 1986, Sutherland and Anderson 1987). While, initially, high population levels of prey living in dense beds might be thought to afford the prey a sense of protection, it would be more optimal for a mobile predator, such as a crab, to remain in areas where prey are in high densities (Boulding and Hay 1984); the time it would take to locate and dig up buried prey would be less in a high density area, therefore allowing the predator to conserve energy. High prey densities

may also motivate crabs to forage more intensively because they are tactile and chemosensory predators (Elner and Hughes 1978). As prey density increases, the concentration of prey chemical cues also increases as does the probability that the predator will locate a prey item. In field studies, Hill (1979) found that the mud crab, *Scylla serrata*, spent most of its time in areas where there were high natural densities of infauna, and several studies found that blue crabs, *Callinectes sapidus*, show a marked increase in total prey consumption when densities of prey were also increased (Ebersole and Kennedy 1995, Micheli 1997). Although *C. japonica* did not show any impacts on benthic macroinvertebrate community structure, results from laboratory experiments indicate that predation by *C. japonica* is likely to impact populations of small bivalves in both intertidal and subtidal soft-sediment habitats when it becomes abundant.

Field survey

There was no detectable impact of *C. japonica* on the macroinvertebrate benthic community structure of the Waitemata Harbour even after their appearance more than 10 years ago and their subsequent establishment. Differences between Hayward et al.'s (1997) survey in the Waitemata Harbour and the one completed in this study were driven by two ephemeral invasive bivalve species whose abundances cannot be attributed to the presence of *C. japonica*. The prey taxa likely to have been targeted by *C. japonica*, such as bivalves, showed no particular tendency to decline in numbers between the 1990's and 2008. These field survey results parallel those from the field experiment, showing a relatively low impact of this invasive crab species on native biodiversity at this point in time. While it is important to note that differences between Hayward et al.'s (1997) study and this one could be confounded by inconsistencies in identifying macroinvertebrate species, this should only slightly influence the reported values for specific species and not change the overall trends.

The Waitemata Harbour has been successfully invaded by at least 66 nonindigenous marine species over the last 100 years (Hayward 1997, Cranfield et al. 1998, Inglis et al. 2005). In this study, differences between the community composition found by Hayward et al. (1997) and the 2008 survey were driven largely by the explosion of populations of the invasive ephemeral Asian date mussel *Musculista senhousia* and the invasive bivalve *Theora lubrica* in 2008. A similar study by Lohrer et al. (2008) also found increased numbers of *M. senhousia* and *T. lubrica* in the Waitemata Harbour when compared to Hayward et al. (1997). Like this study, Lohrer et al. (2008) found decreased species richness and abundance of other species at sites where *M. senhousia* densities were high. While these increases in *M. senhousia* populations may be short-lived due to the episodic population crashes because of their high densities, they may reflect an alteration in benthic-pelagic coupling and trophic dynamics and ultimately alter this soft-sediment habitat (Lohrer et al. 2008). As these invasive bivalve

species are opportunistic (i.e. high recruitment, rapid growth, short life), they may have been able to colonize recently disrupted sites in the harbour faster than native species.

Although the apparent increase of these other invasive organisms cannot directly be attributed to the presence of *C. japonica*, a common theory in marine invasion ecology is that the appearance of one invader may positively influence the success of other invaders (e.g. “invasional meltdown”; Simberloff and Von Holle 1999). For example, the presence of *C. maenas* is thought to have aided the later introduction of another invasive crab, *Hemigrapsus sanguineus* along the northeast coast of the USA (Lohrer and Whitlatch 2002) and of the exotic clam *Gemma gemma* along coastal California (Grosholz 2005). If *C. japonica* is found to preferentially consume non-indigenous bivalves such as *M. senhousia*, *T. lubrica* or *L. orientalis*, it would certainly benefit from the high densities of these species in the Waitemata Harbour. Therefore, it is plausible that the establishment of these invasive prey items may have facilitated the later invasion by *C. japonica* but this hypothesis needs to be experimentally answered.

If the appearance of *C. japonica* in the Waitemata Harbour was having a substantial effect on the marine benthic community, changes in the abundance and size structure of prey populations, and not necessarily prey diversity, would have been apparent (Peterson 1979). However, due to the lack of population estimates of *C. japonica* in the Waitemata Harbour, it is possible that the population is actually small enough that they would not make an impact throughout the harbour. *C. japonica* may have contributed to the decrease in abundance of some species, but the degree of change alone is not enough evidence to blame *C. japonica* for their reduction in numbers. For example, populations of native predators may be having more of an impact on populations of invasive bivalves; snapper (*Pagrus auratus*) diets in the Waitemata Harbour were found to be composed largely of the invasive bivalves *M. senhousia* and *L. orientalis* (Lohrer et al. 2008). Although it is much more difficult to determine in this case, indirect effects of predation on marine benthic communities may occur due to sediment disturbance (Woodin 1978) and/or multiple trophic interactions (Kimbrow et al. 2009). Also, long term anthropogenic perturbations to the Waitemata Harbour may have influenced the densities of native species irrespective of the arrival of an exotic predator. For example, the apparent increase in *M. senhousia* and *T. lubrica*, along with *L. orientalis*, is thought to coincide with the decreases in abundance of the horse mussel *Atrina zelandica* and the heart urchin *Echinocardium cordatum* (Lohrer et al. 2008). Both native species are functionally important benthic marine species (Norkko et al. 2001, 2006, Thrush et al. 2002, Hewitt et al. 2006), and their decreases in abundance may have facilitated the invasions of other bivalves (Rhoads and Young 1970, Woodin 1976, Thrush 1988, Wilson 1991,

Tamaki 1994, Widdicombe and Austen 1999, Lohrer et al. 2005, Norkko et al. 2006, Pillay et al. 2007).

Further field investigations are needed to elucidate the role of *C. japonica* among northeastern New Zealand's intertidal and subtidal marine community. Combining multiple trophic levels, an investigation into the predation patterns of this species could uncover the overreaching, multiple, complex interactions between different trophic levels in these communities. For example, alteration of benthic prey populations could not only be affected by predation by epibenthic consumers like *C. japonica* but also be indirectly affected by higher trophic predators (i.e. sea birds, elasmobranches) that can modify the behavior of these epibenthic predators. As predator numbers may fluctuate throughout the year as population numbers and diet change, any predator impact is likely to vary seasonally. Therefore, a long-term enclosure experiment spanning several, if not all, seasons is needed to fully understand the impacts of *C. japonica*. A comprehensive study would need to take all of these factors into account.

Conclusions

The high densities of *Charybdis japonica* at certain localities within northeastern New Zealand, their effectiveness as predators of juvenile bivalves and their large appetites suggest a potentially important role for these predators in restructuring the prey communities in habitats into which they have been introduced. However, it is unknown if this intense predation can modify the structure of benthic soft-sediment communities through direct or indirect trophic cascades as field experiments and comparisons with historical surveys do not indicate that *C. japonica* is having a negative impact on native biodiversity even though they were introduced almost a decade ago. It is important to remember that although this study did not find any impacts of *C. japonica* on the benthic community at this time, it does not mean that *C. japonica* is not currently altering the community structure or will not influence the community dynamics in the future. The total impact of *C. japonica* on benthic communities will be influenced from both the individual and population level; a combination of the consumption rate of the individual as well as the total abundance of *C. japonica* will synergistically work together to determine the influence of this invasive species on benthic macroinvertebrate community structure. Continued monitoring of the spread of *C. japonica* and more comprehensive field experiments are needed to determine the impact of this invasive species on New Zealand's intertidal and subtidal marine communities.

Chapter Four

Temperature and salinity tolerances of Stage 1 zoeae predict possible range expansion of an introduced portunid crab, *Charybdis japonica*, in New Zealand

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Introduction

Describing the spread and distribution of marine invasive species is inherently complex and difficult to observe or document in the natural environment. Therefore, even with limited resources, the prediction of possible areas of establishment and spread of invasive species has become an important tool in management and eradication efforts (Kolar and Lodge 2001; deRivera et al. 2007; Vander Zanden and Olden 2008). Enhanced predictive capability allows for the establishment of monitoring programs in critical areas and increases the chances of early detection and eradication (Simberloff 2009). However, predictions are especially difficult when basic ecological knowledge of reproduction, larval development and survival of the species in its new habitat is absent.

In this study we follow the approach of deRivera et al. (2007) by determining temperature and salinity tolerance ranges of Stage 1 zoeae to predict the possible range expansion of an introduced marine species in New Zealand. The Asian paddle crab *Charybdis japonica* (Crustacea: Decapoda: Portunidae) was first discovered in the Waitemata Harbour, New Zealand (Fig. 4.1) in 2000, and its introduction is most likely the result of larval transfer in ballast water (Gust and Inglis 2006). Although adult *C. japonica* are able to acclimate to a broad scale of salinities (from 30 to 14‰) and temperatures (native mean monthly temperatures from 4 to 34°C) (Gust and Inglis 2006; Hong-Yu et al. 2008) in their native range, larvae may have narrower tolerance ranges that could prevent *C. japonica* from establishing new populations in New Zealand. Temperature and salinity are two of the most influential abiotic factors that may affect distribution ranges of invasive species like *C. japonica*, as they strongly influence survival, growth and development of crab larvae (Brett 1979; Sulkin et al.

1996; Anger 2001; Baylon and Suzuki 2007; Bravo et al. 2007) and ultimately the successful establishment of a species in a new environment (Epifanio et al. 1998; Rudnick et al. 2000; Gilman 2006; Sanford et al. 2006; deRivera et al. 2007; Storch 2009). Understanding how Stage 1 *C. japonica* zoeae tolerate temperature and salinity fluctuations in newly invaded habitats may aid researchers in forecasting potential areas of spread as this invasion progresses in New Zealand's coastal and estuarine environments.

Methods

Gravid *C. japonica* were collected from the Weiti River on the Whangaparaoa Peninsula of New Zealand (36° 38.4' S, 174° 43.6' E, Fig.4.1) from January to March 2009 in baited oval-shaped collapsible 'Opera house' traps. The dimensions of the traps were 640 x 470 x 200 mm (l x w x h) with a diagonal mesh size of 20 mm and an entrance funnel opening into the trap with a diameter of 90 mm. Crabs were removed from the trap, individually placed in 10 litre buckets containing seawater from the Weiti River and transported ca. 50 km to the Leigh Marine Laboratory. At the laboratory, the crabs were maintained in individual buckets containing 20 litres of UV-treated and 1 µl filtered seawater (FSW hereafter) at ambient temperature, under a natural light regime, with air supplied by bubblers. Ambient seawater temperature during the experimental period was 20.9°C on average, with maximum and minimum values of 22°C and 19°C respectively. The crabs were fed daily 1 adult mussel (*Perna canaliculus*) or oyster (*Crassostrea gigas*), and any uneaten food was removed during exchange of 90% of the seawater. Larval release was checked between 8am and 10am daily.

Once hatching occurred, active Stage 1 zoeae displaying positive phototaxis were collected for either the temperature or salinity experiment. Five separate experiments were conducted during February to March 2009, each testing zoeae from a different female (carapace width [CW] 55 to 70 mm). In order to elucidate thermal and salinity thresholds, not every temperature or salinity level was repeated for each brood; instead, smaller experimental ranges were tested with each subsequent brood.

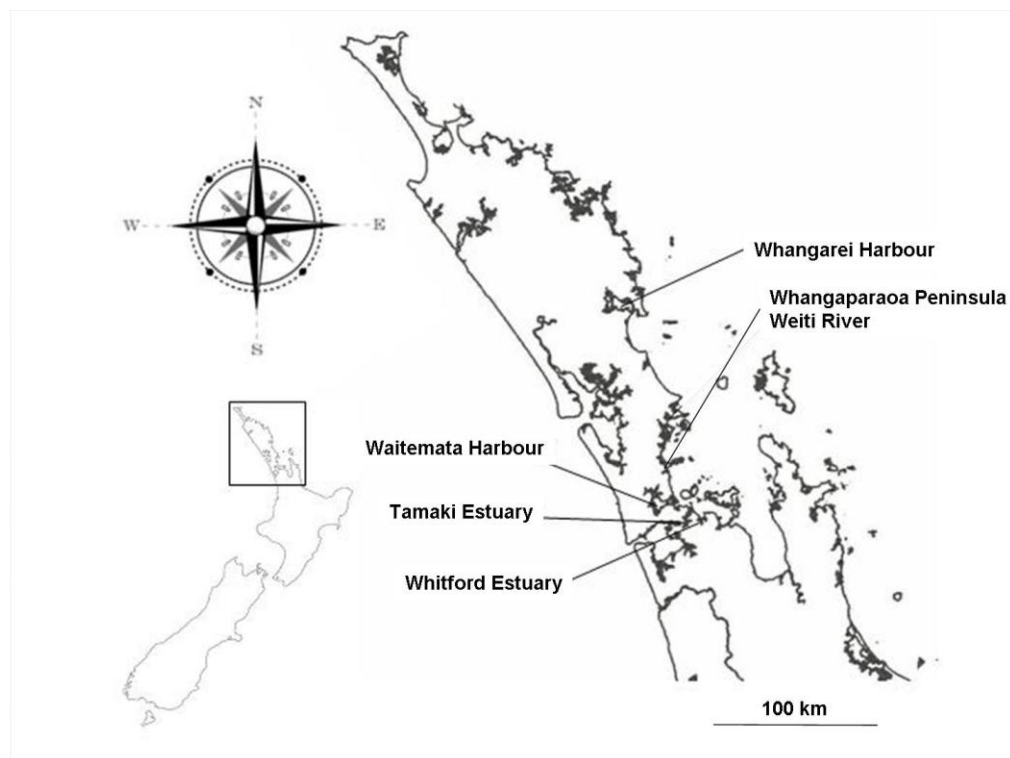


Figure 4.1. Known locations of *Charybdis japonica* in northeastern New Zealand. Gravid females used in the experiments were collected from the Weiti River.

Temperature treatments

Stage 1 *C. japonica* zoeae were exposed to experimental seawater temperatures between 11 and 43°C at an ambient salinity of 35‰. A constant temperature gradient ($\pm 1^\circ\text{C}$) was prepared using a large aluminum block (50 x 30 x 10cm, l x w x h) fitted with recirculating hot and cold water baths (Julabo, Labortechnik GmbH, Germany) at each end. As the block contained 10 columns with 6 rows, we could simultaneously test up to 10 different temperature levels, each with 6 replicates. 10 to 20 Stage 1 zoeae were transferred into 20 ml glass scintillation vials containing FSW, the lid loosely sealed and the vial placed in the temperature block and left for ca 10 minutes to equilibrate. To determine if the temperature block was influencing larval survival, for each experiment we ran a set of control vials (N = 9) at room temperature (23°C) outside the aluminum block. No food was added to either the experimental or control vials during the experiment as Jiang and Wang (2004) found that 18 hours starvation did not affect the growth of Stage 1 *C. japonica* zoeae. Zoeal survival in all vials was assessed after 3, 6, 9, 12 and 24 hours by removing the lid of each vial and counting and removing any dead zoeae. Zoeae were considered dead if they did not respond with movement to any prodding by a plastic Pasteur pipette. Simultaneously with the assessment of survival at each time interval, water temperature was recorded with a digital water resistant thermometer (Dick Smith Electronics, $\pm 1^\circ\text{C}$). Dissolved oxygen content in the vials was checked after 24 hours in the first round of experiments by

placing a Microx TX3 oxymeter (PreSens Precision Sensing GmbH, Germany, $\pm 1\%$) sensor in a randomly selected vial from each temperature level.

Salinity treatments

The effect of salinity on the survivorship of Stage 1 *C. japonica* zoeae was examined by exposure to salinities between 5‰ and 45‰ at room temperature of 23°C. Higher salinities were produced by the addition of rock salt to FSW; lower salinities were produced by dilution of FSW with UV treated, 1 μ m filtered rainwater. 10 to 20 Stage 1 zoeae from each of the five females (CW 55 to 70 mm) were abruptly transferred from buckets with ambient salinity into 20 ml glass scintillation vials containing 20 ml of either FSW at ambient salinity (control 35‰) or into vials with one of the 4 to 6 experimental salinities (N = 9 replicates) and the lid loosely sealed. Zoeae were counted and observed for mortality after 1, 2, 4, 6, 8, 12 and 24 hours as described in the temperature treatments. Dissolved oxygen content in the vials was checked after 24 hours as described for the temperature treatments.

Statistics

Estimates of the temperature or salinity at which 50% of Stage 1 zoeae died, referred to as median lethal temperature, LT_{50} , or median lethal salinity, LS_{50} , were calculated from the mean survival data as sigmoidal dose-response relationship curves (with variable slope) for each duration of exposure using GraphPad Prism 5.

To determine the possible effect of the aluminum block, zoeal survivorship in the control vials was compared to the survivorship in vials in the aluminum block at the same temperature for two of the temperature experiments using non-parametric Mann-Whitney-U tests to compare two independent samples.

Potential areas of spread

The potential for *C. japonica* to complete Stage 1 zoeal development north and south of its present range in northeastern New Zealand was examined by comparing sea surface temperature and salinity records over the past ten years with the temperature and salinity tolerance thresholds determined experimentally. Temperature and salinity data were obtained for the reproductive period of *C. japonica* (November to April; Fowler, *unpublished data*) from numerous sources around New Zealand including the National Institute for Water and Atmospheric Research, Auckland Regional Council, Northland Regional Council, Nelson City Council, Taranaki Regional Council, University of Otago Portobello Marine Laboratory, Hawkes Bay Regional Council, Environment Southland,

Environment Bay of Plenty, Tasman Bay Regional Council, Environment Canterbury, and the Otago Regional Council.

Results

Temperature

C. japonica Stage 1 zoeae were extremely tolerant of a broad range of temperatures (Fig. 4.2A), with survivorship only affected by temperatures outside the environmental relevance for New Zealand (Fig. 4.3). After 6 hours, $\geq 95\%$ of Stage 1 zoeae survived temperatures ranging from 11.3 to 35.9°C (Fig. 4.2A). Survival rates of 100% over 24 hours occurred in all replicates at temperatures of 16, 19, 24 and 25°C with high survival ($\geq 80\%$) when larvae were exposed to 12 to 33°C over the same period (Supplementary Fig. 4.1). At temperatures outside this range, survival decreased with time. For example, after 24 hours of exposure, temperatures $\geq 34^\circ\text{C}$ led to 50% survival, with only 33.1% surviving at 35°C, and 0% surviving at temperatures $\geq 36^\circ\text{C}$. Zoeae held at temperatures $\leq 16^\circ\text{C}$ were still alive but showed reduced activity, although this variable was not quantified. Conversely, zoeae held at between 16 and 33°C remained active even after 24 hours (Supplementary Fig. 4.1).

Survival in the control vials did not differ significantly from survival in vials that were kept in the aluminum block at equal temperature (1st experiment: $U = 459.5$, $p = 0.38$, $N = 44$ in control, $N = 24$ in block; 5th experiment: $U = 726$, $p = 0.81$, $N = 50$ in control, $N = 30$ in block), indicating that the aluminum block had no effect on the survival of the Stage 1 zoeae.

The LT_{50} for Stage 1 zoeae was between 35.9 and 34.1°C, decreasing slightly with increased exposure periods (Table 4.1). There was no lower thermal limit detected in the range of experimental temperatures. LT_{50} estimates for 3 and 6 hours of exposure showed large confidence intervals because of the low mortality over the range of tested temperatures for this period of exposure (Table 4.1, Fig. 4.2A, Supplementary Fig. 4.1).

Dissolved oxygen content in the vials was between 92 and 96% after 24 hours.

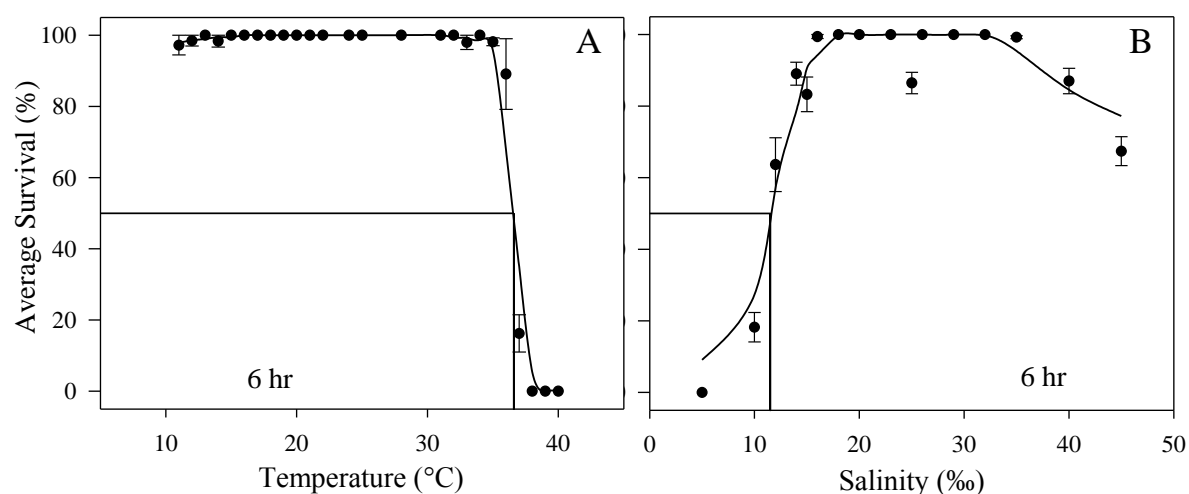


Figure 4.2. Average survival \pm SE (%) of Stage 1 *Charybdis japonica* zoeae reared at different temperatures (A) or salinities (B) after 6 hours. A line was fitted by calculating running averages. In (B), survival data at 25‰ were excluded from the running average. The lines at 50% survival indicate LT_{50} and LS_{50} estimates.

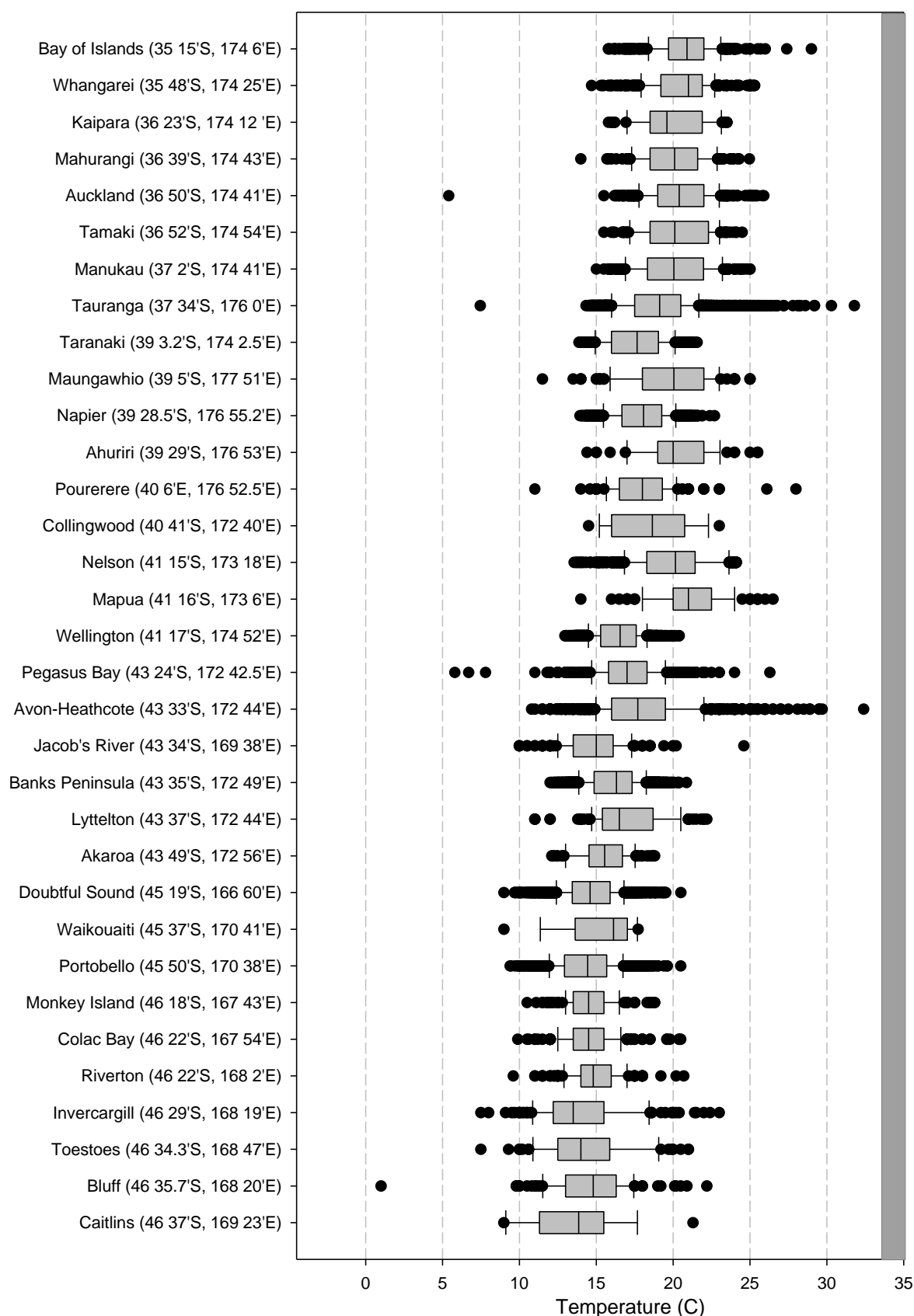
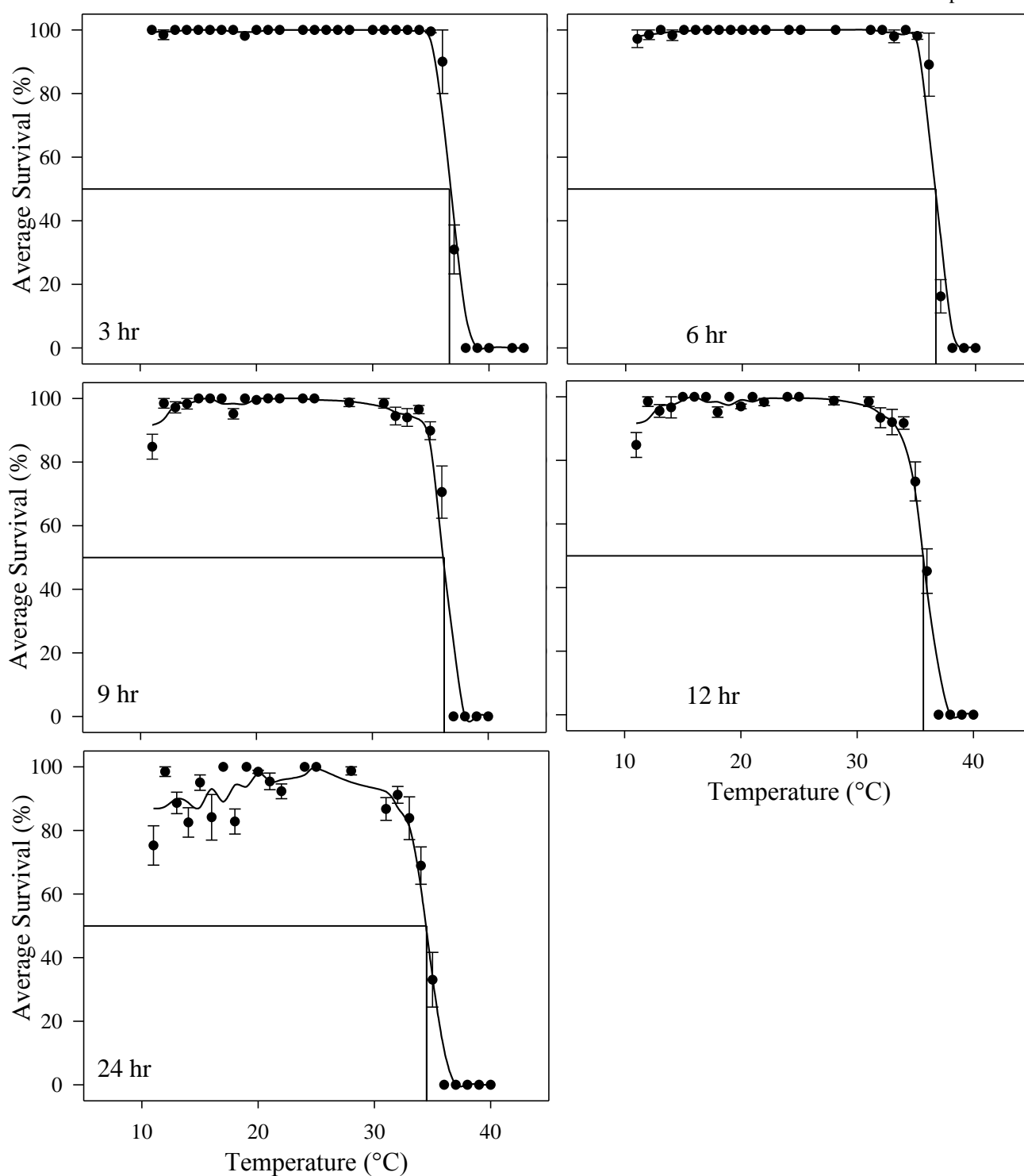


Figure 4.3. Temperature records of bays, harbours and estuaries around New Zealand listed from northerly to southerly latitudes. One measurement point indicates one or an averaged record for one day within the months November - April. The grey area on the right indicates temperatures that Stage 1 *C. japonica* zoeae would not be able to survive, based on LT₅₀ estimates after 24 hours of exposure.



Supplementary Figure 4.1. Average survival \pm SE (%) of Stage 1 *Charybdis japonica* zoeae reared at different temperatures, taken at time intervals of 3, 6, 9, 12 and 24 hours. A line was fitted by calculating running averages. The lines at 50% survival indicate LT_{50} estimates. Salinity was kept constant at ambient seawater conditions (35‰).

Table 4.1. $LT_{50} \pm 95\%$ CI ($^{\circ}$ C) calculated for Stage 1 *Charybdis japonica* zoeae for different durations of exposure to high temperatures.

	3 hours	6 hours	9 hours	12 hours	24 hours
$LT_{50} \pm 95\%$ CI ($^{\circ}$ C)	35.9 ± 78.1	35.8 ± 77	35.8 ± 3.2	35.6 ± 0.9	34.1 ± 1.3

Salinity

Salinity affected the survivorship of Stage 1 *C. japonica* zoeae even within the environmentally relevant ranges that New Zealand waters experience (Fig. 4.4). Zoeae did not tolerate hypo-saline seawater of $\leq 15\text{‰}$, even for short exposure periods (Fig. 4.2B). In contrast, survival was still $>85\%$ after 6 hours exposure in hyper-saline seawater of 40‰ (Fig. 4.2B). However tolerance towards high salinities decreased with increasing duration of exposure. The salinity optimum of Stage 1 zoeae was found in the range of 18 to 35‰ , with survival rates varying from a maximum of $95.8 \pm 1.1\%$ at 35‰ to a minimum of $39.3 \pm 6.7\%$ at 25‰ after 24 hours (Supplementary Fig. 4.2). With the exception of the outlier at 25‰ , 50% survival after 24 hours only occurred at ≤ 19.1 and $\geq 39.6\text{‰}$.

LS₅₀ values were found between $10.8 \pm 0.2\text{‰}$ and $12.8 \pm 0.4\text{‰}$ for exposure of up to 8 hours towards hypo-saline seawater (Table 4.2). With extended exposure, LS₅₀ values increased to $19.1 \pm 0.9\text{‰}$ after 24 hours. In hyper-saline seawater, LS₅₀ values reached $41.5 \pm 0.5\text{‰}$ after 12 hours and decreased to $39.6 \pm 0.7\text{‰}$ after 24 hours.

Dissolved oxygen content in the vials was between 94 and 99% after 24 hours.

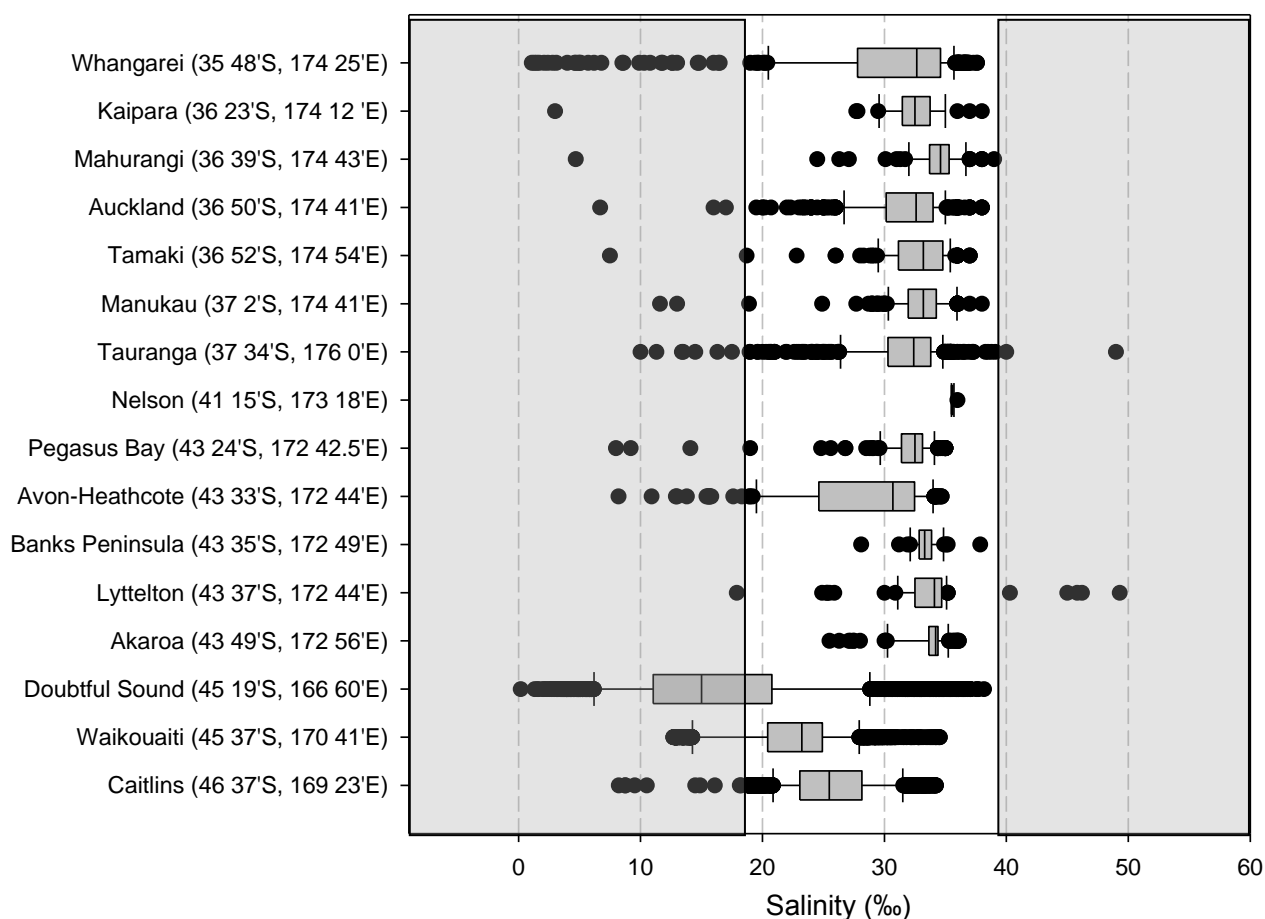
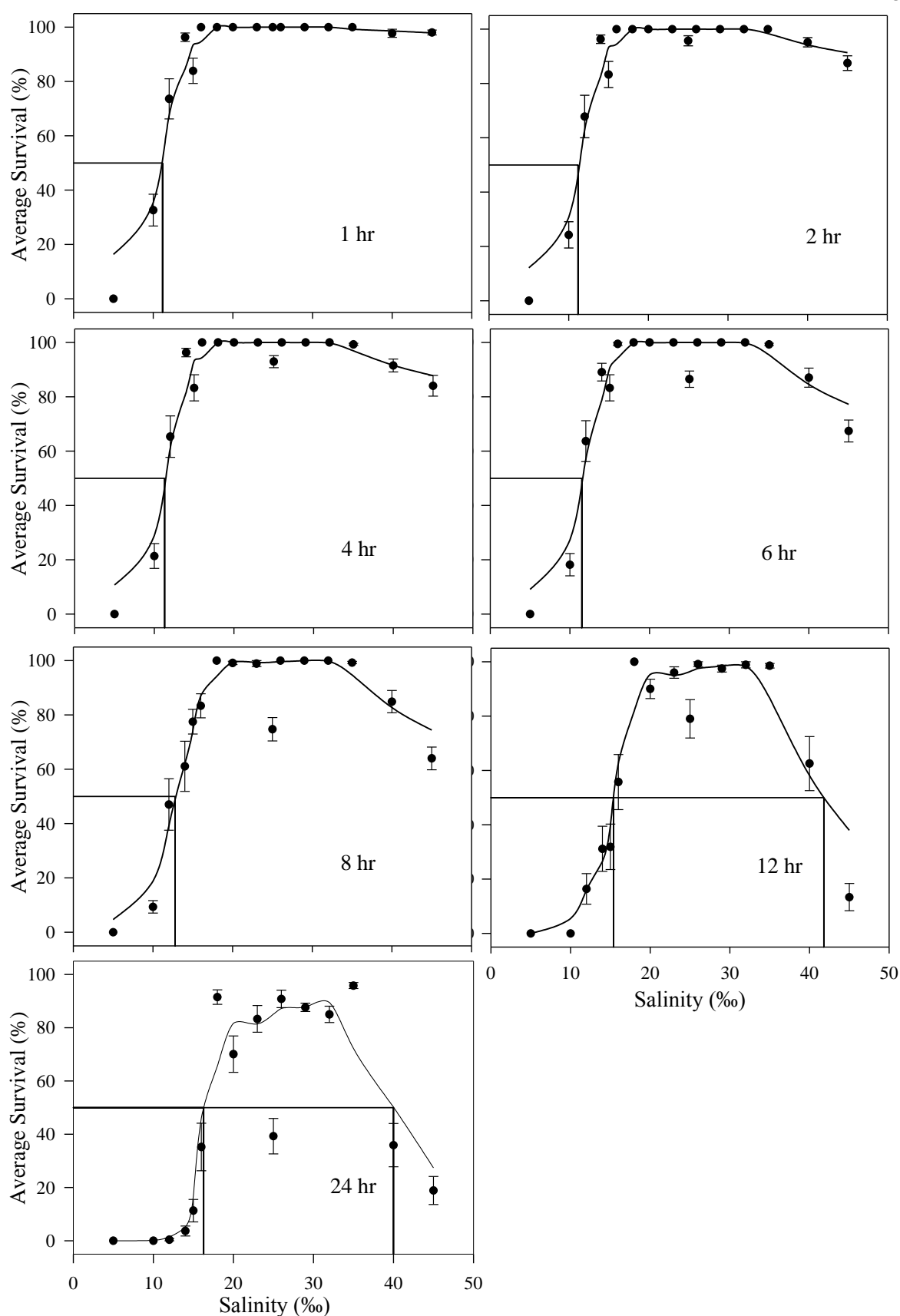


Figure 4.4. Salinity records of bays, harbours and estuaries around New Zealand. One measurement point indicates one measurement in a day or an averaged record for one day within the months November to April. The grey areas show salinities that are lower or higher than the LS_{50} values determined after 24 hours of exposure.



Supplementary Figure 4.2. Average survival \pm SE (%) of Stage 1 *Charybdis japonica* zoeae reared at different salinities, taken at time intervals of 1, 2, 4, 6, 8, 12 and 24 hours. Temperature was kept constant at approximately 23°C. A line was fitted by calculating running averages. Lines at 50% survival indicate LS_{50} estimates. Survival data at 25‰ were excluded from the running average.

Table 4.2. $LS_{50} \pm 95\%$ CI (‰) calculated for Stage 1 *Charybdis japonica* zoeae for different durations of exposure. At 12 and 24 hours both the lower and upper end of the salinity scale tested was lethal, therefore two LS_{50} values were obtained.

	1 hour	2 hours	4 hours	6 hours	8 hours	12 hours	24 hours
$LS_{50} \pm 95\%$ CI (‰)	10.8±0.2	11.2±0.2	11.3±0.2	11.5±0.3	12.8±0.4	15.4 ± 0.5, 41.5 ± 0.5	19.1 ± 0.9, 39.6 ± 0.7

Potential areas of spread

Comparing the experimentally determined temperature and salinity tolerance ranges of *C. japonica* Stage 1 zoeae to potential coastal New Zealand habitats suggests that *C. japonica* could survive at all sites in the North Island and further south to Akaroa Harbour in the South Island (43°49'S, 172°56'E) (Fig. 4.3, 4.4). The upper thermal tolerance limit of the *C. japonica* zoeae is not relevant in New Zealand, therefore, zoeae have the capacity to survive summer temperature maxima (Fig. 4.3). Furthermore, the large salinity tolerance range found for the zoeae indicates that they have the potential of surviving the predominant salinity conditions at these sites (Fig. 4.4). However, it is important to note that a number of sites exhibit daily fluctuation of salinities that are too hypo- or hyper-saline for the optimum for Stage 1 *C. japonica* zoeae. For example, Whangarei Harbour, in which several individual *C. japonica* were collected in May 2009, showed a salinity gradient of 1.5 to 24.4‰ over 40 hours during the breeding month of January 2006 (Auckland Regional Council 2009). If the zoeae hatched on those days and were not able to escape those hypo- or hyper-saline conditions, they would most likely not be able to survive.

Discussion

The dispersal and population establishment of *Charybdis japonica* beyond its present range depends on the influence of several biotic and abiotic factors such as physiological stress, starvation, competition, predation, sinking and advection of the early stage zoeae (reviewed in Morgan 1995). Here we have shown that unfed, unacclimated Stage 1 *C. japonica* zoeae can tolerate a wide range of temperatures and salinities, with optima between 12 and 33°C ($LT_{50} \geq 34^\circ\text{C}$) and 18 and 35‰ (LS_{50} at ≤ 19.1 and $\geq 39.6\%$). These tolerance values are within the environmental ranges of most of New Zealand's estuaries and harbours during *C. japonica*'s reproductive period, and include the optimal temperatures found for zoeal laboratory rearing in their native range (27 to 30°C to megalopae, Yatsuzuka 1952; $24 \pm 1^\circ\text{C}$ to Stage 3 zoeae, Jiang and Wang 2004).

The tolerance ranges and mortality estimates reported here apply to only the first stage of *C. japonica*'s zoeal development. There may be sub-lethal responses to temperature and salinity, particularly at the extremes, that were not evident here due to the short duration of the experiments but

that may appear in later developmental stages (see Pechenik 1987). For example, long exposure to low temperatures and salinities can delay molting and extend the duration of development in crab zoeae and megalopae (Hai et al. 1998; Baylon and Suzuki 2007). Low salinities, in particular, can decrease respiration and digestion rates (Anger et al. 1998), which result in reduced dry body weight and lipid content (Torres et al. 2002). However, even if the larvae are able to survive temperature and salinity fluctuations, they experience further risks that increase mortality as they continue their development in the plankton due to starvation, predation, and offshore transport (Rumrill 1990, Morgan 1995, Vaughn and Allen 2010).

Further, temperature and salinity tolerances of crustacean larvae can differ between developmental stages and may also depend on the environmental conditions experienced by developing embryos (reviewed in Pechenik 1987). Female brachyuran crabs attach their embryos externally, giving them the ability to osmoregulate on their own (Charmantier et al. 2001; Taylor and Seneviratna 2005). This may allow the embryos to acclimate to low salinities during embryogenesis and positively impact their ability to tolerate low salinities after hatching (Charmantier et al. 2002; Gimenez 2002; Gimenez and Torres 2002). This is true for Stage 1 zoeae of several crab species that have higher tolerances than later stage larvae (Lough 1976; Anger 1991, 1998; Cieluch et al. 2004; Brodie et al. 2007). Enhanced tolerances in the first zoeal stage, through hyper-regulation, may enable zoeae to endure brackish estuarine waters until they migrate in later developmental stages to higher, more stable open ocean salinities by advection or swimming (Cieluch et al. 2004). With further development, their regulatory ability and thus, the ability to tolerate low salinities may increase again, producing adults with high hyper-regulatory capacities (Charmantier and Charmantier-Daures 1991; Cieluch et al. 2004; Taylor and Seneviratna 2005). As *C. japonica* adults migrate in and out of estuaries that experience the full range of environmental variables, it will be important to determine the temperature and salinity tolerances of all developmental stages in future research.

Zoeal survival in *C. japonica* will also be influenced by fluctuations in sea surface temperatures and salinities in estuaries and harbours related to physical features such as residence time (the range in New Zealand is 1.5 and 24 days, Heath 1976), water temperature and depth, proximity to freshwater sources, season and wind. For example, in the Waitemata Harbour, which has a residence time range of 6 to 7 days (Williams 1986), *C. japonica* has been captured at sites that experience temperature ranges of 17 to 26°C and salinity ranges of 25 to 37‰ during the breeding season (Auckland Regional Council 2009). In its native range, development through the six *C. japonica* zoeal stages takes a minimum of 17 days after hatching, with Stage 1 taking a minimum of 3 days (Yatsuzuka 1952). If a gravid female spawned in the upper Waitemata Harbour, zoeae might mature to the third

developmental stage before reaching the oceanic temperature and salinity conditions of the harbour entrance 20 km away. However, if water currents retained larvae in the upper reaches, progression through all the zoeal and megalopae stages might occur in the generally warmer and lower salinity conditions of the estuary. This may become particularly important for larvae at higher latitudes where the oceanic temperature may be much cooler than the shallower estuarine water.

Although the impact of *C. japonica* on New Zealand's native marine species remains unclear at the present time, this large (up to 110 mm CW) portunid crab is a significant predator on important benthic invertebrates and may play a key role in structuring communities (Fowler, *in prep.*). In its native range, *C. japonica* preys upon a large variety of benthic species including bivalves, crustaceans, cephalopods and fish and may also catch squid and shrimp (Ai-Yun and Yang 1991; Weimin et al. 1998). It can be expected that *C. japonica*, once it occurs in high densities, will consume high numbers of bivalves and other benthic marine fauna in New Zealand (Fowler, *in prep.*). Based on the results presented here, the temperature and salinity tolerances of *C. japonica* Stage 1 zoeae do not appear to be a significant barrier to *C. japonica*'s continued spread in temperate New Zealand. Additionally, as Stage 1 zoeae show enhanced survival at temperatures $\geq 16^{\circ}\text{C}$, and optimal rearing conditions at temperatures $> 24^{\circ}\text{C}$ (Yatsuzuka 1952; Jiang and Wang 2004), the warmer seawater temperatures predicted under global climate change for New Zealand (1.5 to 3°C increase, Salinger and Hicks 1990) may facilitate the expansion of the species southwards into areas normally too cold for larval development (e.g. deRivera et al. 2007). We therefore predict that, as a result of larval and/or adult dispersal from populations within New Zealand and/or additional introductions from overseas, *C. japonica* will spread and establish populations in other harbours and estuaries on the North Island within the next decade.

Chapter Five

Interactions between an invasive predator, *Charybdis japonica*, and a similar native predator, *Ovalipes catharus*, in northeastern New Zealand

Introduction

There are two stages to any invasion: (1) introduction, colonization and establishment of a species in a new area, and (2) spread and replacement of, or coexistence with, native species. The success or failure of a species, once it has dispersed to a new environment, is influenced by at least three factors: (1) the amount of resources available to the invader and their ability to utilize these resources, (2) the pattern of resource use among native organisms that the invader must compete against, and (3) the strength and organization of interspecific competition within the community and the ability of the invader to successfully enter the community structure (including both positive and negative interactions) (Bruno et al. 2003, Dunstan and Johnson 2007). Those species that compete strongly with native species for resources such as food and space tend to establish themselves quickly and effectively in a novel community (Dunstan and Johnson 2007).

As a group, crustaceans have been highly successful invaders (Weis 2010). Their aggressive antagonistic behaviors (i.e. visual displays, physical combat) often enable them to win disputes over a limited resource such as food and/or shelter and has been instrumental to the success of several invasive crab species (McDonald et al. 2001, Jensen et al. 2002, deRivera et al. 2005, Williams et al. 2006, MacDonald et al. 2007, Roche and Torchin 2007, Gibley et al. 2008, Dauvin et al. 2009). This superior competitive ability has even been shown to restrict the distributions of similar native crabs or even other invasive crabs (Lohrer and Whitlatch 2002, Hunt and Behrens Yamanda 2003, deRivera et al. 2005, Kraemer et al. 2007, Belair and Miron 2009, Breen and Metaxas 2009). In several cases, it is a matter of the invasive being a larger, superior species, but even smaller or equally sized invasives have been shown to competitively dominate native species for resources (i.e. McDonald et al. 2001, deRivera et al. 2005, Williams et al. 2006). However, despite the importance of competitive exclusion for prey and/or shelter for determining the success of mobile invasive species in novel environments, limited research has been conducted concerning the interspecific interactions between native and invasive crabs for a single resource (Gibley et al. 2008). Therefore, in this study, we aimed to describe the changes in feeding behavior of a native crab when exposed to a novel invasive crab.

An invasive Asian paddle crab, *Charybdis japonica*, was first recorded in 2000 by Auckland fishermen and immediately distinguished from the only similarly sized endemic paddle crab (*Ovalipes*

catharus) by their highly aggressive nature (i.e. claw waving and pinching motions) (Webber 2001). Although indigenous throughout East Asia (Wee and Ng 1995), *C. japonica* has colonized and established reproducing populations in northeastern New Zealand (Gust and Inglis 2006, Jones and Browne 2006, Chapter 2). Attaining a maximum size of 110mm carapace width in its native range, *C. japonica* is an abundant intertidal predator that consumes benthic bivalves, crustaceans, fish, and cephalopods (Weimin et al. 1998). The largest known population of *C. japonica* in New Zealand is currently located in Auckland Harbour at depths of 13m (see Fig. 2.1) (J MacDonald, *personal communication*) and occupies several habitat types, including sediment suitable for the commercially important indigenous portunid crab *O. catharus* (Gust and Inglis 2006).

Like *C. japonica*, *O. catharus* is a large (up to 150mm carapace width), versatile and opportunistic predator found off sandy beaches and in harbours and estuaries to 15m depth (Armstrong 1985, Davidson 1987, Wear 1988). A comparison of the prey of the two species indicates significant dietary overlap, and both are known to consume conspecifics and interspecifics (Davidson 1987, Wear and Haddon 1987, Weimin et al. 1998, Fowler, *unpublished data*). Although diel or seasonal movement patterns are not known for *C. japonica* in New Zealand, *O. catharus* juveniles are known to settle in sheltered harbours and estuaries while adults migrate to the more sheltered parts of harbours, bays, and estuaries to molt and mate (Wear 1982, Osborne 1987a, 1987b). Trapping surveys in Auckland Harbour in 2002/2003 caught both species, with *C. japonica* abundance increasing and *O. catharus* abundance decreasing each subsequent year (Gust and Inglis 2006). Although it is unknown as to when the apparent decline in *O. catharus* and increase in *C. japonica* began, trapping by the Ministry of Agriculture and Forestry Biosecurity New Zealand (hereafter MAFBNZ) in Auckland Harbour has shown this consistent trend over the past eight years, with the most obvious disparity between populations during the February 2010 survey (J MacDonald, *personal communication*). Since its introduction, *C. japonica* populations have been expanding along the New Zealand coastline (Gust and Inglis 2006, Jones and Browne 2006), which may intensify their antagonistic competitive interactions with *O. catharus* and ultimately determine the abundance and distribution of both species. The potential for niche and habitat overlap between the species indicates the need to assess, for predictive purposes, the possible effects of this invasive portunid on its indigenous competitor.

Besides displacing native *O. catharus* from their shared habitat, it is also possible that adult *C. japonica* prey upon juvenile and adult *O. catharus*. While predation may have the most direct impact, other behavioral interactions (i.e. removal from refugia, interrupted reproduction) may be equally important as native species that have been competitively displaced from preferred areas may encounter more predators or have decreased access to food (Gibley et al. 2008).

In this study, the inter- and intraspecific behavioral interactions of similarly sized individuals of the two species were investigated in the presence of a single food source. In separate controlled experiments, an individual crab was allowed to start to consume a single prey item, after which a competitor was introduced and their interactions recorded. If, in competition for a single prey item, *C. japonica* retained control of the prey item or stole it from *O. catharus*, *C. japonica* will have the potential to outcompete *O. catharus* during encounters while foraging in the natural environment. In particular, the following questions were asked: (1) How will competition with *C. japonica* affect the feeding behavior of *O. catharus*? (2) How does *O. catharus* respond to aggressive actions initiated by *C. japonica*? (3) Can *O. catharus* displace *C. japonica* from prey items? (4) Is it possible for the two species to share food?

Methods

Study organisms

Intermoult *C. japonica* were collected from the Weiti River on the Whangaparaoa Peninsula of New Zealand (36° 38'24 S, 174° 43'38 E, see Fig. 2.1) in oval-shaped collapsible traps baited with a single pilchard (*Sardinops sagax*) at approximately 2m depth. Intermoult *O. catharus* were collected from Omaha Beach (36° 20'00 S, 174° 46'90 E), where *C. japonica* have not been trapped, using the same methods. The dimensions of the traps were 64 x 47 x 20cm (l x w x h) with a diagonal mesh size of 20mm and an entrance funnel opening into the trap (diameter 90mm). *C. japonica* traps were allowed to fish for a 24hr tidal cycle; *O. catharus* traps were checked at 30 min intervals. Trapped crabs were transported to the Leigh Marine Laboratory. *C. japonica* were maintained in individual aquaria (40 x 50 x 30cm) each containing ~60L of unfiltered natural seawater at ambient temperature, under a light regime of 12L:12D, with air supplied by bubblers at a low pressure. *O. catharus* were separated by sex and maintained in a large tank (152.5 x 120 x 20cm) containing ~365L of unfiltered natural seawater under the same conditions. All crabs were fed chopped pilchard until satiation every other day but were isolated and starved for 48hr prior to the experiments to standardize hunger levels and to ensure feeding during trials. To limit the effect of crab size on the outcome of the trial, the carapace width (hereafter CW) of each test crab was determined to the nearest 1mm using dial callipers and only those crabs between 57 and 67mm CW with all appendages intact were used in trials.

Experimental design

To isolate and quantify the antagonistic interactions between *C. japonica* and *O. catharus*, we examined their behavioral interactions in the presence of a single mussel (*Perna canaliculus*) in the

laboratory. Because the behavior of the crabs may depend on which species was given food first (i.e. priority effects), 12 experimental treatments were included that combined all possible single and multiple species combinations of both predators and sexes, allowing for each species/sex to initially control the single food item (Table 5.1). Five replicates of each treatment were run, and crabs were randomly assigned to each treatment. A total of 23 male *O. catharus*, 24 female *O. catharus*, and 20 male *C. japonica* were used. Female *C. japonica* were not used in these experiments as sufficient numbers could not be obtained. Crabs from both species that were experimentally used twice were allocated to treatments randomly, with the constraint that they could not be allocated to any of the following three groups of treatments more than once: (1) interspecific interaction, (2) intraspecific interaction or (3) solitary. This was intended to prevent any influence of prior experience on the outcome of the second trial for an individual crab. Crabs were kept for 1wk prior to experiments to allow for acclimatization and 1wk after to monitor for molting and death. One crab molted within a week of the conclusion of an experiment, and that trial was repeated using new crabs.

All experiments were conducted during the dark cycle of the 12L:12D light regime between January 28 and February 17, 2010 as both *O. catharus* (Clark 1978) and *C. japonica* (Fowler, *unpublished data*) are more active at night. Each isolated experimental chamber (27.5 x 20.5 x 27cm) contained ~10.5L (19cm water depth) of continually circulating unfiltered natural seawater. Before each trial, crabs were placed in the experimental chamber and separated using an opaque plastic partition for 24hr to acclimatize. At the start of a trial, a single mussel (*P. canaliculus*, shell length 50.7 – 63.8mm) was cut open, halved, and given to one crab. *P. canaliculus* was chosen as the prey item as it is found in the natural diet of *O. catharus* (Wear and Haddon 1987) and *C. japonica* (Chapter 2). Once the crab had started to consume the mussel, the lid separating the two crabs was removed and the trial commenced.

All trials were videotaped for 60min using a Swann CCD video camera (KC54140, 420TVL) mounted 1.5m above the chambers. Signals from the camera were directed to a PCTV2 USB frame grabber then to the program H264 Webcam 3.53 (Timhillone Software), where it was recorded. An LED infrared illuminator (TAFU TF-30M80) with a range of 30m and IR angle of 80° was used as the light source. Cronin (1986) found that brachyuran crabs cannot detect infrared light and similar methodology has been employed previously to record nocturnal crab behaviour (Weissburg and Zimmer-Faust 1994, McDonald et al. 2001, Williams et al. 2006). Due to equipment limitations, four video trials were simultaneously conducted and two rounds of night observations were completed, for a total of eight trials each night.

Video files of each trial were later quantitatively analysed for the following categories: (1) total time in possession of the mussel, (2) total time in aggressive stance, (3) total time spent on evasion tactics (i.e. swimming both while eating and after eating and time spent on the side of the experimental chamber), (4) total number of aggressive actions (i.e. attacks during and after feeding and shoves), (5) total number of successful and unsuccessful displacements from the mussel, (6) total time both competitors had possession of the mussel and were either exhibiting a tug-of-war scenario or were both amicably feeding together, and (7) total time in combat (time in which one competitor was holding onto another, not allowing it to escape). Average duration, counts, and proportions were then categorized as H (high), M (medium) or L (low) as outlined in Table 5.2.

Table 5.1 Predator treatments included in the laboratory experiment to examine the behavioural interactions between the invasive crab *Charybdis japonica* and a similar native crab *Ovalipes catharus*. Numbers given are individuals per chamber. The asterisk denotes which species was allowed to start consuming the mussel at the beginning of each trial. A single mussel (*Perna canaliculus*) was used as prey in each of the 12 treatments. Each treatment was replicated five times. Abbreviations: OM, male *O. catharus*; OF, female *O. catharus*; CM, male *C. japonica*.

Treatment no.	Predator(s)		
	OM	OF	CM
1	1*	-	-
2	-	1*	-
3	-	-	1*
4	1*	1	-
5	1	1*	-
6	1*	-	1
7	1	-	1*
8	-	1*	1
9	-	1	1*
10	2	-	-
11	-	2	-
12	-	-	2

Table 5.2 Categories of response variables used for the analysis of the behavioral interactions of the endemic crab *Ovalipes catharus* and the invasive crab *Charybdis japonica* in the presence of a single mussel (*Perna canaliculus*).

Response variable	H (high)	M (medium)	L (low)
(1) Total time in possession of the mussel	≥ 1000 sec	500 – 999 sec	0 – 499 sec
(2) Total time in aggressive stance	≥ 1000 sec	500 – 999 sec	0 – 499 sec
(3) Total time spent on evasion tactics	≥ 1000 sec	500 – 999 sec	0 – 499 sec
(4) Total number of aggressive actions	≥ 100 actions	50 – 99 actions	0 – 49 actions
(5) Proportion of successful displacements	41 – 60%	21 – 40%	0 – 20%

Results

Mussel possession

There was a reduction in the average mussel possession time (AMPT) for both sexes of *O. catharus* when they were paired against male *C. japonica* instead of conspecifics (Table 5.3A). Female *O. catharus* showed higher AMPT when paired with their same sex than with male *O. catharus* and had a higher AMPT than *O. catharus* males when they were paired with male *C. japonica* (Table 5.3A). Male *C. japonica* AMPT remained high throughout all combinations with both sexes of *O. catharus* except for a slight decrease when they were paired with female *O. catharus* and were given the mussel first (Table 5.3A). When male *C. japonica* were paired with conspecifics, those given the mussel first retained it throughout the trial, drastically reducing the AMPT of the second male *C. japonica* (Table 5.3A).

Aggressive displays

In all combinations, male *O. catharus* exhibited a low to medium average duration of aggressive displays (ADAG) while male *C. japonica* consistently showed high ADAGs (Table 5.3B). Female *O. catharus* demonstrated low ADAGs throughout all combinations (Table 5.3B).

Evasion tactics

When both male and female *O. catharus* were paired with conspecifics, there was little time spent on evasion tactics (Table 5.3C). However, when both sexes of *O. catharus* were paired with male *C. japonica*, the average time of evasion tactics (ATET) increased dramatically (Table 5.3C). Male *C. japonica* showed no evasion tactics when paired with either sex of *O. catharus*. However, when paired against conspecifics, the male *C. japonica* that was not given the mussel first exhibited a higher ATET (Table 5.3C).

Aggressive actions

In all experimental combinations, both male and female *O. catharus* exhibited a low average number of aggressive actions (ANAA) towards their competitors irrespective of who received the mussel first (Table 5.3D). Male *C. japonica*, however, consistently showed a medium to high ANAA towards both sexes of *O. catharus*, but decreased ANAA directed towards male conspecifics if they were not given the mussel first (Table 5.3D).

Table 5.3 Response variables of the endemic crab *Ovalipes catharus* and the invasive crab *Charybdis japonica* in all sex / species combinations (each combination n=5) relative to whether the crab was given the food first or not. The average of the response variable was categorized as H (high), M (medium), or L (low) as outlined in Table 1. Letters (L, M or H) apply to crabs in rows (i.e. In Male *O. catharus* / Female *O. catharus* pairings in **A**, when the male was allowed initial possession of the food (“First Male *O. catharus*”), it obtained it, on average, for a low period of time; when the male was not given the food first (“Second Male *O. catharus*”) during the same pairings, it had an average medium possession time of the food). The mean \pm SE for each is placed in parentheses next to the corresponding letter. A single mussel (*Perna canaliculus*) was used as prey in each of the trials.

A. Average time of possession of the food item

	Male <i>O. catharus</i>	Female <i>O. catharus</i>	Male <i>C. japonica</i>
First Male <i>O. catharus</i>	M (801 \pm 278)	L (381 \pm 171)	L (91 \pm 41)
Second Male <i>O. catharus</i>	M (999 \pm 328)	M (536 \pm 294)	L (55 \pm 52)
First Female <i>O. catharus</i>	H (1421 \pm 254)	H (1501 \pm 628)	L (406 \pm 143)
Second Female <i>O. catharus</i>	H (1308 \pm 258)	M (927 \pm 485)	M (588 \pm 234)
First Male <i>C. japonica</i>	H (1492 \pm 550)	M (757 \pm 398)	H (1280 \pm 583)
Second Male <i>C. japonica</i>	H (1006 \pm 235)	H (1430 \pm 306)	L (169 \pm 122)

B. Average duration of aggressive displays

	Male <i>O. catharus</i>	Female <i>O. catharus</i>	Male <i>C. japonica</i>
First Male <i>O. catharus</i>	M (586 \pm 51)	L (422 \pm 183)	M (712 \pm 519)
Second Male <i>O. catharus</i>	M (958 \pm 567)	L (312 \pm 119)	L (333 \pm 241)
First Female <i>O. catharus</i>	L (279 \pm 83)	L (383 \pm 182)	L (472 \pm 241)
Second Female <i>O. catharus</i>	L (241 \pm 56)	L (448 \pm 159)	L (411 \pm 161)
First Male <i>C. japonica</i>	H (1863 \pm 306)	H (1448 \pm 312)	H (1025 \pm 360)
Second Male <i>C. japonica</i>	H (1754 \pm 230)	H (1162 \pm 257)	H (1153 \pm 376)

C. Average time of evasion tactics

	Male <i>O. catharus</i>	Female <i>O. catharus</i>	Male <i>C. japonica</i>
First Male <i>O. catharus</i>	L (213 ± 96)	L (276 ± 125)	H (1290 ± 217)
Second Male <i>O. catharus</i>	L (73 ± 23)	L (417 ± 347)	H (1204 ± 175)
First Female <i>O. catharus</i>	L (51 ± 38)	L (235 ± 150)	H (1035 ± 189)
Second Female <i>O. catharus</i>	L (65 ± 24)	L (440 ± 170)	M (723 ± 294)
First Male <i>C. japonica</i>	L (0)	L (0)	L (337 ± 283)
Second Male <i>C. japonica</i>	L (0)	L (0)	H (1064 ± 455)

D. Average number of aggressive actions

	Male <i>O. catharus</i>	Female <i>O. catharus</i>	Male <i>C. japonica</i>
First Male <i>O. catharus</i>	L (22 ± 4)	L (27 ± 6)	L (1 ± 0)
Second Male <i>O. catharus</i>	L (31 ± 16)	L (16 ± 6)	L (2 ± 1)
First Female <i>O. catharus</i>	L (35 ± 13)	L (38 ± 12)	L (1 ± 1)
Second Female <i>O. catharus</i>	L (38 ± 13)	L (21 ± 4)	L (2 ± 1)
First Male <i>C. japonica</i>	H (111 ± 13)	M (54 ± 14)	M (56 ± 15)
Second Male <i>C. japonica</i>	H (111 ± 20)	M (76 ± 5)	L (29 ± 17)

Successful and unsuccessful displacements from the mussel

Male *O. catharus* had a low to medium average success rate of displacements (ASRD) when they attacked any other sex or species (Table 5.4). Although male *O. catharus* averaged the highest number of aggressive attacks against their competitors, their displacement success rate was relatively low (Fig. 5.1). Female *O. catharus*, however, exhibited a high ASRD against male *O. catharus* and a low ASRD against male *C. japonica* (Table 5.4, Fig. 5.1). The ASRD of male *C. japonica* was not affected at all by either their competitor's sex or species and remained a steady medium ASRD (Table 5.4). Although male *C. japonica* showed lower average numbers of aggressive attacks on all competitors, they had the highest proportion of those attacks being successful independent of the sex or species of their competitor (Fig. 5.1). However, male *C. japonica* had no more success gaining control of the mussel in the presence of either sex of *O. catharus* than against its own conspecifics (Fig. 5.1).

Table 5.4 Average percentages of attacks (\pm SE) that were successful displacements by the endemic crab *Ovalipes catharus* or the invasive crab *Charybdis japonica* in all sex / species combinations. Average percentages of attacks that were successful displacements was categorized as H (high), M (medium), or L (low) as outlined in Table 1. Letters (L, M or H) apply to the attacking crabs in rows (i.e. In Male *O. catharus* / Female *O. catharus* pairings, when the male was the attacker, it successfully displaced the female only 0 – 20% (L) of the time; when the female was the attacker during the same pairings, it was able to successfully displace the male 41 – 60% of the time (H).). The mean percentage of attacks that were successful displacements (\pm SE) for each category is placed in parentheses next to the corresponding letter. A single mussel (*Perna canaliculus*) was used as prey in each of the trials. Each combination incorporated data from both the crab that was given the mussel first and their competitor; therefore each combination was replicated 10 times.

Attacker	Defender		
	Male <i>O. catharus</i>	Female <i>O. catharus</i>	Male <i>C. japonica</i>
Male <i>O. catharus</i>	M (37 \pm 11)	L (17 \pm 8)	M (22 \pm 13)
Female <i>O. catharus</i>	H (52 \pm 10)	M (26 \pm 11)	L (20 \pm 11)
Male <i>C. japonica</i>	M (40 \pm 14)	M (38 \pm 12)	M (38 \pm 14)

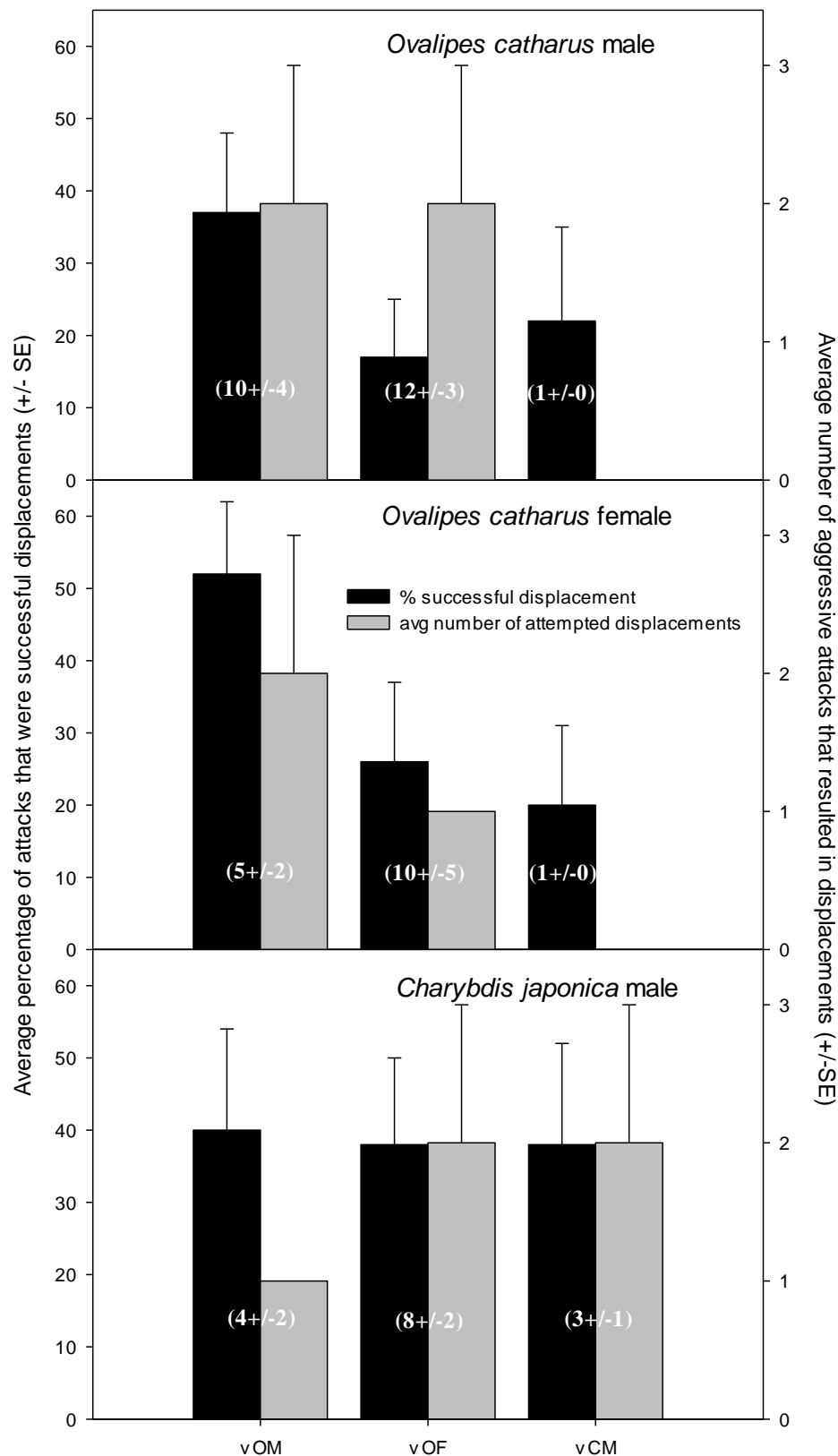


Figure 5.1 Feeding events by *Ovalipes catharus* males and females and *Charybdis japonica* males competing for an opened mussel (*Perna canaliculus*) in video observations (n=10 for each bar). The mean percentage (\pm SE) and average number of attacks that were successful displacements (instances when an attack resulted in the adversary relinquishing the mussel) (\pm SE) are shown. The average number of attacks (both successful and unsuccessful) (\pm SE) is shown in parentheses for each combination. Abbreviations: OM, male *O. catharus*; OF, female *O. catharus*; CM, male *C. japonica*.

Food sharing

The highest percentage of food sharing occurred in the combined *O. catharus* / *O. catharus* trials, while the lowest occurred in the *O. catharus* / male *C. japonica* trials (Table 5.5). Food sharing occurred in almost half of all male *C. japonica* / male *C. japonica* trials (Table 5.5). In the male *O. catharus* / male *C. japonica* trials, there was no difference in the frequency at which both competitors had possession of the mussel when compared to which competitor was given the mussel first; however, the average duration of the interaction increased four times in cases when male *C. japonica* were given the mussel first (Table 5.5). In the female *O. catharus* / male *C. japonica* trials, there was a two fold increase in the frequency in which both competitors had possession of the mussel when *O. catharus* was given in the mussel first, but the duration of the interaction decreased by half in these interactions (Table 5.5).

Table 5.5 The frequency and duration each combination of the invasive crab *Charybdis japonica* and the endemic crab *Ovalipes catharus* had possession of the mussel (*Perna canaliculus*) at the same time. The asterisk denotes which species was allowed to start consuming the mussel at the beginning of each trial. A single mussel was used as prey in each of the trials. Each combination was replicated five times, except for the single sex and species combinations in which both sets of trials letting each of the crabs begin eating first were combined. Abbreviations: OM, male *O. catharus*; OF, female *O. catharus*; CM, male *C. japonica*.

<i>Combination</i>	<i>% of all trials where both were on food at the same time</i>	<i>Average time (sec) ± 1 SE both on food at same time</i>
OM v OM	100	34.0 ± 6.5
OM* v OF	100	34.8 ± 30.1
OM v OF*	80	66.4 ± 42.3
OM* v CM	20	0.4 ± 0.4
OM v CM*	20	2.0 ± 2.0
OF v OF	60	23.4 ± 8.8
OF* v CM	40	0.8 ± 0.6
OF v CM*	20	1.6 ± 1.6
CM v CM	40	14.6 ± 8.6
Total O v O	85	36.6 ± 9.0
Total O v C	25	1.2 ± 0.6
Total C v C	40	14.6 ± 8.6

Combat time

Combat time, during which one competitor was holding onto another, not allowing it to escape, was recorded in seven out of 60 trials; out of those seven trials, combat time was only observed once

during all *O. catharus* / *O. catharus* combinations during a male / female combination when the male was given the mussel first. In this instance, the male attacked the female and held her for six seconds. The average combat time (\pm SE) observed for the three *O. catharus* / male *C. japonica* combinations was 562.3 ± 551.7 sec and only occurred in female *O. catharus* / male *C. japonica* pairings. In all three cases (out of a total of 10 trials), the male *C. japonica* attacked and held the female *O. catharus*. In one of these cases, the male *C. japonica* attacked and held the female *O. catharus* for 27 min and 46 sec, and the female *O. catharus* shed both a chelae and walking leg at different times to escape. The male *C. japonica* fed on both of these appendages, but this feeding was not included in the data analysis. Combat interactions occurred in three out of the 10 male *C. japonica* / male *C. japonica* pairings and lasted for an average (\pm SE) of 492 ± 303.5 sec. Although there were aggressive interactions during most trials involving crab pairings, there were no instances of conspecific or interspecific killings.

Discussion

The success of crab invaders in outcompeting similar native species for a single resource has been documented for only a few species (summarized in Table 5.6). In the present study, male individuals of an invasive Asian paddle crab *Charybdis japonica* dominated both male and female native New Zealand paddle crabs *Ovalipes catharus* in one-on-one competition for food, regardless of which crab possessed the food initially. First possession of the resource apparently did not confer any advantage on the possessor, which has also been noted in other crab interactions (McDonald et al. 2001, Jensen et al. 2002, MacDonald et al. 2007). While male and female *O. catharus* exhibited the ability to successfully commandeer prey from each other, their inability to successfully defend the food or obtain it from *C. japonica* demonstrates the much more aggressive nature of the invasive predator. *C. japonica* individuals frequently displaced *O. catharus* of both sexes that were previously feeding by striking out with their chelae, while *O. catharus* usually failed to successfully acquire the prey if *C. japonica* was feeding. *O. catharus* were able to displace *C. japonica* from the prey in some trials, but generally this occurred near the end of the hour when *C. japonica* had already consumed most of the mussel flesh. These results suggest that male *C. japonica* may have an advantage over, or at least decrease the prey available to, *O. catharus*, which were not successful in defending or acquiring the prey item.

Video observations reveal that male *C. japonica* behave aggressively towards *O. catharus* and conspecifics of equal size when competing for a prey item; *O. catharus* showed low levels of aggressive behaviors throughout all trials and increased time spent evading *C. japonica*. While *C. japonica* attacked *O. catharus* and conspecifics with their chelae, actively trying to grasp or nip their opponent, *O. catharus* often only shoved their competitors using the outward side of their chelae. The

proportion of trials and the average time spent sharing food, in which both crabs were amicably feeding on the prey at the same time, was highest and longest in duration in *O. catharus* conspecific combinations; this decreased in interspecific trials. Other similarly sized conspecific crab predators also show lower levels of aggression towards one another than when paired with interspecifics (Huntingford et al. 1995, Lee 1995, Hunt and Behrens Yamanda 2003).

Intraspecific cannibalism and interspecific predation is known to occur in many species of crabs, including *O. catharus* and *C. japonica* (Davidson 1987, Wear and Haddon 1987, Fowler, *unpublished data*), and can regulate population size, reduce intraspecific competition and be a nitrogen diet supplement (Klein Breteler 1975, Kneib et al. 1999). Although *C. japonica* were competitively dominant and have been observed to consume *O. catharus* in a laboratory setting (Fowler, *personal observation*), it seems that they do not kill or consume *O. catharus* in the presence of an alternative food source. The one instance in this study of *C. japonica* attacking and holding a female *O. catharus* for almost 28 min resulted in *O. catharus* shedding a chela and walking leg to escape; *C. japonica* did not actively remove the appendages but did consume the flesh from them. It can be hypothesized that if *C. japonica* does not kill *O. catharus* in the confined tanks, it is highly unlikely that they do so in the natural environment where escape is much easier. Based on the lack of predation observed in the presence of an alternative food source during these laboratory trials, direct predation by *C. japonica* alone cannot explain the low abundance or absence of *O. catharus* seen in subsequent trappings in Auckland Harbour over the past several years. However, it has been shown that similar sized competitors seldom kill each other (Huntingford et al. 1995, Lee 1995), and interactions between two differently sized competitors (i.e. adults and juveniles) more often lead to predation (i.e. Hunt and Brehens Yamada 2003). Also, *O. catharus* can reach 150mm CW whereas *C. japonica* can only grow to 110mm CW; therefore, it is possible that the natural interactions between these individuals could be different from what was observed in this experiment. As this study concentrated on similarly sized individuals and it has been observed that *C. japonica* kill and consume *O. catharus* in the laboratory, inter- and/or intraspecific predation may occur in natural conditions between different life stages and may impact the distribution of both species.

The abundance and distribution patterns of one crab species can directly impact the abundance levels and distribution patterns of co-existing crab species by predation on and / or competition between species (Lohrer and Whitlatch 2002, Hunt and Behrens Yamanda 2003, deRivera et al. 2005, Kraemer et al. 2007, Belair and Miron 2009, Breen and Metaxas 2009). However, the competitive superiority of *C. japonica* over *O. catharus* will only be of consequence where the two have overlapping habitat ranges. While *C. japonica* is mostly found in sandy sheltered areas (Gust and

Inglis 2006), *O. catharus* is more commonly found on oceanic sandy beaches (McLay, *personal communication*). However, *O. catharus* juveniles are known to settle in the sheltered harbours and estuaries where *C. japonica* is currently trapped extensively, and *O. catharus* adults migrate to harbours, bays, and estuaries to molt and mate (Wear 1982, Osborne 1987a, 1987b). Despite the seasonal movement patterns of *O. catharus* and the known overlap of their habitat and distribution with *C. japonica* in New Zealand, there is doubt as to whether these species will interact to any great degree (Gust and Inglis 2006, Jones and Browne 2006). However, comparisons of diet between the two species revealed a strong dietary overlap, providing the impetus for interactions due to food availability if the two species do overlap in range (Wear and Haddon 1987, Davidson 1987, Weimin et al. 1998, Chapter 2). Forced by their smaller chelae size to consume prey items within a limited size range, there may be an increased prevalence of antagonistic interactions between juveniles of both species for similar prey. Although the species' distributions may only overlap temporally, the possibility that *C. japonica* may come into contact and compete with recently settled juvenile *O. catharus* as well as mating adults begs the question as to whether the invasive crab may ultimately affect the recruitment patterns of *O. catharus*.

Trapping surveys in Auckland Harbour in 2002/2003 caught both species of crabs but never in the same trap (Gust and Inglis 2006). Overall, traps caught more *C. japonica* than *O. catharus* each year (Gust and Inglis 2006), and there has been a decrease in *O. catharus* abundance over time with the most obvious disparity in February 2010 (J MacDonald, *personal communication*). It is important to note, however, that these trapping surveys were completed quickly and may only show a snapshot of each species' distribution patterns. Although highly unlikely, it is possible that *O. catharus* are still in the areas they have historically occupied but are not appearing in the traps; a more feasible explanation, based on the results of this study, is that trapped *C. japonica* exclude *O. catharus* from occupied traps or from the entire area with their aggressive displays. However, it would also be expected that if *O. catharus* entered a trap first, *C. japonica* would not be deterred and both crabs would be caught unless *C. japonica* consumed *O. catharus* while in the trap. The aggressive behavior and known predation of *Cancer productus* on *C. maenas* on the west coast of the USA is thought to influence the trapping ratios of these species in areas where they coexist (Hunt and Brehens Yamada 2003). Therefore, it is feasible that the aggressive behavior of *C. japonica* may be influencing the range of *O. catharus* on two different spatial scales. While the possible active avoidance by *O. catharus* of *C. japonica* may reduce interspecific competition and allow both species to coexist in the same area, it may have overreaching effects that ultimately drive *O. catharus* out of part of its historical range. Spatial and temporal interspecific avoidance has been shown in other crab species (Navarrette and Castilla 1990, Stehlik et al. 2004). While laboratory trials from this study suggest that *C. japonica* has the potential to

influence the catch rate of *O. catharus*, further investigations over wider temporal and spatial scales are needed to determine if the distribution of the native crab is, in fact, changing.

Over time, the successful removal and sustained exclusion of *O. catharus* from previously occupied territory could have substantial effects on the population structure of this species and the ecosystem as a whole. As a predator of New Zealand's soft-sediment open ocean and estuarine environments, *O. catharus* is an important trophic species that helps regulate the natural balance of marine benthic communities (Haddon and Wear 1993). Although it is possible for *C. japonica* to fulfill the role of an important predator, the removal or exclusion of *O. catharus* from its natural range can have over-reaching impacts on trophic cascades. For example, differences in foraging between invasive and native crabs and anti-predator responses of prey can disrupt native food webs and lead to a loss of marine biodiversity and ecosystem function (Kimbro et al. 2009). Alternatively, competition between species for food and/or space may alter the predation pressure exerted by *O. catharus* on the shared prey, thus upsetting the ecosystem balance (e.g. intraguild predation; Griffin 2006, Griffin and Byers 2006).

However, the overall results from this study should be viewed cautiously as both species are highly mobile intertidal and subtidal predators, and their interactions are likely to be complex due to many factors (i.e. interference and/or exploitative competition, predation, and intraspecific cannibalism). To induce competition in this experiment a single prey item was presented to two starved crabs in a confined space, therefore eliciting maximum antagonistic behavior for a limited resource. Competition is extremely difficult to demonstrate in natural environments (Byers 2000), and the ultimate prerequisite (by definition) is a limiting resource. As it is unknown as to whether food is a limiting resource for either species in natural conditions, the overall consequences of the superior competitive ability of *C. japonica* in the field remains questionable. Giving one crab the prey item at the beginning of the trial eliminated the time it took for crabs to search for food and may not be directly applicable to situations in nature as in most cases individuals may not have to compete and, if they do, each would have the option of fleeing with the prey item (Jensen et al. 2002). For instance, the prolonged escape response by *O. catharus* during their interactions with *C. japonica* may enable *O. catharus* to effectively win such trials, keep possession of the prey, and swim away instead of surrendering it to *C. japonica*. It is also possible that *O. catharus* simply avoids all confrontations with *C. japonica* and moves to unoccupied space if they come into contact with one another, as seen with *Callinectes sapidus* conspecifics (Mansour and Lipcius 1991). Only in interspecific trials did *O. catharus* exhibit prolonged swimming, which may indicate their preference to escape from *C. japonica* rather than compete. As such, there are likely some qualitative and quantitative behavioral differences

between the laboratory settings and natural conditions. Given the limited scope of the experiments, this study should be viewed as a starting point for further investigations into the interactions between *C. japonica* and *O. catharus*, as understanding the dynamics of species interactions is critical to mapping the possible distribution and impact of *C. japonica* in northeastern New Zealand. Combined with field manipulations and long-term monitoring projects, more studies are needed to ascertain the possibility of competition between the species and the exclusion of either species from previously occupied territory.

Table 5.6 Results of experimental manipulations involving invasive and native crabs competing for a limited resource.

Invasive Species	Native Species	Limiting Resource	Superior Competitor	Reference
<i>Charybdis japonica</i>	<i>Ovalipes catharus</i>	Prey	<i>C. japonica</i>	This study
<i>Carcinus maenas</i>	<i>Cancer magister</i>	Shelter	<i>C. maenas</i>	McDonald et al. 2001
		Prey	<i>C. maenas</i>	McDonald et al. 2001
	<i>Cancer irroratus</i>	Prey	Neither	Belair and Miron 2009
	<i>Hemigrapsus oregonensis</i>	Shelter	<i>H. oregonensis</i>	Jensen et al. 2002
		Prey	<i>C. maenas</i>	Jensen et al. 2002
	<i>Callinectes sapidus</i>	Prey	<i>C. maenas</i> ¹	deRivera et al. 2005
		Prey	<i>C. maenas</i>	MacDonald et al. 2007
	<i>Homarus americanus</i> ⁵	Prey	Neither ²	Williams et al. 2006
		Prey	<i>C. maenas</i>	Rosson et al. 2006
<i>Hemigrapsus sanguineus</i>	<i>Callinectes sapidus</i>	Shelter	<i>C. maenas</i> ³	Rosson et al. 2006
		Prey	Neither	MacDonald et al. 2007
<i>Eriocheir sinensis</i>	<i>Carcinus maenas</i>	Shelter	<i>E. sinensis</i>	Gibley et al. 2008

¹While *C. sapidus* consumed more *C. maenas* than the limiting prey, *C. maenas* consumed more of the limiting prey and is listed as the superior competitor for the shared prey. ²Whichever crustacean was given access to the prey item first retained possession and was deemed the superior competitor. ³*C. maenas* was not interested in obtaining access to the shelter and rather hunted the lobster, *H. americanus*, as a prey item. *H. americanus* viewed the shelter as effective protection from predation and not a limited resource. Therefore, ultimately, *C. maenas* consumed many *H. americanus* and can be viewed as the superior overall competitor. ⁵All the species mentioned in the table are crabs except for *H. americanus*, which is a lobster.

Conclusions

Due to the availability of food and space, lack of natural enemies and suitable environmental conditions, it appears that *C. japonica* has filled an unoccupied niche in New Zealand and will continue to thrive (Fowler et al. 2011, Chapter 2). This study should be viewed as a starting point for further investigations into the interactions between *C. japonica* and *O. catharus*, as understanding the dynamics of species interactions is critical to mapping the possible distribution and impact of *C. japonica* in northeastern New Zealand. Combined with field manipulations and long-term monitoring projects, these studies are needed to ascertain the possibility of competition between species and the exclusion of either species from previously occupied territory.

Chapter Six

General Discussion

Overview

It is estimated that only 10% of all introduced species establish themselves in a new environment, and, of these, only 10% actually expand their range (Williamson 1996). Many successful invasive organisms are thought to have proliferated due to combinations of biological and/or ecological pre-adaptations that have aided their integration into novel environments (Mayr 1965, Kolar and Lodge 2001). These include, but are not limited to, fast growth, the ability to reproduce sexually and asexually, rapid reproduction, high dispersal ability, phenotypic plasticity, tolerance of a wide range of environmental conditions, consumption of a broad range of prey items, competitive superiority, association with humans, and a history of other successful invasions (Williams and Meffe 1998). The most successful marine invasive species tend to have high fecundities, short generation times, and broad environmental tolerances (Fofonoff et al. 2003). However, while both successful and unsuccessful invaders as well as native species may possess combinations of these traits, the outcome of an invasion is ultimately determined by complex ecosystem interactions. For example, although larvae and adults of the non-native swimming crabs *Scylla serrata* and *Portunus pelagicus* have been found infrequently in New Zealand waters and exhibit many of the traits of successful invaders, they are unable to breed due to the cooler sea surface temperatures (Dell 1964, Wear and Fielder 1985, Webber 2001). Predicting the outcome of an invasion is extremely difficult, but studying the biological and ecological traits of a successful new species in its invaded range will help to identify those key attributes that influence the success rate.

This thesis aimed to describe such characteristics of the newly invaded Asian paddle crab, *Charybdis japonica*, in northeastern New Zealand, and to incorporate those attributes into global predictions of successful invasive species and their ecosystem effects. Descriptions of population demography and morphometric analyses were used to provide information on the biological attributes of *C. japonica* (Chapter 2), while laboratory and field experiments investigated how *C. japonica* was interacting with the native community (Chapter 3, 4, 5). The individual chapters in this thesis have been formatted as separate manuscripts, each with their own discussion. This general discussion synthesizes that data and concisely details specific biological and ecological characteristics of *C. japonica* that may have aided this species' success in New Zealand.

Biological characteristics of *Charybdis japonica* that may have made it successful

Life history traits of invasive crustaceans that may enable them to succeed in new environments include a long larval life that facilitates dispersal, rapid growth and maturation, short generation times, high fecundity, the ability to produce multiple broods in succession, and broad tolerances to environmental variables (Weis 2010). Not including the megalopa stage, the six zoeal stages of *C. japonica* remain in the water column for at least 18 days (Yatsuzuka 1952). Although this is not a particularly long larval life, it does allow for the potential of spread by ocean currents during this time. In New Zealand, the fast growth rate of juveniles and the differential allocation of growth by the two sexes of *C. japonica* allow for early maturation of this species, which is hypothesized to occur after one year at between 40 and 50mm carapace width (Chapter 2). Although not unusually fecund for invasive species, *C. japonica* females can produce up to approximately 400,000 eggs per brood in New Zealand and spawn over six months (Chapter 2). *C. japonica* can store sperm from multiple males for up to seven days and produce up to three broods a season in their native range (Kim 2001); this has yet to be confirmed in invasive populations. Although this is not a particularly long time for sperm storage, a single female which is storing sperm could be transported long distances and create new broods in a novel environment. Comparisons of zoeal survival rates to historical sea surface temperatures and salinities show that *C. japonica* Stage 1 zoeae tolerate a broad range of temperatures and salinities and could survive natural conditions throughout New Zealand (Chapter 4). Combined with their long larval life during which they could be spread via ocean currents, this gives *C. japonica* the potential to invade other New Zealand estuaries and harbours (Chapter 4). As *C. japonica* continues to exhibit qualities of a *r*-selected species in its invaded range, it appears that this species may have attributes that allow it to be successful and will continue to spread throughout New Zealand.

Ecological characteristics of *Charybdis japonica* that may have made it successful

Those species that have a broad diet and/or habitat range tend to fare well as invaders, as they are able to take advantage of a variety of prey types (Weis 2010). *C. japonica*'s generalized omnivorous diet of plant material, molluscs, crustaceans, and polychaetes allows for the opportunistic exploitation of a diverse range of food resources throughout all seasons (Chapter 2). Laboratory studies in Chapter 3 show that *C. japonica* consumes several different bivalve species, and, along with the diet composition analysis in Chapter 2, predict that *C. japonica* would have a strong impact on New Zealand's marine benthic communities. Based on the diverse species composition of *C. japonica*'s gastric mills collected from the Weiti River (Chapter 2), it could be assumed that *C. japonica* has little direct impact on established adult beds of mature shellfish comprising species of commercial or recreational importance in northeastern New Zealand (*Paphies australis*, *Perna canaliculus*, *Austrovenus stutchburyi*, and *Pecten noveazelandiae*). However, *C. japonica* could influence the

recruitment of these species through heavy predation of small bivalves, exemplified by the appearance of only juvenile *P. canaliculus* shells in the gastric mills and the ability of a single individual to consume up to 42 juvenile bivalves in 24 hours (Chapter 3). High juvenile mortality has important implications for prey population maintenance and is a serious threat to the successful management of commercial bivalve resources (Belding 1930, Hanks 1961, Galtsoff 1964), especially for populations of the green-lipped mussel (*Perna canaliculus*) and pipi (*Paphies australis*) in New Zealand (Chapter 3). Although it was hypothesized that *C. japonica* has altered the natural marine benthic community since their introduction, there was no observable significant effect of *C. japonica* predation on benthic macroinvertebrate community structure in the field experiment or field survey. The discrepancy between their voracious diet in the laboratory and the lack of an altered marine community abundance and/or structure in the field may be due to numerous factors (see Chapter 3 for detailed explanations), including experimental design. It is possible that *C. japonica* is having an impact on the benthic marine system that was not found in this study but could be discovered in subsequent field experiments and surveys. The high densities of *C. japonica* at certain localities within northeastern New Zealand, their effectiveness as predators of juvenile bivalves and their large appetites suggest a potentially important role for these predators in restructuring prey communities that may not be apparent at this point in time (Chapter 3).

Successful invaders are most often those species that are able to utilize the maximum amount of resources (i.e. food, space) in lieu of their native competitors (Dunstan and Johnson 2007). In nearly all cases of marine crab invasions, predator-predator aggression has also been thought to influence the success rate of invaders by determining the superior competitor (Snyder and Evans 2006). Male *C. japonica* individuals dominated both male and female native New Zealand paddle crabs *Ovalipes catharus* in one-on-one competition for food, regardless of which crab possessed the food initially (Chapter 5). While *O. catharus* was often able to successfully commandeer prey from conspecifics, *C. japonica* individuals frequently displaced *O. catharus* that were previously feeding, and behaved aggressively towards *O. catharus* and conspecifics of equal size when competing for a prey item. *O. catharus* showed low levels of aggressive behaviours throughout all trials and spent most of their time evading *C. japonica*. These results suggest that male *C. japonica* may have an advantage over, or at least decrease the prey available to, *O. catharus*, which were not successful in defending or acquiring the prey item. Although it appears that *C. japonica* is not influencing the catch rates of *O. catharus* in the Waitemata Harbour by direct predation, the apparent simultaneous increase in *C. japonica* and decrease in *O. catharus* populations (J. MacDonald, Ministry of Agriculture and Forestry Biosecurity New Zealand (MAFBNZ), pers. comm.), could be related to the much more aggressive nature of *C. japonica* and seemingly demure response of *O. catharus*. While the possible active avoidance by *O. catharus* of *C. japonica* may reduce interspecific competition and allow both species to coexist in the

same area, it may have overreaching effects that ultimately drive *O. catharus* out of part of its historical range. Although the species' distributions may only overlap temporally (i.e. in embayments during the reproductive season), the possibility that *C. japonica* may come into contact and compete with recently settled juvenile *O. catharus* as well as mating adults begs the question as to whether the invasive crab may ultimately affect the recruitment rates of *O. catharus*.

As hypothesized, *C. japonica* exhibits several ecological attributes that may allow them to become successful invaders. Their broad diet range, voracious appetite, and competitive superiority have enabled them to coexist alongside native New Zealand species for at least a decade. While the availability of an open niche and the lack of natural enemies may have aided their success, *C. japonica* would not have been able to survive and spread without these characteristics.

Comparisons with other successful crab species

C. japonica shares many important biological and ecological characteristics with other successful invasive crabs. Successful invasive crabs are usually short-lived, with rapid growth to maturity (e.g. Ryan 1956, Turoboyski 1973, Berrill 1982, Epifanio et al. 1998, Dineen et al. 2001, Dauvin et al. 2009) and usually produce large quantities of larvae in both their native and invaded ranges (e.g. Broekhuysen 1936, Berrill 1982, Crothers, 1967, Takahashi et al. 1985, Fukui 1988, Siddiqui and Ahmed 1992, Lemaitre 1995, Tavares and de Mendonca 1996, McDermott 1998, Mantelatto and Garcia 2001, Rudnick et al. 2003, Vinuesa 2007, Audet et al. 2008, Ozcan et al. 2010). Previous work comparing intraspecific egg size and reproductive output in decapod species have shown that these variables increase with latitude, most likely as an effect of decreasing temperature (Jones and Simons 1983, Lardies and Castilla 2001, Brante et al. 2003). However, comparisons of the reproductive potential of several invasive crabs in their native and invaded ranges show that based on total egg number and size at maturity, these species do not gain any advantage by moving to a new environment (Table 6.1). Other invasive crab species are known to have broad environmental tolerances (e.g. Williams 1984, Welcomme and Devos 1991, Cohen et al. 1995, Epifanio et al. 1998, Petersen 2006, deRivera et al. 2007, Roche and Torchin 2007) and habitat requirements (e.g. Cohen et al. 1995, Grosholz and Ruiz 1996, Dineen et al. 2001, Dauvin et al. 2009, Dittel and Epifanio 2009). Many other successful invasive crabs have been shown to have opportunistic, generalist feeding approaches which may increase their survival rate in new habitats (e.g. Cohen et al. 1995, Lohrer and Whitlatch 1997, McDermott 1998, Dineen et al. 2001, Ledesma and O'Connor 2001, Rudnick and Resh 2005, Baeta et al. 2006). For several species of invasive crabs, the ability to effectively compete with native species for resources, such as food and shelter, has been instrumental to their success (e.g. Grosholz et al. 2000, McDonald et al. 2001, Jensen et al. 2002, deRivera et al. 2005, Rossong et al. 2006, Williams et al. 2006, MacDonald et al. 2007, Roche and Torchin 2007, Gibley et al. 2008, Breen

and Metaxas 2009, Dauvin et al. 2009). While these characteristics cannot guarantee the success of a crab invader, they may help it to thrive in a new environment.

Table 6.1 Aspects of the reproductive biology of several successful invasive crabs. Data collected from specimens in their native range is shown in the left hand columns while data from invasive populations is listed on right.

	Native range			Invasive range			Sources
	Size at maturity	CW(mm)	# eggs	Size at maturity	CW(mm)	# eggs	
<i>Charybdis japonica</i>	39-53mm	46.8-76.8	94,226 – 473,151	40 - 55mm	49.5 - 78.8	26, 285-414, 461	Kim 2001, Chapter 2
<i>Charybdis hellerii</i>	N/A	80-117	22,517-292,050	35mm	36-41	42,016-152,583	Siddiqui and Ahmed 1992, Lemaitre 1995, Tavares and Mendonca 1996, Mantelatto and Garcia 2001, Ozcan et al. 2010
<i>Carcinus maenas</i>	15-31mm	16-30	18,500-200,000	28-50mm	N/A	140,00–200,000	Broekhuysen 1936, Berrill 1982, Crothers, 1967, Vinuesa 2007, Audet et al. 2008
<i>Hemigrapsus sanguineus</i>	14-18mm	N/A	56,000	12mm	12-31	2,621-43,622	Takahashi et al. 1985, Fukui 1988, McDermott1998

A global model of successful marine invasive species

Although the impacts of some marine invasive species are apparent after only one or two years, the vast majority show synergistic effects on the native system that may not be noticed until a decade or more later (Crooks and Soule 1999, Mooney and Cleland 2001). While an initial introduction can seem harmless, with only a few individuals found, the later population explosion and subsequent spread and impact of an invasive species can catch both the environment and the people who manage it off guard. However, combating each and every single non-native species is not energy, resource, or cost efficient. If there was a quick checklist or global model that could rank suspected invasive species according to invasibility potential, it would help managers and ecologists determine the relative risk of that particular species. Incorporating the biological and ecological attributes of many successful invasive species into an ecosystem matrix is the first step in making a global model to predict the success rate of any invasive species.

Models that incorporate characteristics of known invaders, such as the environmental tolerances, habitat, and larval distribution patterns, along with attributes of the environment are useful for determining the rate of spread and predicting the impact of a particular species (Hayes and Barry 2008). While this thesis does not include any novel models or frameworks for predicting the success of invasive species, the data collected from these studies can be used in several different existing species distribution models (reviewed in Guisan and Thuiller 2005). Moles et al. (2008) developed a framework for understanding and predicting which attributes are most likely to succeed in a given environment while also considering the traits of resident species and the environmental conditions. The drawback with this approach is that researchers need ecological information on thousands of resident species, but the output is a predicted distribution of traits under different environmental conditions and the recognition of vacant niches in the invaded ecosystem. Other models take a different approach; Romanuk et al. (2009) developed a food web theory of invasion success, which describes the invader in terms of its trophic function as mediated by native species' trophic activities and the structural complexity of the invaded food web (i.e. a niche model). Previously published data concerning environmental tolerances and/or habitat suitability have been used recently to predict invasion success and potential spread in other aquatic ecosystems and could be applied to the *C. japonica* invasion within New Zealand and abroad (i.e. Chapter 4, deRivera et al. 2007, Kilroy et al. 2008). In a similar method, Miller et al. (2007) created a model to predict invasion success based on the underlying biology of successful and failed molluscan invaders that would be applicable to geographically disparate marine ecosystems. They found that high historical abundance, broad salinity

tolerance, and a direct developmental mode were key biological attributes that differentiated successful molluscan invaders from failed ones. While successful invasive crabs may also have high historical abundance and broad salinity tolerances, none are known to have direct development (C McLay, *personal communication*). However, using Miller et al. (2007) as a proxy, collation of data from this thesis and numerous other sources may suggest other similar patterns for invasive crabs.

There are few studies that have incorporated numerous biological and ecological species characteristics to show invasibility risk and potential spread in marine systems, and more comprehensive modeling approaches are needed in the field of predictive invasion biology. While certain species may be predicted to be successful invaders based on key biological or ecological attributes, environmental and demographic stochasticity can influence their ability to invade. At this point, no single model or list of attributes can predict with overall certainty the success of an invader. However, due to the rapid decision making process required by management, plans against invasive species must be made with, in some cases, little or no biological or ecological basis. The models listed above provide a way to quickly assess the invasibility potential of a particular species and formulate an early risk management response.

Conclusions

While an invasive species may exhibit certain characteristics that would make it a formidable invader in one area, there is no single attribute that guarantees their success in other novel environments. Rather it is a combination of biological and ecological traits and how they relate to different environments that contribute to the overall success of an invasive species. While comparisons with other successful crab invaders may elicit powerful theories as to why certain species succeed, overall comparisons between successful and unsuccessful introductions are needed to ascertain exactly what drives these patterns (e.g. Miller et al. 2007). As unsuccessful introductions are usually not known or described, comparisons with similar non-invaders of the same genus could be used in lieu of actual data on failed invasions. Using the biological and ecological data described in this thesis, comparisons with either failed invasions by other brachyuran crab species or with non-invasive brachyuran crab species may highlight particular characteristics that may aid successful invaders.

C. japonica is a highly fecund species that may be able to produce multiple broods a season and whose larvae have a planktonic existence for several weeks, which enables them to be transported long distances (Chapter 2). Able to survive a broad range of salinities and temperatures as both larvae and adults, it appears that their distribution will not be affected by these factors (Chapter 4). *C. japonica* decreases its numbers of parasites in invaded communities (Miller et al. 2006), which may allow

individuals to spend more energy on growth and reproduction (Chapter 2) and attain a larger body size. This strategy may contribute to their ability to successfully compete with and dominate native species like *Ovalipes catharus* by driving them from shared prey items (Chapter 5). The introduction and spread of *C. japonica* has the potential to change coastal communities around New Zealand due to the crab's predatory habits and its tolerance of a wide range of habitats and conditions. In both its native and introduced habitat, *C. japonica* is an opportunistic omnivore that has a broad diet comprising many taxa, and high predation rates on juvenile bivalves suggest that *C. japonica* can become an important predator in marine benthic communities in New Zealand (Chapter 3). Due to these biological and ecological attributes of *C. japonica* and a depauperate number of crab species in New Zealand, it appears that this invasive species will continue to thrive and proliferate in its new habitat. However, the ultimate impact of *C. japonica*'s presence on New Zealand's marine benthic community remains unknown.

Implications of this thesis

This thesis fills several gaps in the invasion literature. First, it helps to define biological and ecological characteristics that combine to influence the success of invaders. The case study of *C. japonica* exemplified the need to address multiple attributes to fully understand how and why certain species succeed. This thesis gives other researchers a better understanding of the factors affecting invasion success and may be combined with attributes of other successful invaders to improve predictive abilities. Second, while *C. japonica* has been an established invasive species in New Zealand for almost a decade, little research has been done on its effects on the natural environment or its biological attributes. This thesis provides such information that may be useful when predicting the impacts of this species on native species and may ultimately be used in future eradication efforts that take into account its biological and ecological parameters. Third, experimental manipulations were employed to elucidate the possible consequences of the invasion by *C. japonica*. Combining laboratory experiments, field surveys, and field manipulations, this thesis outlines several of the most likely impacts of this invasion. The synergistic view of the mechanisms and consequences of the invasion by *C. japonica* in New Zealand from this thesis proved to be a well-rounded approach to studying this invasion.

Future research

Charybdis japonica will continue to spread around the coastline of the North Island of New Zealand in the next decade. Therefore, it becomes imperative to use the information collected in this study to highlight specific areas for routine surveillance. With the environmental tolerances described

in this thesis, future studies will be able to synergistically combine ocean current models, larval development times, and larval tolerance in response to environmental fluctuations to more accurately predict the progression of this invasion. Simple plankton tows around selected harbours during the summer season would be effective in describing the range of *C. japonica* larvae and highlighting embayments at risk for an introduction. The collection of larvae would also be important in establishing whether certain populations are self-sustaining. However, while larval dispersal and recruitment are central to the stability of the population, the ability of adults to move between embayments also poses a real risk. Therefore, harbours and estuaries from the Bay of Islands to Tauranga should have monthly trapping protocols in place now, especially during the summer months, to quickly and effectively identify the presence of *C. japonica* when it finally does arrive. However, it may not be possible to perform a complete eradication of this species in a single season due to their highly mobile nature and tendency for a low catch-per-unit-effort. Trappings and hand collections concentrated around the beginning of the breeding season (November) and throughout the summer may impact population levels in future years due to decreased recruitment numbers. Recreational fishing of *C. japonica* by the public in newly invaded environments or old ones (i.e. Waitemata Harbour) may also influence population levels and decrease the cost associated with large trapping events.

There are still many unanswered questions concerning the biology and ecology of *C. japonica* in New Zealand. For instance, does *C. japonica* migrate due to season, sexual maturity (i.e. breeding aggregations), or age? If so, a concentrated trapping effort during this time may have an effect on population numbers. Does *C. japonica* have any predators that will be able to keep the population in check? The native paddle crab has many fish and elasmobranch predators (Mitchell 1984, McLay 1988) that may prey upon *C. japonica* as well. Will *C. japonica* decrease numbers of economically and ecologically valuable shellfish to cause substantial damage? Continued monitoring of targeted areas such as green-lipped mussel farms and pipi nursery grounds for both the presence of *C. japonica* and indications of their predation becomes imperative if this question is to be answered. Will *C. japonica* influence the catch rates and distribution patterns of the native New Zealand paddle crab? As *Ovalipes catharus* is the basis for a small fishery around New Zealand, the knowledge of fishermen in these areas will be crucial to understanding the dynamics between these two similar species. Forming associations with fishermen and educating them about *C. japonica* may provide more information about the species and its movement patterns that could not be elucidated from one-off trappings completed every six months. Based on all of the available information, it appears that *C. japonica* is a permanent addition to New Zealand waters. As this thesis is the first biological and ecological study of *C. japonica*, there are many avenues for further research, including the ones outlined above, that should

be explored and documented. As it is a relatively new invader, the process and impacts of the invasion of *C. japonica* will be of interest to international scientists and managers alike.

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