# PREDATOR-PREY INTERACTIONS BETWEEN THE EUROPEAN GREEN CRAB (*CARCINUS MAENAS*) AND BIVALVES NATIVE TO PRINCE EDWARD ISLAND

**A Thesis**

**Submitted to the Graduate Faculty**

**in Partial Fulfillment of the Requirements**

**for the Degree of Master of Science**

**Department of Biology**

**Faculty of Science**

**University of Prince Edward Island**

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**April 2011**

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*Your file Votre référence*
*ISBN:* 978-0-494-82248-7
*Our file Notre référence*
*ISBN:* 978-0-494-82248-7

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# ABSTRACT

The commercial harvesting and culture of American oysters (*Crassostrea virginica*), blue mussels (*Mytilus edulis*), and soft-shell clams (*Mya arenaria*) has long been an important source of economic income for rural areas of Prince Edward Island (PEI). However, as seen in other bivalve industries elsewhere (Dare et al. 1983), the sustainability of PEI's bivalve industries are threatened by the establishment of the non-indigenous European green crab (*Carcinus maenas*). The green crab is a predator of most bivalves and has the ability to greatly reduce the population size of its prey in virtually every coastal habitat (Cohen et al. 1995, Mascaro & Seed 2000).

To document their potential population growth and impact, trapping surveys were carried out during 2008, 2009 and 2010 in two prime bivalve harvesting estuaries located in southern PEI: North River and Bedeque Bay. The trapping surveys confirmed that there is an ongoing spread of green crabs into new shellfish habitats while rapidly increasing in previously established areas.

To help prioritize future research, this study explored size-dependent green crab prey preference on *C. virginica*, *M. edulis*, and *M. arenaria* in a coastal system of PEI. Using two sizes of prey (15-25 and 25-35 mm shell length; SL) and three different experimental manipulations, small (35-45 mm carapace width; CW), medium (45-55 mm), and large (55-75 mm) green crabs were given a choice among these three bivalves and their daily feeding rates were monitored over the course of three days. For both prey sizes, green crabs showed an early feeding preference for soft-shell clams and, only as they declined in numbers, a switch towards mussels and subsequently towards oysters.

Such changes in order and timing of prey preference were directly related to differences in prey shell thickness, a fairly reliable indicator of prey shell-strength.

As the *C. virginica* industry is believed to be the most threatened by the green crab invasion, three types of experiments in the laboratory and the field were utilized to assess predation rates exhibited by small (35-45 mm CW), medium (45-55 mm), and large (55-75 mm) green crabs feeding on small (5-15 mm SL), medium (15-25 mm), large (25-35 mm), and extra-large (35-50 mm) oysters. All experiments lasted three to five days but oyster mortality was assessed on a daily basis. Overall, the outcome of green crab-oyster predator-prey interactions was heavily dependent on both oyster size and crab size. While almost no predation occurred on extra-large oysters, large and medium green crabs preyed heavily on all other sizes, usually in the first three days of manipulation. Small and medium oysters were the most vulnerable to predation but reached a partial size refuge at ~35 mm SL.

Under that size threshold, oysters remain highly vulnerable and require management measures in order to secure their sustainability. As green crabs continue to spread in PEI and the Gulf of St. Lawrence, further mitigations strategies are likely to be needed. The results presented in this thesis provide the foundation for future developments of these mitigation strategies.

# ACKNOWLEDGEMENTS

First and foremost, I would like to thank Dr. Pedro Quijon for giving me the opportunity to study under his supervision at UPEI. The incredible assistance and support he has provided is more than any student could expect from their supervisor. I am also grateful to my supervisory committee members Dr. Jeffrey Davidson and Dr. Shawn McKenna for their thoughtful comments, feedback, and suggestions during the course of this program, and also Dr. Gilles Miron, the external examiner at my thesis defense.

For field and laboratory assistance, there are many people who I would like to thank. First, I would like give a special thank you to Luke Poirier, Kristen Murray, and Dan McNeil (UPEI-Biology) for their great assistance during the field seasons of 2009 and 2010. It has been a pleasure working with all of these individuals. I also thank Erica Watson and Crystal Laroque (Department of Fisheries and Oceans-Gulf Division) for their assistance in the field. I thank the Biology Department (UPEI) and the Shellfish Research Group (AVC-UPEI) for the use of facilities, equipment, and vehicles. I am also grateful to Tim Barrett (UNB) for his advice with statistical analyses. Finally, I would like to thank my fellow graduate students and lab mates, Mitchell MacMillan, Melanie Rossong, and Kevin Sorochan for all their assistance and the insightful discussions during our time spent together over the last two years.

I would like to thank the PEI Shellfish Association and the Atlantic Shrimp Corporation for providing funding for this project through an Aquaculture and Fisheries Research Initiative Grant to Dr. Quijon and Dr. Davidson. I also thank graduate support from the National Science and Engineering Research Council (NSERC) and the generous support of UPEI'S Dr. J. Regis Duffy Graduate Scholarship in Science.

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# Chapter 1. INTRODUCTION AND OBJECTIVES

## 1.1. Introduction

The commercial harvesting and culture of bivalve species has long been an important source of economic income for rural areas of Prince Edward Island (PEI), Atlantic Canada, and many coastal areas worldwide. In 2007, for example, harvest and culture of blue mussels (*Mytilus edulis*), American oysters (*Crassostrea virginica*), and soft-shell clams (*Mya arenaria*) had a combined landed value of approximately $28 million in PEI. However, as seen in other bivalve fisheries elsewhere (Dare et al. 2003), the sustainability of these shellfish industries are increasingly threatened by the establishment of aquatic invasive species. Aquatic invasive species are known to cause a wide array of ecological impacts and cause considerable economic damage throughout the world (see review by Lovell and Stone 2005). Such ecological impacts include but are not restricted to displacement and loss of native species, possible extinctions of endemic species, altered or disrupted habitats, and changes in distinctive trophic levels and food webs (Cohen et al. 1995; Lovell and Stone 2005). In the marine system, economic costs of invasive species are often associated with biomass reductions of commercially harvested or shellfish organisms and fouling on aquaculture infrastructure, such as ship hulls, wharfs, and aquaculture gear (Lovell and Stone 2005).

One invasive species particularly detrimental for shellfish resources is the European green or shore crab (*Carcinus maenas*). This species, originally native to European waters, is now found throughout many parts of the world including both the east (Audet et al. 2003) and west coasts of North America (Cohen et al. 1995), parts of

Australia (Thresher et al. 2003; Ahyong 2005), South Africa (Le Roux et al. 1990), and Argentina (Hidalgo et al. 2005). On the east coast of North America, green crabs were first reported in 1817 around the New York and New Jersey areas (Audet et al. 2003) after arriving on fouled hulls or in the solid ballast of wooden ships (Cohen et al. 1995). Since their initial arrival, the crabs expanded northward and reached the coast of Maine in the early 1900's. By 1951, the green crabs were present in Canadian waters, specifically, in the Bay of Fundy (Audet al. 2003). Throughout the following several decades, green crab populations expanded around the southwestern tip of Nova Scotia and along the province's Atlantic shoreline. Shortly after, a rapid population expansion, partly linked to a re-invasion from European populations, occurred and is still ongoing (Roman 2006; Blakeslee et al. 2010). In 1995, green crabs were found along the west coast of Cape Breton Island and soon after in 1997, were confirmed for the first time in the southern Gulf of St. Lawrence and Prince Edward Island (Audet et al. 2003). In 2004, the green crab was also identified in the Magdalen Islands, Quebec (Paille et al. 2006). Although the green crabs were reported again in the area in low numbers during 2005 and 2006, as of December 2006 there was no evidence of a population becoming established (Paille et al. 2006). The most recent invasion took place in Newfoundland the northernmost limit of distribution for the region (Klassen and Locke 2007).

The green crab is a predator of most bivalves, including the American oyster, the blue mussel, and the soft-shell clam, three commercially important bivalve species in the Atlantic region (Miron et al. 2005). Besides their importance to their corresponding harvesting and aquaculture industries, these species also contribute to the health of the shoreline ecosystem by maintaining water quality and providing essential habitat for an array of other species. For example, *C. virginica* and *M. edulis* form extensive reefs and beds that provide biogenic habitat, and enhance the diversity and abundance of benthic organisms such as polychaetes, nemerteans, decapods, gastropods, and other bivalves (Grabowski et al. 2005). As these organisms are common prey for fish and other mobile epibenthic species, the habitats formed by *C. virginica* and *M. edulis* indirectly increase the abundance of fish and other mid-trophic level species in an area (Lenihan et al. 2001). *C. virginica*, *M. edulis*, and *M. arenaria* are also filter feeding organisms that remove large quantities of organic and inorganic particulate matter and nutrients from the water column (Gerristen et al. 1994; Nelson et al. 2004). As a result, these bivalves influence the amount of phytoplankton and primary production in estuarine areas, and improve overall water quality, especially in areas where they are abundant (Gerritsen et al. 1994; Mann 2000).

In most aquaculture areas, predation on small sized bivalves by epibenthic predators is an important source of bivalve mortality and limits the overall productivity of the industries (e.g., Bisker and Castagna 1987; Flimlin and Beal 1993). Therefore, the arrival of any invasive predatory species is a justified cause of concern for the shellfish industry. Green crabs are notorious bivalve predators and have the ability to reduce the population size of their prey in virtually every habitat (Cohen et al. 1995, Mascaro & Seed 2000, Floyd and Williams 2004). As bivalves make up the majority of prey items in the diet of green crabs (Elner 1981), many of the early, noticeable impacts of green crab are on these species. For example, in the 1950's the annual production of the New England soft-shell clam fishery (*M. arenaria*) in the northeastern United States was drastically reduced shortly after the arrival and establishment of green crab populations in the region (Ritchie 1976). More recently in the 1990's, a green crab invasion has been implicated for substantial declines of two native clam species on the west coast of North America (*Nutricola tantilla* and *Nutricola confuse)* (Grosholz et al. 2000).

The impacts of green crab invasions extend well beyond bivalves. The crabs are also known to compete with other crustaceans and vertebrates for food and space (McDonald et al. 2001; Rossong et al. 2006; Williams et al. 2006) and can indirectly influence entire marine benthic communities (Baeta et al. 2006). For example, in laboratory experiments with adult green crabs and juvenile American lobsters (*Homarus americanus*), Rossong et al. (2006) found that green crabs constantly dominated feeding trials and displaced lobsters from shelters. Green crabs are also important predators of many gastropod species including the intertidal snail, *Littorina obtusata* (Rochette et al. 2007; Edgell and Rochette 2009). Rochette et al. (2007), in particular, demonstrated that green crabs may be responsible for thicker shells in *L. obstusata* in some areas as an induced defence against predation. Green crabs can also be detrimental for other invertebrates and plant species by altering and disrupting their local habitat (Davis et al. 1998; Garbary and Miller 2006). For example, green crab foraging methods are particularly damaging to eelgrass beds as they dig large burrows on the sediment and can also tear and cut at the sheath bundle of the grass (Garbary and Miller 2006; Malyshev 2009). The loss of eelgrass beds can be quite detrimental to benthic communities as they provide habitat for an array of organisms, and are a critical feature of healthy estuarine ecosystems in Atlantic Canada and elsewhere.

Given the ecologic and economic importance of these bivalve species to the region, the quantitative assessment of predator-prey green crab-bivalve interactions represents a critical step towards the understanding of the impacts associated with green crab invasions. Furthermore, knowledge on the vulnerability of bivalve populations to green crab predation is essential for the identification of appropriate mitigation strategies, and finally for improving our preparedness for future invasions. This study includes four main parts that aim to address the insufficient knowledge available about these particular interactions.

A literature review (Chapter 2) where aspects, such as those mentioned above as well as others, pertaining to bivalves and green crab invasions are discussed. Some of these aspects include the importance of bivalves in relation to the fishery and aquaculture industries, their ecological roles, and common sources of mortality such as diseases, competition, and predation. The literature review also focuses on the invasion history of the green crab and the attributes that make this species a successful invader. The review also discusses the ecological and economic impacts associated with green crab invasions, reviews the literature focusing on predation upon bivalve populations and the methods that have attempted to control green crab impacts.

In the second part of the study (Chapter 3), green crab predation on three relevant bivalve species is assessed by running a series of predator-prey (green crab-bivalve) manipulations in enclosures under both field and laboratory conditions. In that chapter, green crab prey preferences, when given a choice among *C. virginica*, *M. edulis*, and *M. arenaria,* are examined in detail to better understand the potential impacts of green crab invasions and to prioritize future research. Currently in PEI, the fishery and aquaculture industry for *C. virginica* is believed to be the most at risk from the green crab invasion. Unlike the off-bottom culture of *M. edulis*, a substantial part of the *C. virginica* fishery relies on the harvesting of wild beds or the seeding of unprotected bottoms. Similarly, the *C. virginica* industry is considerably larger in scale in comparison to the *M. arenaria* industry (Gillis et al. 2000).

For the reasons summarized above, the third part of this study (Chapter 4) uses predator-prey manipulations in the laboratory and field that focus solely on green crab predation on various sizes of *C. virginica*. To identify potential differences associated to predator and prey size, the experiments in both chapters (3 and 4) were conducted with three distinctive sizes of crabs and various sizes of bivalves. As changes in the timing of predation in crab-bivalve interactions may be relevant for the overall outcome of these manipulations and they are seldom reported in the literature, in chapters 3 and 4 bivalve mortality was monitored daily during the course of all the experiments (three to five days).

Finally, the last part of this thesis (Chapter 5) summarizes the main results obtained during the development of this research project, discusses their implications for the management of oyster beds and proposes a series of recommendations to the industry in the form of effective mitigation measures against green crab predation.

## 1.2. General and specific objectives

i) To study prey preferences in a coastal predator-prey system

- To assess green crab prey preferences among *M. edulis*, *C. virginica*, and *M. arenaria* in both field and laboratory conditions
- To identify potential differences in prey preference associated to predator and prey size.

- To relate prey preferences to differences in shell thickness, a main predictor of shell strength.
- To identify potential short-term variations in prey preference occurring within the time frame of the feeding trials.

ii) To study green crab-American oyster predator-prey relationships

- To measure green crab feeding rates while foraging on *C. virginica* in both field and laboratory conditions.
- To identify potential differences in crab feeding rates associated to predator and prey size.
- To determine the period of most intense foraging within the time frame of the feeding trials.

iii) To assess and propose green crab mitigation measures

- To review alternative mitigation strategies currently used for the mitigation of green crab impacts.
- To propose potential mitigation measures that are practical, cost-effective, and suitable for the PEI industry.

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# Chapter 2. LITERATURE REVIEW

## 2.1. *Crassostrea virginica, Mytilus edulis,* and *Mya arenaria*

Along with quahogs (*Mercenaria mercenaria*), American oysters (*Crassostrea virginica*), blue mussels (*Mytilus edulis*), and soft-shell clams (*Mya arenaria*) are three of the most valuable shellfish resources in Prince Edward Island (PEI) and Atlantic Canada (PEIDAFA 2005). The commercial fisheries for *C. virginica* and *M. arenaria* have a long history in both PEI and Atlantic Canada (FAO 2009). In the last several decades, the culture of *C. virginica* and *M. edulis* have become increasingly important in the region, whereas *M. arenaria* has lagged behind and, among other clam species, has become the focus of diversification efforts (Miron et al. 2005). Besides their commercial value, these species are also ecologically important as they provide food and habitat for many marine organisms and are known to improve water quality (Kennedy 1996). As a result of their ecological and economical importance, these bivalves have received much attention in the literature. Some aspects of this literature including their biology, contributions to ecosystem health, and their importance to the fishery and aquaculture industries are discussed below.

### *2.1.1. Biology and life history*

*C. virginica*, *M. edulis*, and *M. arenaria* are all species belonging to the class Bivalvia (Raven et al. 2005). Bivalves are marine and freshwater molluscs characterized by the presence of two lateral valves (shells) hinged together, encasing the soft body tissue of the organism. Bivalves are generally sessile filter feeders, with siphons and gills used for water, food, and oxygen intake. Several aspects of the life history of *C. virginica*, *M. edulis*, and *M. arenaria* are similar. After the release of eggs and sperm into the water column, external fertilization occurs almost immediately. The fertilized eggs develop into free swimming larvae within six to 12 hours and are released into the water column where they remain for up to three to four weeks in the case of *C. virginica* (PEIDAFA 2005) and *M. edulis* (Seed 1976) and up to six weeks for *M. arenaria* (Abraham and Dillon 1986). To settle, *C. virginica* larvae search for a suitable substrate, such as rocks, shells, and man-made structures, and release a cement-like adhesive to become physically attached (PEIDAFA 2005). *M. edulis* and *M. arenaria* larvae settle on suitable substrates by attaching themselves with byssal threads (Seed 1976; Abraham and Dillon 1986). For *M. arenaria* suitable substrates includes soft bottoms such as clay, sand, and mud (Beal and Vencile 2001; Beal 2006) while suitable substrates for *M. edulis* includes most hard substrates such as rocks, bivalves, and man-made structures (Jones et al. 2009). While *M. edulis* and *C. virginica* remain sessile after settlement (PEIDAFA 2005), soft-shell clams develop a muscular foot, become able to move, and eventually burrow into the sediment (Abraham and Dillon 1986).

Populations of *C. virginica* are found along the eastern coast of North America from the Gulf of St. Lawrence, Canada to the Gulf of Mexico. Populations are also found in the Caribbean and along the coasts of Brazil and Argentina (Carriker and Gaffney 1996). Although found in sea water, within their range, *C. virginica* is typically most abundant in estuaries and coastal areas of low salinity (Carriker and Gaffney 1996). Within these areas, *C. virginica* is found on hard and soft-bottoms in both the littoral and sublittoral zones, and commonly associated with reefs.

*M. edulis* has a broad distribution and populations of the species are found throughout many parts of the world (Gosling 1992). In the Pacific Ocean, the mussel is found from Alaska to California in the east (Burger and Gochfeld 2006) and along the Asian coast in the west (Gosling 1992). In the Atlantic Ocean, *M. edulis* is found from the Canadian Arctic to North Carolina, USA. The mussel is also found in Greenland and European waters, including the Mediterranean Sea and North Africa (Gosling 1992). Within their range, *M. edulis* is commonly found in both the littoral and sublittoral zones, and are known to live in both brackish water estuaries and open shores. Due to their fast growth and high recruitment, *M. edulis* populations are usually dominant in their associated marine communities (Enderlein and Wahl 2004).

*M. arenaria* is originally native to the east coast of North America, from the Canadian subarctic to Cape Hatteras, North Carolina. The species was introduced to the west coast of North America however, and is now found from Alaska to California (Powers et al. 2006). Within this range, *M. arenaria* is typically found along the coast in estuaries and bays in clay, mud, or sand bottoms (Mackenzie and McLaughlin 2000). The clam consists of a thin shell composed of two symmetrical valves that gape at each end, exposing the soft body and an elongated siphon (Abraham and Dillon 1986). Their siphon allows the clam to use its muscular foot to burrow into the sediment to mean depths of 13 cm, or deeper in the presence of predators (Flynn and Smee 2010; Whitlow 2010). As the siphon is required to extend to the surface to filter feed for food, the length of the siphon is generally limiting to the burial depth of the clam (Whitlow 2010).

### *2.1.2. Importance to the fishery and aquaculture industries*

*C. virginica*, *M. edulis*, and *M. arenaria* are all commercially important bivalves throughout their range and have a long history in the commercial fishery and aquaculture industry. Within Canada, *C. virginica* is exclusively fished and cultured in the Atlantic region. In this region, the wild fishery and aquaculture industry produced 3 582 metric tonnes for a total landed value of $8.121 million CAD in 2007 (DFO 2009). In particular, PEI was responsible for producing 2 596 metric tonnes, that contributed a landed value of $5.7 million CAD to the province's economy (PEIDFARD 2007).

As *M. edulis* is found throughout many parts of the world, many countries have fishing and aquaculture industries directed toward this species. In 2007, there was close to 300 000 metric tonnes of *M. edulis* produced worldwide (FAO 2009). Some of the world's major producers include France, Denmark, Ireland, Netherlands, United Kingdom, Canada, and the United States (FAO 2009). In Canada, 23 872 metric tonnes were landed in 2007 and had a total value of $33.94 million CAD (DFO 2009). Of the total Canadian *M. edulis* production, PEI was responsible for approximately 71% with 17 502 metric tonnes and value of $21.8 million CAD (DF0 2009).

*M. arenaria* is harvested and grown in areas of Atlantic Canada and in the eastern and western United States (FAO 2009). In 2007, over 8 229 and 410 metric tonnes of clams were landed in the eastern and western United States, respectively. The total landings contributed to a value of almost $24.3 million USD. Similarly, in Canadian waters, 1,026 metric tonnes were produced in 2007 (DFO 2009) of which 189 metric tonnes originated from PEI and had an approximate landed value of $486 000 CAD (PEIDFARD 2007).

### *2.1.3. Natural history and ecological roles*

Besides their economic importance to the commercial fishery and aquaculture industries, *C. virginica*, *M. edulis*, and *M. arenaria* have very important ecological roles in marine benthic communities. For example, *C. virginica* can form extensive oyster reefs and act as a foundation species for many organisms (Grabowski et al. 2005; Kimbro and Grosholz 2006). The physical structure of the reefs provide habitat in the form of hard substrate and refuge shelters (Kennedy 1996). This type of habitat increases the diversity and abundance of associated benthic marine organisms such as polychaetes, nemerteans, decapods, gastropods, and other bivalves (Grabowski et al. 2005). As these organisms make up the majority of juvenile fish prey, oyster reefs indirectly increase the abundance of juvenile and adult fish in the area (Lenihan et al. 2001). Additionally, as they are filter feeders, *C. virginica* removes large quantities of organic and inorganic particulate matter and nutrients from the water column (Gerristen et al. 1994; Nelson et al. 2004). As a result, *C. virginica* populations can largely influence the amount of phytoplankton and primary production in estuarine areas, and improve overall water quality in areas where they are abundant (Gerritsen et al. 1994; Mann 2000).

*M. arenaria* and *M. edulis* are also suspension feeders and are able to filter large quantities of water. They therefore also contribute to water quality improvement in many bays and estuaries (Gerritsen et al. 1994). In fact, in some regions, *M. edulis* cultivation has even been suggested as a method to improve water quality in environmentally degraded estuaries (Stybel et al. 2009). Mussels in habitats like sedimentary bottoms play similar roles as oysters, as they become foundation species that generate a physical habitat previously not available for other species. Mussel beds formed by *M. edulis* also modify the physical characteristics of the habitat by increasing their stability and complexity. *C. virginica*, *M. edulis*, and *M. arenaria* are also ecologically important organisms as they are an integral part of benthic marine food webs and interact with many organisms (Mann 2000). For example, some organisms may have a commensal relationship and even provide food for these bivalves (e.g., Seed 1976; Abraham and Dillon 1986; Ford and Tripp 1996). Other organisms however may directly or indirectly compete with these bivalves or act as pests and predators, and contribute to their mortality (e.g., White and Wilson 1996; Miron et al. 2005; Whitlow 2010).

### 2.2. Natural sources of bivalve mortality

Severe environmental conditions, such as exposure to freezing temperatures, ice scour, and heavy sedimentation are all causally related to *C. virginica* (Galtsoff 1964), *M. edulis* (Seed 1976), and *M. arenaria* (Abraham and Dillon 1986) mortality. However, these environmental factors also mediate mortality resulting from an array of biological interactions. While a few species may have commensalistic relationships with *C. virginica*, *M. edulis*, and *M. arenaria*, many others act as agents of disease outbreaks, or are direct or indirect competitors, pests, and predators (e.g., Bower 2007a; Kennedy et al. 2009; Carver et al. 2010). Together, these organisms are responsible for substantial mortality levels in bivalve populations, and are reviewed with some detail in the paragraphs that follow.

### *2.2.1. Common diseases in C. virginica, M. edulis, and M. arenaria*

Disease has been identified as an important source of *C. virginica* mortality since the first reported outbreak in the early part of the 20th century (Ewart and Ford 1993). This outbreak first occurred in the Malpeque Bay region of Prince Edward Island, Canada, and became known as the Malpeque Disease. This infection was responsible for the mortality of over 90% of the natural *C. virginica* population in Malpeque Bay, which at the time was a world famous harvesting area (PEIDAFA 2005). The Malpeque Disease later spread into New Brunswick in the 1950's and had a devastating effect on *C. virginica* populations in that region. Although the agent causing the disease is still unknown (Ewart and Ford 1993; Ford and Tripp 1996), it is believed to still be present in these areas with current *C. virginica* populations descending from strains that developed a resistance to the disease (McGladdery and Bower 1999).

Since Malpeque Disease, many other severe outbreaks of infectious diseases of *C. virginica* have occurred throughout its range. The most common are known as MSX (Multinucleated Sphere X; *Haplosporidium nelsoni*), Dermo (*Perkinsus marinus)*, SSO (Seaside Organism; *Haplosporidium costale*), and JOD (Juvenile Oyster Disease; *Vibrio* spp.). While these diseases can cause high levels of mortality and are a major cause for concern, outbreaks of Dermo and JOD have so far only been reported along the eastern United States but have not been reported in Canadian waters (Bower 2005; Bower 2006*a*). In contrast, MSX and SSO have both been reported in northeastern United States and Atlantic Canada (PEIDAFA 2005; Bower 2007a; Bower 2007b). MSX has only been found in the Bras d'Or Lakes of Cape Breton, Nova Scotia (Bower 2007a), whereas SSO has been found at non-lethal levels in PEI waters but has not caused *C. virginica* mortality in the province (PEIDAFA 2005).

In *M. edulis* and *M. arenaria* populations, several disease outbreaks have been reported to cause high levels of mortality in different areas throughout the world (e.g., Bower 2009; Bower 2010). One of the most well known diseases in *M. edulis* is caused by a parasitic copepod (*Mytilicola* spp.) (Bignell et al. 2008) and is known as red worm disease (Bower 2009; Bower 2010). Of the two species that cause red worm disease in *M. edulis*, *M. intestinalis* is only found in European waters (Bower 2009) while *M. orientalis* is found along the west coast of North America including British Columbian waters (Bower 2010). Also along the west coast of North America, considerable mortalities of *M. edulis* have been linked to a disease similar to leukemia, known as haemocytic neoplasia of mussels (Elston et al. 1988). Similarly, on the west and east coast of North America, including Atlantic Canada, *M. arenaria* suffer from the equivalent disease in clams, haemocytic neoplasia of clams (Bower 2006b). In PEI, mass mortalities of *M. edulis* in the 1970's were attributed to another disease caused by *Labyrinthomyxa* sp. (Li and Clyburne 1979). However, later studies on mussels in the province found no significant levels of the disease and it is no longer believed to be a considerable source of mortality in the area (Mallet et al. 1990).

### *2.2.2. Competitors and pests of C.* ***virginica, M. edulis, and M. arenaria***

Other organisms present in the marine environment can also compete with oysters, blue mussels, and soft-shell clams for available resources such as food and space. If competitors are abundant and competition is severe, this type of interaction can result in actual mortality of larvae, spat, and/or adult bivalves (Seed 1976; MacKenzie 1970; White and Wilson 1996; McNair and Smith 1999). Beginning with larvae, fouling organisms, such as algae, bryozoans, sponges and molluscs, can compete with oysters and mussels by reducing their settling success. These competitors can settle on available substrate and prevent larvae from settling, either by completely covering the substrate (physically) or by emitting settling inhibiting substances (chemically; White and Wilson 1996).

After *C. virginica* larval settlement, competitors with faster post-settlement growth can kill many newly settled spat by overgrowth (Galtsoff 1964; MacKenzie 1970). In the case of many species, such as the native to PEI slipper shell (*Crepidula fornicata*) (LeBlanc et al. 2003), overgrowth can cause high levels of mortality by inflicting severe physical damage to *C. virginica* spat (MacKenzie 1970). With certain species of calcareous bryozoans and tunicates, overgrowth can be responsible for smothering or suffocating oysters by completely covering them (MacKenzie 1970; White and Wilson 1996). One such species of tunicate, native to PEI, is the sea grape (*Molgula* spp.) which can cause severe oyster spat mortality, especially in years of high abundance (MacNair and Smith 1999). Other tunicates species affecting bivalve populations in PEI and the southern Gulf of St. Lawrence include the clubbed tunicate (*Styela clava*), the vase tunicate (*Ciona intestinalis*), the golden start tunicate (*Brotryllus scholesseri*), and the violet tunicate (*Botrylloides violaceus*) (Locke et al. 2007). These four invasive species have all arrived to PEI and the southern Gulf of St. Lawrence since 1997 and have become nuisance species for the bivalve aquaculture industry, in particular the culture of *M. edulis* (Ramsay et al. 2008a). Not only do these invasive tunicates attach to aquaculture equipment and increase the associated production costs (Ramsay et al. 2008b), they are also reported to ultimately reduce mussel productivity through competition for food and space (Daigle and Herbinger 2009). For example, mussels on heavily fouled culture lines are reported to have decreased meat yields, lower growth rates, and an increase in overall mortality (Daigle and Herbinger 2009).

Reduced growth and survival rates resulting from competition for food are also reported for *C. virginica* populations (Zajac et al. 1989; White and Wilson 1996; PEIDAFA 2005). The most common examples of organisms competing for food with *C. virginica* include slipper shells, various barnacle species, (White and Wilson 1996), and *M. edulis* (PEIDAFA 2005). As soft-shell clams are usually burrowed in the sediment, competition for food and space is usually less severe than in other species (Abraham and Dillon 1986). However, intraspecific competition (Beal 2006) and competition for food with the amethyst gem clam (*Gemma gemma*) (Sanders et al. 1962) has been documented in some regions and has been attributed to reduced growth rates of juvenile *M. arenaria* populations. While competition between wild *C. virginica* and *M. arenaria* populations has been reported to some extent in the literature, the effect of cultured *C. virginica* on wild *M. arenaria* populations is now an area of current interest and recent research (see Abgrall et al. 2010).

Organisms which do not directly compete or prey on bivalves, but have a negative impact on their health, and ultimately on their survival rate, are often referred to as pests. One of the most common and damaging pest is the boring sponge (*Cliona celata*), found throughout the Atlantic coast of North America (Galtsoff 1964; MacKenzie 1970; Carver et al. 2010), including waters surrounding PEI and the southern Gulf of St. Lawerence

(PEIDAFA 2005). The boring sponge infects bivalves such as *C. virginica* and causes the shell to erode (Carver et al. 2010). With shell erosion, the shell is weakened and the organism becomes more vulnerable to predation and disease with age (Carver et al. 2010). The boring sponge, which is reported to infect up to 25-30% of the individuals in some estuaries in New Brunswick, is also a serious concern for aquaculture industry as the infected individuals have substantially decreased market values (Carver et al. 2010). The bristle worm or mud worm (*Polydora* spp.) is another pest with similar effects as the boring sponge (White and Wilson 1996; PEIDAFA 2005). As seen in the boring sponge, these worms bore into the shells of bivalves and cause them to become brittle and, indirectly, reduce their survival rate.

The green algae, *Codium fragile* ssp. *tomentosoides,* commonly known as the oyster thief is another known pest of American oysters. Originally native to Japan, the oyster thief was first confirmed in the Gulf of St. Lawrence in 1996 (Garbary et al. 1997) and has since spread to most estuarine areas of PEI (PEIDAFA 2005). This invasive species can attach to adult oysters, and the buoyancy of the plant can cause the attached oysters to float away. In areas of strong currents and tidal action, oysters and attached plants can be washed on shore or into shallow waters exposing the oysters to desiccation and possible ice scour (Garbary et al. 1997).

### *2.2.3. Common predators of oysters, blue mussels, and soft-shell clams*

The soft bodied tissues of bivalve species are protected from predators by a calcareous shell of varying thicknesses according to species. The thickness of the shell is a main predictor of shell strength (Elner 1978: Zuschin and Stanton 2001), and one of the main deterrents of predation (Boudling 1984; Leonard et al. 1999; Newell et al. 2007). *C. virginica*, for example, has a thicker shell compared to many other bivalves (White and Wilson 1996) which predators are required to penetrate in order to feed on body tissues. *M. edulis* has a somewhat thinner shell but as they grow in shell length, they also grow proportionally in shell width and shell height. The increase in volume, or cross sectional area, can reduce mortality from predators such as crabs as they become difficult to manipulate and crush with their claws (Kaiser et al. 1993). The tight clumps or clusters that *M. edulis* forms also acts a defense to predators and reduces their overall vulnerability to predation (Kaiser et al. 1993; Seed and Hughes 1995). *M. arenaria* on the other hand can be quite vulnerable to predation as they have a much thinner shell than most bivalves, as well as an exposed siphon (Whitlow 2010). *M. arenaria* however is capable of burrowing themselves into the sediment and reaching a possible spatial refuge from various predatory species (van der Veer et al. 1998; Whitlow et al. 2003).

Despite their defensive features, *C. virginica*, *M. edulis*, and *M. arenaria* face many predators throughout their natural range. Many of these predators have developed specialized appendages which allow them to break into the shells of bivalves. These predators include mollusks, echinoderms, crustaceans, fishes, birds, and mammals (Flimlin and Beal 1993). Generally, small individuals or spat are the most at risk to predation, as larger adults are bigger in size and have thicker shells (White and Wilson 1996). Sea stars, such as *Asterias forbesi* and *Asterias vulgaris,* are some of the most common and well known predators of most bivalve species (Flimlin and Beal 1993; Kennedy et al. 2009). While both species of sea stars are common along the northeastern coast of the United States (Flimlin and Beal 1993), *A. vulgaris* is the main predator in PEI waters (Miron et al. 2005). To prey on bivalves, a sea star pulls apart the two valves, extends its stomach inside the opening, and digests and absorbs the body tissue (Flimlin and Beal 1993; White and Wilson 1996; Kennedy et al. 2009). Sea stars, having been known to consume over 15 individuals of *C. virginica* spat per day, can be responsible for considerable bivalve mortality each year (Flimlin and Beal 1993). Especially in years of high abundances, sea stars can be quite detrimental to shellfish populations (Kennedy et al. 2009).

Another important predator of American oysters is a carnivorous gastropod commonly known as the Atlantic oyster drill (*Urosalpinx cinerea*) (Flimlin and Beal 1993; White and Wilson 1996; Harding et al. 2007; Kennedy et al. 2009). As their name suggests, oyster drills prey on oysters by boring a small hole into the shell, allowing them access to the body tissue (Harding et al. 2007; Kennedy et al. 2009). Originally found from southern Nova Scotia to northeastern Florida (Flimlin and Beal 1993), oyster drills were first present in PEI waters in the early 1900`s. Recently however, growing populations have become established in many harvesting and growing areas in the province, making them an increasingly important source of *C. virginica* mortality (PEIDFARD 2006). Besides solely preying on oysters, oyster drills are also known to prey on *M. edulis* and to a lesser extent, *M. arenaria* (Harding et al. 2007). Another carnivorous gastropod, the dog whelk (*Nucella lapillus)* is also responsible for considerable *M. edulis* mortality in intertidal areas throughout the world including eastern Canadian waters (Hunt and Scheibling 1998). Several worm species can also be important predators of many bivalve species and can cause considerable mortality each year. For example, the oyster flatworm (*Stylochus ellipticus*) is a common predator of all sizes of *C. virginica* (Newell et al. 2007).The flatworm preys on the body tissue of oysters by entering through the opened valves (Flimlin and Beal 1993; Newell et al. 2007). Although abundant in areas such as the Chesapeake Bay, PEI is at the northern limit of the oyster flatworm's range (White and Wilson 1996). In *M. arenaria* populations, the milky ribbon worm (*Cerebratulus lacteus*) is another important predator that can limit the abundance of *M. areanaria* and is also found in PEI waters (Bourque et al. 2001).

Several species of fish and birds are common bivalve predators in many parts of eastern North America. *M. arenaria*, for example, is vulnerable to a wide variety of fish predators including the striped killifish (*Fundulus majalas*) and the common mummichog (*Fundulus heteroclitus*) (MacKenzie and McLaughlin 2000). Many species of gulls and sea ducks are known to prey on both *M. arenaria* (Abraham and Dillon 1976; Flimlin and Beal 1993) and *M. edulis* (Hamilton et al. 1999; Dionne et al. 2006), and likely cause considerable mortality each year. Although little information exists on the extent to which fish prey on *C. virginica* in Atlantic Canada, several known predators are located in estuarine areas of the north eastern United States. Several fish species that prey on *C. virginica* include the toadfish (*Opsanus tau*), the cow-nosed ray (*Rhinoptera bomasis*), and the summer flounder (*Paralichthys dentatus*) (White and Wilson 1996). Although these species prey on oysters, predation by fish is generally not considered a major problem (Flimlin and Beal 1993). Furthermore, those same fish species, as well as others, can also be beneficial to oyster populations. These fish species can reduce the overall predation on oysters by preying on various species of crabs (Abbe and Breitburg

1992; White and Wilson 1996), one of the main predators on bivalve beds (e.g., Mascaro and Seed 2001a,b; Floyd and Williams 2004; Miron et al. 2005).

Crabs are some the most common and abundant predators of commercially grown bivalves (Flimlin and Beal 1993) and are likely responsible for much of the *C. virginica* (Elner and Lavoie 1983; Bisker and Castagna 1987; White and Wilson 1996), *M. edulis* (Mascaro and Seed 2001a; Breen and Metaxas 2008), and *M. arenaria* (Ebersole and Kennedy 1995; Floyd and Williams 2004) mortality each year. Crabs are capable of opening bivalves by chipping away valve edges, forcing the two valves apart, and by crushing the entire shell (Flimlin and Beal 1993). Various crab species such as the stone crab (*Menippe mercanaria*), the blue crab (*Callinectes sapidus*), the rock crab (*Cancer irroratus*), and the mud crabs (Family Xanthidae) are known to prey on shellfish along the Atlantic coast of North America (Mackin 1959; Elner and Lavoie 1983; Flimlin and Beal 1993; White and Wilson 1996). In estuarine areas of PEI, native crab species known to prey on commercially important bivalves include the native rock crab (*C. irroratus*) (Miron et al. 2005) and several species of mud crabs (PEIDAFA 2005), the black fingered mud crab (*Dyspanopeus sayi*) and the white fingered mud crab (*Rhithropanopeus harrisii*). With the invasion of European green crab (*Carcinus maeanas*) to North America in the 1800's (Audet et al. 2003), this species quickly became recognized as a predator of most bivalves in the region, including *C. virginica*, *M. edulis*, and *M. arenaria* (Elner 1981; Flimlin and Beal 1993). The green crab, which was first confirmed in PEI in 1997 (Audet et al. 2003), is now expanding across the island and emerging as an important predator of commercially grown bivalves in the area (Miron et al. 2005).

## 2.3. The European green crab

European green crabs are medium sized, intertidal, brachyuran crabs belonging to the Portunidae family. These crabs grow to about 50-80 mm carapace width (CW) and are commonly characterized by their dark green colour, which can vary from brown, orange, and red depending on moulting status (Behrens Yamada and Hauck 2001). The crabs are identified by the presence of five lateral teeth of approximately equal size on both sides of the rostrum, which is composed of three lobes between the eyes. The fifth pair of walking legs is slightly dorso-ventrally flattened, an adaptation for swimming. However, in this species the swimming legs are less pronounced than in other portunid species (Behrens Yamada and Hauck 2001). The green crab has an exceptional tolerance to a wide variety of environmental conditions and a long planktonic larval stage, making it an excellent invasive species that is now found throughout many parts of the world (e.g., Carleton and Cohen 2003). Accordingly, much literature exists on the biology of the green crab, its invasion history, and the ecological impacts caused in newly invaded areas. A portion of that literature has been reviewed below.

### *2.3.1. Biology and environmental tolerance*

The native range of the green crab covers the eastern Atlantic Ocean, ranging from central Norway to the coast of northwest Africa. The range extends as far east as the Baltic Sea, and as far west as Iceland and the Faeroe Islands. The crabs however, are not present in the Mediterranean Sea, instead a congeneric species, *Carcinus aestuarii*, occupies the region (Williams 1984). Within their range, green crabs occupy a wide variety of habitats at varying depths. Although found in coastal waters up to 18 m deep

(Elner 1981), throughout their range green crabs are typically found in estuarine areas from the intertidal zone to depths of about 5-6 m (Crothers 1968). Within this depth, the crabs are found in many habitats including coastal areas with hard substrates such as rock and shell but are usually most abundant in sheltered areas with soft substrates such as eel grass beds and mud flats (Grosholz and Ruiz 1996; Jamieson et al. 1998).

Green crabs typically live to be about 5-7 years of age and reach sexual maturity at about 2-3 years (Berrill 1982). In their European home range, sexual maturity is reached at 23.0-45.00 mm carapace width (CW) for females and at 42.0 mm CW for males (d'Udekem d'Acoz 1993 as cited by Sharp et al. 2003). However, in an estuarine area in the southern Gulf of St. Lawrence (Basin Head, PEI), Audet et al. (2008) found sexual maturity was not reached until a larger size of 36.90-43.79 and 44.32-49.48 mm CW, for females and males, respectively. The larger size at sexual maturity in the southern Gulf of St. Lawrence is reportedly due to colder climate conditions in the region compared to the warmer European waters.

In the Gulf of St. Lawrence, reproductive events for green crabs tend to occur at least a month later than in the northeastern United States, and follow a different cycle in their native European range (Sharp et al. 2003; Audet et al. 2008). Such differences among regions are again likely attributed to different climatic conditions (Audet et al. 2008). In PEI, mating usually peaks around mid-September and ranges from August to December (Audet et al. 2008). However, in the warmer waters of Maine, mating frequency generally peaks in August, and in Europe, mating occurs continuously throughout the year (Berrill 1982). After mating and egg fertilization, the female carries the eggs under her abdomen for several months before they develop into free-swimming larvae and are released into the water column (Broekhuysen 1936 as cited by Klassen and Locke 2007). In North American waters, females spawn once a year and can have up to 185 000 eggs in one brood (Carlton and Cohen 1995). In the European range however, spawning events happen at least twice a year (Broekhuysen 1936 as cited by Sharp et al. 2003). The larvae may then remain in the water column for more than 80 days before settling on the bottom (Thresher et al. 2003).

Green crabs are capable of tolerating a wide range of environmental conditions, allowing them to successfully expand and adapt into new areas (Audet et al. 2008). The crabs are able to withstand temperatures from less than 0 to greater than 35°C (Hidalgo et al. 2005). Foraging and general activity however is greatly reduced at temperatures less than 7°C in the New England states (Ropes 1968) and at less than 5°C in the southern Gulf of St. Lawrence (Belair and Miron 2009a). Adult green crabs are also capable of surviving environments with salinities ranging as low as 4‰ (Crothers 1967) to as high as 52‰ (Carlton and Cohen 1995). Early benthic stages are, however, less tolerant to environmental conditions than adult crabs. Both egg development and larvae require a narrower range for temperature and salinity (Crothers 1967). The adult crabs are also reasonably tolerant to hypoxic conditions, although the degree to which they are affected is dependent on both salinity and temperature (Legeay and Massabuau 2000). Under the right conditions, the crabs are reported to be able to survive out of water for up to ten days (Crothers 1968), greatly increasing their chance to be accidentally transported to new areas. The ability of the crabs to withstand harsh environmental conditions, as well as their high fecundity and long planktonic larval stage, make them excellent global invaders that are now found in many areas well outside of their natural range (Roman 2006).

### *2.3.2. Invasion mechanisms and history, worldwide to Atlantic Canada*

Although green crabs have a long lasting planktonic larval stage which could easily allow short range expansions (Roman and Palumbi 2004), human mediated transport is almost certainly responsible for the trans-oceanic expansion of green crabs (Carleton and Cohen 2003). Carlton and Cohen (2003) and Cohen et al. (1995), in an attempt to determine the methods for green crab invasion, identified several possible transport mechanisms. They noted that early invasions were most likely the result of crab transport in solid ballast, such as rocks, or from transport on fouled or bored hulls of wooden ships. However, with the decline of solid ballast and wooden ships, more recent invasions are more likely caused by other mechanisms (Cohen et al. 1995; Carlton and Cohen 2003). Transport in ballast water is considered the most likely mechanisms for the recent green crab invasions (Cohen et al. 1995; Carlton and Cohen 2003). Both green crab larvae and juveniles were documented in ballast water and with their long lasting larval stage, green crabs are capable of surviving long trans-oceanic voyages (Carlton 1985). In the case of the western North American invasion, Cohen et al. (1995) identified transport in commercial fisheries products such as bait worms and American lobsters (*Homarus americanus*) as a possible transport mechanism. Before these products were shipped, they were traditionally packed with seaweed, and accidentally any associated invertebrates, including green crabs. Cohen et al. (1995) also recognized that green crabs are a widely studied organism and accidental release by universities and researchers could be a potential transport mechanism. Although few documented examples exist, the intentional release of green crabs into new areas for food and commercial fishery purposes may have also contributed to their global spread (Cohen et al. 1995; Carlton and Cohen 2003).

With their exceptional tolerance to a wide variety of environmental conditions (Crothers 1967; Ropes 1968; Legeay and Massabuau 2000; Hidalgo et al. 2005; Bélair and Miron 2009a) and the ability to live out of water for several days (Crothers 1968; Darbyson et al. 2009), it is not surprising that green crabs are now found well beyond their native range, throughout many parts of the world. Outside of European waters, the crabs were first reported on the eastern coast of North America in 1817 in the New York and New Jersey areas and have since expanded northwards (Audet et al. 2003). Another trans-oceanic expansion occurred around the early 1900's, when populations of the green crab became well established along parts of the Australian coast (Thresher et al. 2003; Ahyong 2005). Later, in 1983, the crabs were documented in waters near Cape Town, South Africa and since established large populations in that region (Le Roux et al. 1990). The crabs first invaded the west coast of North American in 1989, in the San Francisco Bay area (Cohen et al. 1995). Isolated to that area for several years, the green crabs are now found along most of the California coast (Grosholz and Ruiz 1996), as well as Oregon since 1998 (Jamieson et al. 1998) and Washington since 1999 (Behrens Yamada et al. 2005). Recently, isolated populations of green crabs on the western coast of Vancouver Island, British Columbia (BC) were also documented (Gillespie et al. 2007). Even more recently in 2003, a well established population of green crabs was confirmed in the South American waters of Argentina (Hidalgo et al. 2005).

Since their first report in the New York and New Jersey areas in 1817 (Audet et al. 2003), it was not until the beginning of the 1900's when the crab first reached the coast of Maine (Audet et al. 2003). It was then another fifty years later, in 1951, before the crabs were reported in Canadian waters, in the Bay of Fundy region of New Brunswick (NB) (Audet et al. 2003). In the next several years, the crabs expanded around the southwestern tip of Nova Scotia (NS) and began slowly making their way northward along the province's Atlantic shore before reaching Chedabucto Bay around 1985 (Audet et al. 2003). As the crabs were first identified in St. Georges Bay and the west coast of Cape Breton Island around 1994 and 1995, the crabs are believed to have entered the southern Gulf of St. Lawrence through the Strait of Canso (Audet et al. 2003). Upon their arrival into the southern Gulf, the crabs rapidly expanded throughout the region moving westward along the Northumberland Strait side of NS before reaching NB waters in 2002 (Audet et al. 2003).

In 1997, the green crabs were first confirmed in Prince Edward Island waters in the Cardigan River system at the eastern end of the province (Audet et al. 2003). Green crab populations then rapidly expanded into the areas of Naufrage and Vernon Bridge in 1998, and North Lake and Wood Islands in 1999 (Klassen and Locke 2007). On the south shore of PEI, the crabs expanded westward and reached the Charlottetown Harbour water system in 2000 and Victoria in 2001 (Klassen and Locke 2007). Meanwhile, on the north shore of the province, the crabs expanded as far west as Savage Harbour by 2001. From 2000 to 2006, there was no reported expansion of green grab populations in the province however in previously invaded regions populations continued to grow and became well established (Klassen and Locke 2007). As of the March 2011, the known range of the green crab extends as far west as Enmore River on the south shore and New London Bay on the north shore (Aaron Ramsay, PEI Department of Fisheries, Aquaculture, and Rural Development, Pers. Comm.)

Recent molecular research found little genetic similarity between the crabs along the eastern seaboard of the United States and southern NS and the crabs found in the southern Gulf of St. Lawrence and eastern NS (Roman 2006). The author provides genetic evidence that the crabs in the southern Gulf and eastern NS are more closely related to the cold tolerant crabs of northern Europe, from areas such as Norway and the Faeroe Islands, and are likely the result of a new introduction. The author also suggests that the recent rapid expansion throughout the Gulf of St. Lawrence is due to the introduction of cold tolerant green crabs and provides a shipping route between Canso, NS and Mongstadt, Norway as the possible invasion vector. After their initial expansion throughout PEI, the green crabs later spread into more northern regions of the Gulf of St. Lawrence. In 2004, an isolated population was reported in the Grand Entrée Lagoon of the Magdalen Islands, Quebec (QC) (Paille et al. 2006; Klassen and Locke 2007). Also, in 2007, an established population was observed for the first time in Newfoundland and Labrador (NL) in the North Harbour area of Placentia Bay (Klassen and Locke 2007).

### *2.3.3. Ecological and economic effects of invasion*

The arrival of an invasive species to any new area has the potential to cause a considerable impact on the host ecosystem, as well as the economics of the area (Grosholz and Ruiz 1996; Walton et al. 2002). As green crabs have become well established in many areas outside of their native range in the last century (Audet et al.

2003; Klassen and Lock 2007) much research has been devoted to the impacts they have caused in introduced regions. Green crabs can impact newly invaded ecosystems in several different ways. They are reported to alter and disrupt ecosystem habitat (Davis et al. 1998; Garbary and Miller 2006), compete with other crustaceans and vertebrates for food and space (McDonald et al. 2001; Rossong et al. 2006; Williams et al. 2006), and greatly diminish the local population size of their prey (Walton et al. 2002; Floyd and Williams 2004).

One way green crabs can cause ecological impacts in newly invaded ecosystems is by disrupting the local habitat. For example, Davis et al. (1998) found green crab foraging methods have the potential to cause damage to eelgrass beds and can interfere with eelgrass restoration efforts. Also, in NS, a green crab invasion was blamed for the loss of over 95% of the eelgrass beds in Antigonish Habour and nearby estuaries (Garbary and Miller 2006). Green crab foraging methods are reported to destroy eelgrass beds by creating large burrows and by tearing or cutting the sheath bundle of the grass (Davis et al. 1998; Garbary and Miller 2006; Malyshev 2009). As eelgrass beds provide habitat for an array of benthic organisms, and are a critical feature of healthy estuarine ecosystems, damage to eelgrass beds caused by green crabs can have tremendous impacts on the entire benthic community (Davis et al. 1998).

The ecological implications of green crab invasions also extend to competition with native crustaceans, and when these native crustaceans are commercially valuable, green crabs can negatively affect the economics of an area. On the west coast of North America for example, juvenile and adult green crabs were demonstrated to have a negative impact on the commercially important Dungeness crabs (*Cancer magister*)

(McDonald et al. 2001). In experimental conditions, juvenile green crabs displaced similar sized Dungeness crabs from shelters and consistently dominated in feeding trials. In areas where distributions overlapped, McDonald et al. (2001) proposed that the invasive green crab could have a negative impact on the Dungeness crab fishery through a reduction in recruitment. Jensen et al. (2002) also found that green crabs out competed the native shore crab species (*Hemigraspus oregonesis*) on the west coast of North America. Similarly, on the east coast, MacDonald et al. (2007) found juvenile green crabs usually dominated agonistic interactions with similar sized native blue crabs (*C. sapidus*) and the more recently invaded Asian shore crab (*Hemigraspus sanguineus*). Also, on the east coast, laboratory experiments between adult green crabs and juvenile American lobsters (*Homarus americanus*) found green crabs dominated feeding trials, displaced lobsters from shelters, and even preyed upon lobsters in some trials (Rossong et al. 2006). Furthermore, in experimental trials between adult green crabs and sub-adult lobsters, green crabs continued to dominate feeding trials as they were the first to the food and consistently defended it from larger lobsters (Williams et al. 2006). However, in similar experiments involving green crabs and adult lobsters (>72 mm carapace length), Williams et al. (2009) showed a reversal of dominance with green crabs once the lobsters exceeded 72 mm carapace length (CL). As there is potential spatial overlap between American lobster and green crab habitat in the southern Gulf of St. Lawrence (Rossong et al. 2006), green crabs have the potential to negatively affect the valuable commercial lobster fishery in the region. Furthermore, in the southern Gulf of St. Lawrence, Miron et al. (2005) demonstrated that invasive green crabs have a similar diet as the native rock crab (*C. irroratus*). The authors suggested that this diet, along with their similar habitat preference, may cause competition between the two species, and have an impact on the local rock crab fishery. More recent studies however, addressing the spatial overlap between these two species, suggested that rock crabs and green crabs may be able to co-exist without displacing one another (Bélair and Miron 2009a,b).

Besides competing with crustaceans for food and space, green crabs can also negatively impact local ecosystems in newly invaded areas through predation mechanisms (Walton et al. 2002; Floyd and Williams 2004). For example, in Bodega Bay Harbor on the Californian coast, green crab predation is believed to be responsible for declines of the native shore crab (*H. oregonensis*) (Grosholz et al. 2000). Populations of *H. oregonensis* have decreased by nearly 90% in just three years following the initial green crab invasion to the area (Grosholz et al. 2000). Green crabs have also been shown to be important predators of several gastropod species, including the intertidal snail, *Littorina obtusata* (Rochette et al. 2007; Edgell and Rochette 2009). Rochette et al. (2007) in particular, demonstrated that populations of *L. obtusata* in areas invaded with green crabs have undergone morphological transistions to protect themselves from green crab predation. The authors state these populations have developed thicker, heavier shells, and smaller apertures to reduce the ability of green crab foraging. Green crab predation has also caused declines in several species of amphipods and two native clam species, *Nutricola tantilla* and *Nutricola confuse.* With field and laboratory experiments, Grosholz et al. (2000) suggested these population declines were a direct result of green crab predation. As bivalves are reported to make up a large percentage of the green crab diet (Ropes 1968; Elner 1981; Baeta et al. 2006), most impacts associated with green crabs are on these organisms. In their European home range, green crab predation is attributed to massive population declines of commercially harvested bivalves, such as blue mussels (Dare and Edwards 1976), Pacific oysters (*Crassostrea virginica*) (Walne and Dean 1977), and hard clams (*Mercenaria mercenaria*) (Walne and Dean 1972). In their expanded range, green crabs are attributed to several bivalve population declines throughout the world. One of the most notable cases is the New England soft-shell clam (*Mya arenaria*) fishery in the north eastern United States. After the arrival and establishment of green crab populations in the region, the clam fishery which once produced over 6000 metric tonnes  in the 1940's was decreased to around 900 metric tonnes by the 1950's (Ritchie 1976). While on the west coast of North America, the green crab invasion has also been attributed to substantial declines of two native clam species (Grosholz et al. 2000). Experimental research further suggests that green crabs will also have a negative effect on the venerid clam (*Katelysia scalarina)* fishery in Tasmania, Australia as green crabs predation rates on the clam are much higher than any native predator tested (Walton et al. 2002). In the Gulf of St. Lawrence, Miron et al. (2005) also found green crabs are an important predator of several commercially important bivalve species and suggested green crabs may impact local bivalve fisheries and aquaculture operations in the region.

### 2.4. Bivalve predation by European green crabs

Many crab species are considered to be common predators of bivalves (Flimlin and Beal 1993). European green crabs are no exception as they are aggressive, voracious predators that feed on a wide variety of prey items, including bivalves, crustaceans, algae, and polychaetes (Ropes 1968; Elner 1981; Baeta et al. 2006). Stomach content analyses of green crabs however indicate in most regions these predators rely mostly on bivalves in their diet (Ropes 1968; Elner 1981; Baeta et al. 2006). In their European home range for example, green crabs are known to feed on several species of oysters (Mascaro and Seed 2000*a,b*; Mascaro and Seed 2001*a,b*), mussels (Dare et al. 1983; Baeta et al. 2006; Murray et al. 2007), and cockles (Mascaro and Seed 2000*a,b*; Mascaro and Seed 2001*a,b*). On the west coast of North America, green crabs are well known predators of several oyster and clam species (Palacios and Ferraro 2003). On the eastern coast of North America, the crabs are known predators of various species of significant economic importance, including the hard clam, *M. mercenaria* (Walton and Walton 2001; Miron et al. 2005), *M. arenaria* (Ropes 1968; Floyd and Williams 2004; Miron et al. 2005), *M. edulis*, and *C.virginica* (Miron et al. 2005). As most of these bivalve species are economically and ecologically important, there has been much research devoted to predator-prey interactions between these bivalves and green crabs. This literature has been reviewed in detail in the sub-sections that follow, with a particular emphasis on American *C. virginica*, *M. edulis*, and *M. arenaria*, three of the most commercially important bivalves to PEI (Miron et al. 2005).

### *2.4.1. Prey preferences of green crabs*

Experimental feeding trials suggest green crabs exhibit strong prey preferences when given a choice among several bivalve species of similar size (Cohen et al. 1995; Mascaro and Seed 2000a,b; Mascaro and Seed 2001a,b; Palacios and Ferraro 2003; Miron et al. 2005). With experiments using bivalves from their European home range, both medium (40-50 mm CW) and large (55-70 mm) green crabs showed a preference for

*M. edulis* over similar sized flat oysters (*Ostrea edulis*) and Pacific oysters (*Crassostrea gigas*) (Mascaro and Seed 2000b; Mascaro and Seed 2001a,b). On the west coast of North America, feeding trials with green crabs and local bivalve species also indicated green crabs exhibit species selective prey preferences (Cohen et al. 1995; Palacios and Ferraro 2003). In the southern Gulf of St. Lawrence, Miron et al. (2005) found in multiple choice experiments that *M. edulis* were preferred over *M. arenaria* and *C. virginica*.

The species-selective preferences exhibited by green crabs can be explained in part by the optimal foraging theory (Elner and Hughes 1978). The optimal foraging theory predicts green crabs, as well as other predators, will find, capture, and consume food of highest energetic value while minimizing their time and energy output (Charnov 1976). Factors that influence prey selection, relating to the optimal foraging theory include handling time and required energy for consumption, the prey encounter rate, and the nutrient value of the prey (Elner and Hughes 1978). The main factor that affects handling time and required energy for consumption among various bivalve species is their contrasting shell morphologies (e.g., Boulding 1984; Mascaro and Seed 2000b; Mascaro and Seed 2001a). Such features as shell thickness, shell shape, and the presence or absence of gapes are all important in determining their vulnerability to crab predation (Boulding 1984).

Shell thickness is an important factor influencing prey preference as bivalves with thinner shells are observed to be more vulnerable to crab predation compared to bivalves with thicker shells (Boulding 1984). For example, when comparing predation by the red rock crab (*Cancer productus*) on the thick-shelled and thin-shelled morphs of the Pacific little neck clam (*Protothaca staminea*), the thick-shelled morph was the least vulnerable to predation (Boulding 1984). As shell thickness is noted as a main determinant of compressive shell strength (Elner 1978; Zuschin and Stanton 2001), thicker shells are able to withstand larger compressive loads (Boulding 1984; Leonard et al. 1999; Newell et al. 2007). Thicker shelled bivalves therefore require more crushing force from crab chela and often more compressive pulses (e.g., Elner 1978; Boulding 1984). More crushing force and pulses required for consuming thicker shelled bivalves generally increases handling time, making them less preferred by crabs (e.g., Boulding 1984).

The absence or presence of pedal and siphonal gapes is also an important feature determining prey preference and the vulnerability of bivalve species to crab predation (Boulding 1984; Miron et al. 2005). In feeding experiments, Boulding (1984) found the butter clam (*Saxidomus gianteus*) to be more vulnerable to predation from the red rock crab than the thin shelled morph of *Protothaca staminea*. As these clams have similar shell thickness, the author attributed the siphonal gape of the butter clam for its increase in vulnerability. As gapes provide crabs and other predators immediate access to the soft body tissues, bivalves with gapes are usually more preferred as they are generally easier to handle and require shorter handling times (Boulding 1984).

Shell shape is another important species dependent feature determining the vulnerability of bivalves to crab predation (Boulding 1984; Kaiser et al. 1993; Mascaro and Seed 2000b; Pelacios and Ferraro 2003). Boulding (1984) reported that more inflated, spherical shelled bivalves require more handling time by crabs, and are therefore less preferred. Similarly, Mascaro and Seed (2000b) suggested the minimum shell dimension, such as the shell height or width, of a bivalve is an important feature determining crab handling time. Also, while examining green crab foraging on mussel shaped plaster models, Kaiser et al. (1993) found handling time was not greatly influenced by changes in shell length but increased with increasing height and cross-sectional areas of the models. Therefore, it would be expected that bivalves with at least one small dimension would be more preferred.

Green crabs use both tactile and chemosensory stimuli while foraging for prey, therefore prey preferences are also likely influenced by the encounter rate of prey items (Elner and Hughes 1978; Cohen et al. 1995). While local abundances affect the rate at which green crabs encounter certain bivalve species, the ability of some bivalves to burrow is also an important factor (Boulding 1984; Pelacios and Ferraro 2003; Dudas et al. 2005; Miron et al. 2005). Pelacios and Ferraro (2003) reported green crabs preferred Olympia oysters (*Ostrea conchaphila*) to California soft-shell clams (*Cryptomya californica*) to bent-nosed macoma clams (*Macoma nasuta*). This order of prey preference, the authors noted, was consistent with the burial depth of the clams, which would influence the encounter rate. Similarly, Miron et al. (2005) reported in multiple choice feeding experiments *M. edulis* spread on the sediment surface were preferred over *M. arenaria* buried in the sediment, despite their siphonal and pedal gapes and thinner shells (Dare and Edwards 1981; Brousseau et al. 2001). Both authors however also noted that a deeper burial depth would not only affect encounter rate but also increase handling time as well.

Although burrowing may provide a partial spatial refuge from predators for some bivalves (Boulding 1984; Miron et al. 2005), species such as *M. arenaria* still account for a large portion of the green crabs' diet (Ropes 1968; Elner 1981; Floyd and Williams

2004). Green crabs are capable of burrowing up to 15 cm in search of prey (Ropes 1968) and are able to detect the siphon holes of buried bivalves with their walking legs (Cohen et al. 1995). In single choice experiments Miron et al. (2005) reported green crabs were able to detect and handle burrowed *M. arenaria* without any difficulty. With experiments involving the Asian shore crab (*H. sanguineus*), Brousseau et al. (2001) found buried *M. arenaria* were more preferred over *M. edulis* and *C. virginica.* Furthermore, in feeding experiments on the west coast of North America, green crabs showed a preference for the invasive Asian clams (*Potamocorbula ameruensis)* buried in sediment as opposed to mussels clustered on the surface, suggesting other factors such as shell morphologies are also at play (Cohen et al. 1995).

### *2.4.2. Size selection and maximum vulnerable size*

Besides showing preferences for certain bivalves, green crabs also exhibit preferences for certain sized individuals within a species (Dare et al. 1983; Mascaro and Seed 2000a; Mascaro and Seed 2001b; Floyd and Williams 2004; Miron et al. 2005). Similar to prey preferences, size selection can be partially explained by the optimal foraging theory (Elner and Hughes 1978; Mascaro and Seed 2000a). Regarding size selection, the optimal foraging theory predicts crabs choose a size of prey that would maximize dietary intake while minimizing energy output and handling time (Charnov 1976). For example, Mascaro and Seed (2000b) found green crabs consistently selected intermediate sizes of *M. edulis*. The authors suggested the intermediate sizes may not be the most profitable in terms of dietary value but larger items may be less preferred because they are more difficult to open while smaller items may be less likely to encounter and more frequently dropped. Murray et al. (2007) also demonstrated that green crab predation on *M. edulis* exponentially decreases with increasing prey size suggesting crabs prefer smaller sized individuals. Other authors have also suggested that various crabs species may choose smaller prey as repeatedly attempting to open larger prey can cause chelal damage and wear, reducing their overall foraging ability (Juanes and Hartwick 1990).

For most bivalve species there is also a critical size at which predation by crabs can no longer occur (e.g., Boulding 1984; Floyd and Williams; Miron et al. 2005). This maximum vulnerable size to green crab predation has been reported for several bivalve species. Miron et al. (2005) found that *M. edulis* and *C. virginica* both reach a partial size refuge from green crabs at ~25 mm shell length (SL), a value for *M. edulis* that was also consistent with findings from other studies (e.g, Murray et al. 2007). However, for rock crabs (*C. irroratus*) and American lobsters (*H. americanus*) foraging on *C. virginica*, Elner and Lavoie (1983) reported the critical size to be slightly larger at ~30-35 mm SL. For *M. arenaria*, laboratory experiments by Ropes (1968) showed green crabs are able to prey on individuals larger than their own carapace width. Brousseau et al. (2001) also observed Asian shore crabs preyed on *M. arenaria* by pulling the tissue through the siphonal gapes rather than breaking into the shell. However, in field conditions Floyd and Williams (2004) found only minimal green crab predation on *M. arenaria* of ~55 mm SL and greater but suggested this critical size may be more closely related to the deeper burial depths of larger clams, rather than their overall size.

Size selection and critical size are both shown to increase with increasing predator size (Elner and Hughes 1978) since larger predators have both an increase in chela strength and gape (e.g., Boulding 1984). As bivalves increase in size they may eventually become too large to be handled by chela, decreasing the amount of force a crab can apply (Boulding 1984). To feed on these larger bivalves, Elner and Hughes (1978) showed green crabs chip away at the valve edges of larger mussels rather than completely crush the entire shell. As this method is much slower, the handling time required to open the mussels greatly increases, making this size of prey less preferred. The size at which a bivalve can no longer be handled by a crab is most likely dependent on the minimum shell dimension, rather than the maximum. Therefore, crabs may not make size selections based solely on shell length and may incorporate other shell dimensions such as height and width, and other features such as crushing resistance (Kaiser et al. 1993; Mascaro and Seed 2000a).

As most studies show, green crabs have a preference for smaller sized individuals within a given prey species (Boulding 1984; Floyd and Williams; Miron et al. 2005; Murray et al. 2007), and therefore, younger, smaller individuals are most likely to be affected by a green crab invasion. The decimation of young bivalve stocks can cause steep population declines once the older, larger individuals begin to die off and are not replaced (Floyd and Williams 2005). As the greatest impacts associated with green crabs are closely linked to the buildup of abundant populations (Walne and Dean 1977), several different methods have been applied on the monitoring of green crab numbers and size composition over time (e.g., Baeta et al. 2005; Audet et al. 2008; Polk 2008).

### *2.4.3. Monitoring changes in green crab population size and composition*

Aspects of green crab population dynamics monitored through sampling surveys include such characteristics as population abundance (of larvae, juveniles, and adults), size structure, sex ratio, and number of egg bearing females. When sampling surveys are conducted in a consistent way, such as monthly or seasonally, and with a similar protocol, changes reported overt time should reflect overall changes in the actual population (Lancia et al. 1996). The paragraphs below describe different sampling methodologies for each of the main life history stages in green crabs.

Beginning with larvae, the population dynamics of green crabs are generally measured with plankton tows (Zeng and Naylor 1996; Baeta et al. 2005). Typically, plankton tows use nets of ~50 cm diameter and mesh size ranging from 200 to 500 μm for monitoring green crab larvae (Zeng and Naylor 1996; Baeta et al. 2005). As the volume of water passing through the net can be determined, larval density can be estimated as individuals per cubic meter (ind $m^{-3}$). Another methodology used for measuring the abundance of crab larvae is stationary filter collectors (van Montfrans 1990). In this sampling method, larvae are filtered through a screen and held in a holding container (van Montfrans 1990; O'Connor 1993). When the collector is checked daily, short term patterns associated with changes in temperature, salinity, currents, and tides can be investigated (van Montfrans 1990; O'Connor 1993). In both these sampling methods, the collected green crab larvae can then be further classified into six different larval stages (1 protozoeal, 4 zoeal, and 1 megalopal stage) to determine the larval population structure for the area (Crothers 1967). Methods such as plankton pumps that are deployed in a given area and have the ability to filter water at a pre-defined frequency, can be considered much more accurate for the purpose of studying short-term larval dynamics (Alldredge and King 2009). However, plankton pumps are suitable for smaller sized plankton and rarely do not collect appropriate amount of crab larvae (Alldredge and King 2009)

In order to estimate the abundance of juvenile green crabs, two common methodologies are pitfall traps and minnow traps (e.g. Grosholz and Ruiz 1995). Pitfall traps are generally composed of polyethylene containers (buckets) buried in the sediment so that the top is flush with the surface. These buckets are not baited so juvenile green crabs are passively captured as they walk across the sediment and fall into the buckets. Minnow traps (cylindrical polyethylene or wire mesh traps, with a circular entrance at each end) are also used for targeting juvenile crabs (Grosholz and Ruiz 1995; Behrens Yamada and Gillespie 2008; Ellerbrook 2009). Unlike pitfall traps, minnow traps are baited and rely on the attractiveness of the bait for capturing juveniles. Although, Grosholz and Ruiz (1995) used both baited minnow traps and non-baited pit-fall traps, a direct comparison on their effectiveness was not made as minnow traps were only deployed in areas with hard substrates, where pitfall traps could not be used. In Basin Head, PEI, Audet et al. (2008) also used fry nets (similar to those used for sampling anadromous fish) for capturing juvenile green crabs in the intertidal zone. Fry nets allow the captured juveniles to be easily transported to the laboratory for further measurements such as size and sex to be recorded.

In order to estimate the abundance of adult crabs, the most common methodology is the use of baited traps, like those used in this thesis, with the type of trap generally depending on the region. For example, in early studies conducted in Nova Scotia, modified eel pots were mainly used for capturing green crabs (Tremblay et al. 2006; Polk 2008; Ellerbrook 2009). Similarly, in PEI, modified eel pots (Audet et al. 2008) and commercial lobster traps were used shortly after the initial invasion to the region (Gillis et al. 2000). Recently the use of Fukui traps has become a common method for trapping green grabs (e.g., Hunt and Behrens Yamada 2003; Behrens Yamada 2005; McDonald et al. 2007; Behrens Yamada and Gillespie 2008) and is now the national standard used by the Department of Fisheries and Oceans Canada. Three main advantages associated to this type of traps are their light weight, their ability to collapse, and allow even the largest crabs to enter. In other areas baited traps such as creels (Naylor 1962) and pearl lantern nets (Audet et al. 2003) are also used for targeting adult green crabs.

Passive traps that do not require the use of bait are also used for capturing adult green crabs (e.g., Audet et al. 2008). Non-baited traps such as fyke nets provide the benefit of capturing green crabs during life stages (or at certain hunger levels) when they are not normally attracted to bait. For example, while using both baited modified eel traps and non-baited fyke nets, Audet et al. (2008) reported that more ovigerous females were caught in fyke nets. The capture of ovigerous females through trapping methods such as fyke nets is important as they allow fecundity analyses to be conducted and provide a better overall understanding on the green crab reproduction cycle for the sampling area. Beam trawls are another method for capturing adult green crabs, and have similar benefits as the fyke nets (Baeta et al. 2008). However, this method requires specialized, expensive equipment and can only be used in certain depths and on certain bottom types. Another method that does not rely on bait is sampling using quadrats while snorkeling or SCUBA-diving (Breen and Metaxas 2009). In this method, quadrats can be randomly placed in sampling areas or uniformly placed along pre-measured transects. Although this method is somewhat limited by visibility conditions and depth, and may present limitations associated to the degree of mobility exhibited by crabs in the presence of divers, the use of quadrats should allow the most precise estimation of organisms (Breen and Metaxas 2009).

With the sampling methods described above, direct population estimates can only be made if the collected samples can be directly related to the density of the species (Lancia et al. 1996). This is difficult however due to unknown biases that may arise from these sampling methods (e.g., Tremblay and Smith 2001). These biases include, for example, the under representation of ovigerous females in baited traps (Audet et al. 2008). Alternative methods use mark-recapture techniques to estimate green crab population size and composition (Polk 2008). In this method, individuals of the target population are captured and marked to be uniquely identified and released back into the population (Bell et al. 2003). As the capturing of individuals continues, capture histories of marked and unmarked individuals are recorded and are analyzed to estimate the population size and composition for the area. Mark recapture programs also face their own biases however: natural mortality, tag loss due to molting, and behaviour changes resulting from tagging are all reported to influence population estimates in mark recapture programs (Bell et al. 2003).

The “Zippin method” is yet anther alternative to generate population estimates for green crabs (Zippin 1958; Smith and Addison 2003). The Zippin method involves closing off an area by methods such as fencing and removing the totality of individuals of the target species through trapping (Zippin 1958). Once all of the individuals in the closed area are captured, the density and overall abundance of the target species can be determined. In 2010, a modified Zippin method was tested in Basin Head Lagoon, PEI, in an attempt to monitor the success of a local eradication program (Andrea Locke, pers. comm.). Preliminary results from that area suggest that the Zippin method was ineffective due to gear handling problems and weather issues.

Estimates of green crab population size from both the mark recapture and Zippin methods can provide useful data on the abundance of green crabs in an area but seem heavily dependent on the size and conditions of the area under study, particularly, exposure to wind and currents.

### *2.4.4. Methods to control and mitigate green crab predation*

Due to the negative ecological and economic impacts associated with the establishment of large green crab populations, many control and mitigation strategies have been developed and tested in an attempt to reduce their potential impacts on wild and cultivated bivalve beds (Flimlin and Beal 1993; Lafferty and Kuris 1996; Thresher et al. 2000). Methods suggested for controlling green crab populations include trapping programs and chemical and biological control agents. Mitigation strategies to reduce predation on bivalves include protective nets and fencing, spreading bivalve seed at certain sizes and densities, and changing culturing practices to off-bottom methods (Flimlin and Beal 1993).

Trapping programs, such as subsidized fisheries, have been suggested and even tested in some areas in an attempt to eradicate green crab populations (Thresher et al. 2000). These programs however have not resulted in any evidence that the complete eradication of a fully established green crab population is possible through human intervention alone (Gillis et al. 2000). Furthermore, if a population was removed from an area even at the smallest scale, there is a strong likelihood of re-introduction from established nearby populations (Gillis et al. 2000). Although there is an important commercial fishery in southern Europe, the meat is dark and considered low quality to North American standards (Gillis et al. 2000). Furthermore, the small size of the crab and low meat yield also attribute to the crab being unsuitable for North American markets (Cohen et al. 1995; Lafferty and Kuris 1996). If subsidized fisheries were developed or a bounty placed on green crabs, some argue unwanted results may occur. A subsidized fishery may increase the risk of introduction into new areas and may never completely control the population as participation in the fishery would likely decrease as abundances became diminished (Klassen and Locke 2007).

Chemical agents have also been used to control green crab populations, restrict their movement, and prevent their predation on bivalves (Hanks 1961). To help manage the *M. arenaria* fishery in the New England states, Hanks (1961) evaluated the effectiveness of using bait soaked in pesticides as a control method. The toxic bait proved to be effective against controlling green crab movement and substantially reduced green crab trap catches in the area. The use of toxic bait is also more selective than pesticides that are spread directly on the water either from boats or planes (Hanks 1961). Chemical agents applied directly on the water surface can have unexpected negative effects on entire benthic communities and in some cases destroy important habitat such as eelgrass beds (Feldman et al. 2000). Despite its effectiveness and selectivity (compared to other application methods), the use of toxic bait may not only target green crabs, but all organisms that are attracted to the bait. Therefore, it is certain to have adverse environmental effects well outside of the green crab population and not be considered as a suitable control method.

Biological controls have been traditionally used in terrestrial systems and have recently been adapted as a measure to control invasive species in the marine setting (Lafferty and Kuris 1996; Thresher et al. 2000). Examples of biological controls include introducing predators, parasites, or pathogens of an invasive species into the invaded areas to reduce negative impacts (Thresher et al. 2000). One of the most noted potential control agents for green crabs is the rhizocephalon barnacle, *Sacculina carcini* (Lafferty and Kuris 2000; Thresher et al. 2000; Goddard et al. 2005). This parasitic barnacle castrates both male and female green crabs, inhibiting them from reproducing (Thresher et al. 2000). However, several experimental studies looked at the degree of host specificity in *S. carcini,* and showed that in most areas this parasitic barnacle would not only infect green crabs but also infect native crab species as well (Thresher et al. 2000; Goddard et al. 2005). Therefore, the potential effects of *S. carcini* on native crab species and other decapods would need to be carefully and fully understood before it was introduced as a biological control for green crabs in invaded areas.

Another biological control suggested is the nemertean egg predator, *Carcinonemertes epialti* (Torchin et al. 1996). This predator feeds on the eggs of various crab species but is less host specific than an ideal biological control. Predatory fish, such as the oyster toadfish (*Opsanus tau*), have also been tested for the biological control of crabs. As toadfish feed on crabs, Bisker et al. (1989) demonstrated toadfish placed inside protective enclosures could effectively control mud crab predation on juvenile hard clams. In similar experiments with oysters, Abbe and Breitburg (1992) however found toadfish ate only a minimal number of crabs, and had no apparent affect on oyster survival.

Besides methods of controlling green crab populations, mitigation strategies have also been developed and tested for reducing their impact on commercially important bivalves (Flimlin and Beal 1993). The most noted method is the use of plastic screens or nets to cover cultured shellfish such as *M. arenaria* (Flimlin and Beal 1993; Beal and Kraus 2002; Buttner et al. 2004; Floyd and Williams 2004). These protective nets allow good water flow while excluding green crabs and other predators. Fencing is another option similar to plastic nets and screens (Davies et al. 1980; Beal and Krause 2002). Plastic mesh fences can be constructed around areas of cultured shellfish and physically exclude green crabs and other predators (Davies et al. 1980; Beal and Krause 2002).

Other mitigation methods include stocking or spreading bivalve seed on the bottom at certain sizes or densities that should reduce predation. If bivalves are protected from predators until they reach their maximum vulnerable size, mortality from green crab predation should be greatly reduced (Dare et al. 1983; Flimlin and Beal 1993; Murray et al. 2007; Kamermans et al. 2009). Stocking or spreading seed at certain densities has also been suggested as a method to reduce crab predation. Sponaugle and Lawton (1990) demonstrated that several portunid crab species foraged less efficiently on hard clams (*M. mercenaria*) at low densities. Kamermans et al. (2009) however found spreading *M. edulis* seed at high or low densities had no overall affect on green crab predation. Gillis et al. (2000) also suggested adaptive measures such as switching to off-bottom growing methods or raising existing off-bottom methods further in the water column might also be necessary measures to ensure the sustainability of shellfish aquaculture industries in areas invaded with green crabs.

## 2.5. References

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# Chapter 3. POTENTIAL EFFECTS OF A NON-INDIGENOUS PREDATOR IN ITS EXPANDED RANGE: ASSESSING GREEN CRAB, CARCINUS MAENAS, PREY PREFERENCE IN A PRODUCTIVE COASTAL AREA OF ATLANTIC CANADA

Pickering, T., Quijon, P.A. (in press) Potential effects of a non-indigenous predator in its expanded range: assessing green crab, *Carcinus maenas*, prey preference in a productive coastal area of Atlantic Canada. Mar. Biol.

## 3.1. Abstract

Non-indigenous European green crabs (*Carcinus maenas*) are emerging as important predators of native bivalve populations in estuarine areas of Atlantic Canada. Although well known as omnivorous predators, this species may indeed exhibit marked prey preferences, sometimes for species of high commercial and ecologic value. In this study we investigate size-dependent green crab prey preference on American oysters (*Crassostrea virginica*), blue mussels (*Mytilus edulis*), and soft-shell clams (*Mya arenaria*). Specifically, we utilize three types of experiments to assess preferences exhibited by small (35-45 mm carapace width), medium (45-55 mm), and large (55-75 mm) green crabs when given a choice among small (15-25 mm SL) and then medium (25-35 mm) sized bivalves. All the experiments lasted three days, but in order to identify potential differences on the timing of predation, records of bivalve mortality were obtained on a hourly or daily basis. In experiments conducted in the laboratory and in floating field enclosures, green crabs showed a strong and early preference for soft-shell clams followed by mussels. In most cases, as clam abundance decreased, mussel mortality increased, and as this second choice started to decrease, oyster mortality increased. A preference for soft-shell clams was evident even in bottom cage inclusions, where this species had the ability to burrow into the sediment. We relate the order of prey

preference to species-specific differences in shell thickness, a main determinant of shell strength, and discuss our results in the light of the ongoing spread of green crabs and the sustainability of shellfish resources.

### 3.2. Keywords

Prey preference, European green crabs, *Carcinus maenas*, American oysters, *Crassostrea virginica*, blue mussels, *Mytilus edulis*, soft-shell clams, *Mya arenaria*, manipulative experiments

### 3.3. Introduction

Predator-prey interactions between crabs and prey species such as bivalves (e.g., Elner 1978; Boulding 1984), gastropods (e.g., Hughes and Elner 1979; Lawton and Hughes 1985), and polychaetes (e.g., Tyrrell et al. 2006) have received a great deal of attention in the literature. A substantial portion of that literature has focused on prey preferences, a sometimes complex behavioural decision that we still struggle to fully understand. The preferences exhibited by crabs can be explained in part by the optimal foraging theory (Elner and Hughes 1978) which predicts that crabs, like other predators, will find, capture, and consume prey with the highest energetic value while minimizing their energy output (Charnov 1976, but see also Smallegange and van der Meer 2003 and Smallegange et al. 2008). For crab-bivalve systems as those described here, most of the theory has focused on the choices done by predators while presented with different sizes of a same prey species (e.g. Elner and Hughes 1978; Hughes 1980). However, nothing precludes the application of a similar theoretical background to studies where predators choose among different prey species that may indeed have different nutritional quality (Beukema 1997). Ultimately, a choice of a prey of a given size or a given species is expected to be driven by the maximization of energetic return after prey handling costs (Charnov 1976; Stephens and Krebs 1986).

In crab-bivalve predator-prey systems, at least three well known factors influence energy maximization in the predator: the nutrient value of the prey, crab handling time, and crab-bivalve encounter rates (Elner and Hughes 1978; Hughes 1980). Nutrient value of prey items can vary with size (Elner and Hughes 1978) and species (Beukema 1997; Mascaro and Seed 2001a). In addition, crab handling times are not only related to crab's size, health and hunger levels, but are also driven by features like the bivalve's size, shell thickness, shape, and the presence of siphonal or pedal gapes (Boulding 1984; Kaiser et al. 1993; Mascaro and Seed 2000a, 2001b). Shell thickness in particular is a main indicator of compressive shell strength (Elner 1978; Zuschin and Stanton 2001) that ultimately dictates whether a bivalve will withstand or not large compressive loads like those imposed by the crushing force of a crab chela (Boulding 1984; Leonard et al. 1999; Newell et al. 2007). Shell shape is also an important feature and, indeed, Boulding (1984) reported that more spherical bivalves impose a longer handling time to crabs which was then reflected in relatively low preferences. In contrast, the presence of pedal and siphonal gapes increases the bivalve vulnerability to crab predation (Boulding 1984; Miron et al. 2005) as they facilitate the predator's access to the prey's soft body tissues (Boulding 1984).

Predator-prey encounter rates also influence energy output while foraging, and therefore should influence prey preferences (Elner and Hughes 1978). While prey density increases the rate at which a crab will encounter certain bivalve species, this is counter balanced by the ability of some bivalves to burrow into the sediment seeking a spatial refuge against predation (Palacios and Ferraro 2003; Dudas et al. 2005; Miron et al. 2005). Regardless, burrowing species are still prominent items in the diet of many predatory species, in particular those with the ability to counterbalance bivalve escape with fast, deep sediment digging (Ropes 1968; Elner 1981; Floyd and Williams 2004). The European green crab (*Carcinus maenas*) is a prime example of the latter. This species is able to detect siphon holes of buried bivalves with their walking legs (Cohen et al. 1995) and burrow up to 15 cm deep seeking prey (Ropes 1968). Green crabs are also known for being aggressive foragers that feed on a broad array of small crustaceans, snails, polychaetes and even algae (Ropes 1968; Elner 1981; Baeta et al. 2006). However, stomach content analyses reveal that in both native and expanded regions these predators rely most heavily on bivalve species (Crothers 1968; Elner 1981; Baeta et al. 2006).

The European green crab, originally native to European waters is now found throughout many parts of the world including both the east (Audet et al. 2003) and west coasts of North America (Cohen et al. 1995). On the east coast green crabs were first reported in 1817 around the New York and New Jersey areas of the United States (Audet et al. 2003). Following a northward expansion, by the 1950's green crabs were present in Canadian waters, specifically, in the Bay of Fundy (Audet al. 2003). Throughout the following decades, green crab populations expanded around the southwestern tip of Nova Scotia and along the province's Atlantic shoreline (Audet et al. 2003). A rapid population expansion, partly linked to a re-invasion from northern European populations, occurred more recently and is still ongoing (Roman 2006; Blakeslee et al. 2010). In 1997, the green crab was confirmed for the first time in the shores of the southern Gulf of St. Lawrence and Prince Edward Island (hereafter PEI) (Gillis et al. 2000; Audet et al. 2003).

Throughout their native and expanded ranges the ecological effects of green crabs have been well documented. In their European home range, green crabs are important predators of several species of cockles and oysters (Mascaro and Seed 2000a, b; 2001a, b), and mussels (Dare et al. 1983; Baeta et al. 2006; Murray et al. 2007). Similarly, in North America, green crabs are attributed to substantial declines of eelgrass beds (Garbary and Miller 2006) and have the potential to compete with other crustaceans such as American lobsters (*Homarus americanus*) for food and shelter (Rossong et al. 2006). This crab species is also a well documented predator of several oyster and clam species (Ropes 1968; Floyd and Williams 2004; Miron et al. 2005) and has been attributed to population declines of various clam species on both the Pacific (Grosholz et al. 2000) and Atlantic coastlines (Ritchie 1976). Despite their relatively recent invasion to the southern Gulf of St. Lawrence, green crabs are becoming prominent predators of a broad range of organisms, including most bivalve species (Miron et al. 2005; but see also Quijon and Snelgrove 2008). Given the prominent community and ecosystem roles played by some of these prey species, questions regarding this new predator's preferences, relative feeding rates and the timing of predation remain critical and have obvious implications for shellfish management and sustainability (Miron et al. 2005).

Wild beds of soft-shell clams (*Mya arenaria*), blue mussels (*Mytilus edulis*), and American oysters (*Crassostrea virginica*) are widespread features of the southern Gulf of St. Lawrence shoreline systems. Given the ecologic and economic importance of these species and the ongoing western spread and establishment of green crabs across the province (Aaron Ramsay, PEI Department of Fisheries, Aquaculture and Rural Development, Pers. Comm.), the quantitative assessment of green crab prey preferences represents a critical step in our preparation for further invasions and for the identification of appropriate mitigation strategies. Since multiple factors are involved in the outcome of prey preference studies, their assessment should not be limited to a single approach or type of experiment and should consider potential short-term changes occurring within the duration of the feeding trials. In this study, we used three different types of manipulations, both in the laboratory and the field, to investigate green crab prey preferences when given a choice among blue mussels, soft-shell clams, and American oysters. To identify potential differences associated to predator and prey sizes, we conducted experiments with three distinctive crab sizes and two distinctive size of prey. We then examined one of the potential causes of prey preference, bivalve shell thickness, using it here as a proxy of shell resistance to predation. Our null hypothesis is that prey mortality levels are generally similar and unrelated to green crab size, prey size, and shell thickness, regardless of the time prey have been exposed to the predator. However, based on what is expected from predators that maximize their energetic return (e.g., Hughes 1980; Boulding 1984) we expect prey mortality rates to decrease with increasing bivalve size and shell thickness, and to increase with the size of the crabs used in the feeding trials.

## 3.4. Materials and methods

### *3.4.1. Study area and green crab abundance*

North River is a shallow, soft-bottom estuary embedded in a larger estuarine system (The Hillsborough) on the southern shore of Prince Edward Island (PEI), Canada (Fig. 3.1). Trapping surveys conducted at upper, middle and lower reach sites during the fall seasons of 2008, 2009, and 2010 confirm an ongoing increase in green crab abundances in important bivalve harvesting areas (see Appendix for full data set). This and other microtidal estuaries in the area (e.g. Bedeque Bay) support large wild beds of soft-shell clams, mussels and oysters and constitute some of the most productive shellfish areas of Atlantic Canada (Miron et al. 2005).

### *3.4.2. Collection of green crabs and bivalves for experimental manipulations*

During July-August of 2009 and 2010, green crabs were collected from North River and several other locations across PEI (Bedeque Bay, Basin Head Lagoon, and Souris River). At time of collection, water temperature at these locations ranged from 18-22°C. To reduce variability associated with morphology and gender only intact male green crabs were collected and kept for the experiments (cf. Smallagange and van der Meer 2003). They were classified into three representative size categories based on the size structure gathered from the sampling surveys: small (35-45 mm carapace width; CW), medium (45-55 mm CW), and large green crabs (55-75 mm CW). American oysters were supplied by a private oyster grower whereas soft-shell clams and blue mussels were collected from public beds located in Brackley Bay and Stratford, respectively. Based on values reported in the literature (e.g., Mascaro and Seed 2000; Palacios and Ferraro 2003),

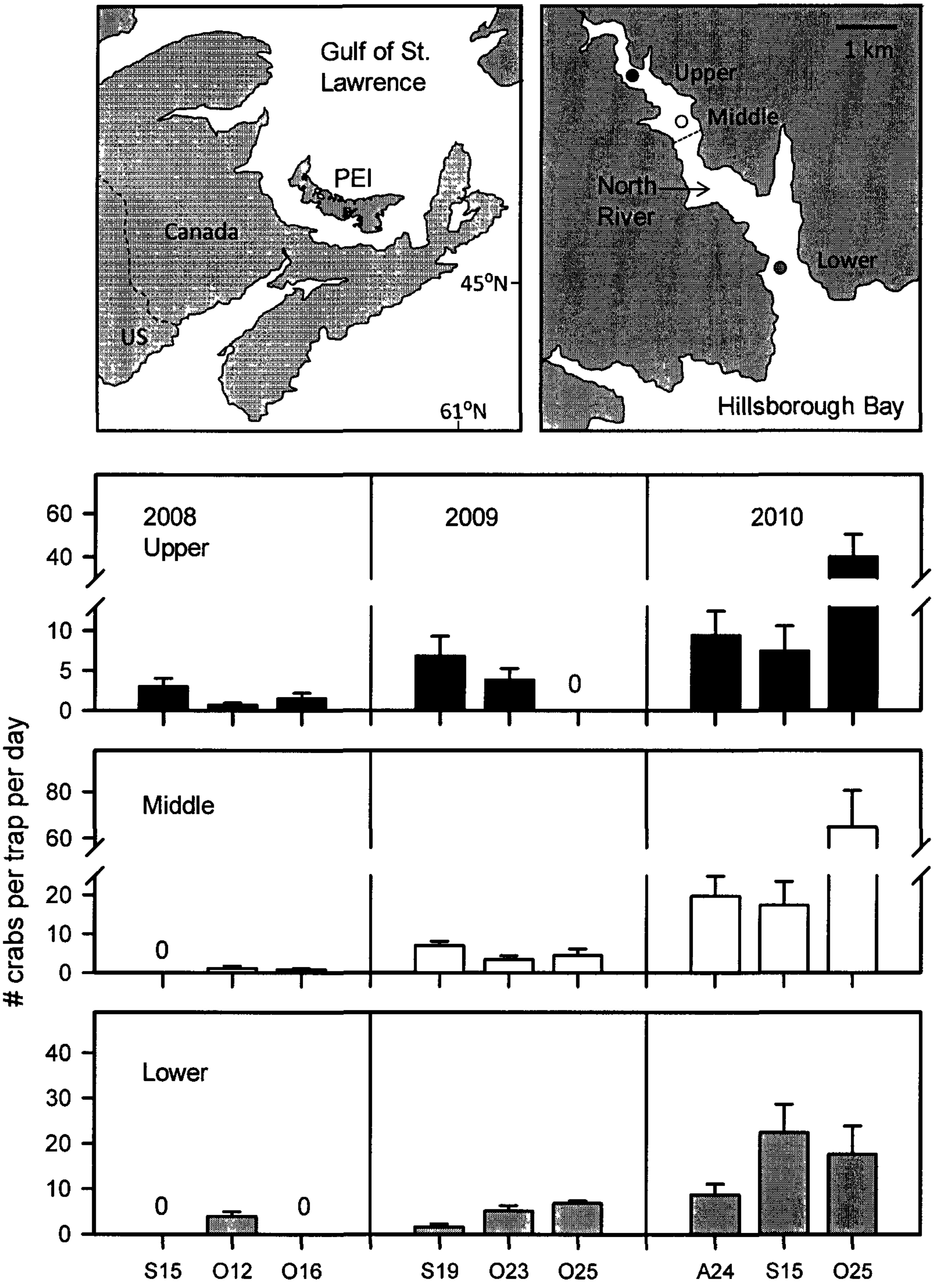

Figure 3.1. Map of North River, PEI, with the location of upper, middle and lower sampling sites for green crabs. Lower panels show corresponding mean (+ SE) trapping abundances of green crabs for each site for different sampling dates during 2008, 2009, and 2010. *A*: August, *S*: September, *O*: October; numbers identify the day of the month.

the three species of bivalves were classified into two size ranges: small (15-25 mm) and medium bivalves (25-35 mm shell length).

### *3.4.3. Laboratory experiments*

Green crab prey preferences were determined by running a series of feeding trials during July-August of 2009 and 2010 in glass tanks with dimensions 21.6 cm wide x 41 cm long x 25 cm high, filled with prepared seawater (18-22 ppt; 18-20˚C) and covered by a hood to avoid crab escape. Photoperiod was maintained at 12 hours of light and 12 hours of darkness. Air stones were placed in each tank and their sides were carefully covered to avoid external visual stimuli (e.g., Palacios and Ferraro 2003). Small, medium and large green crabs were used separately as individual predators for each trial. Based on densities described in the literature (Miron et al. 2005; Palacios and Ferraro 2003), 10 individuals of each bivalve species were added into each individual tank (total n=30 per tank). Six separate trials (3 predator size treatments x 2 prey size treatments) were conducted with 10 replicates for each trial.

### *3.4.4. Field experiments*

Two types of field inclusion trials were held in an estuarine area immediately adjacent to North River during July-August of 2010. The first type of experiment was held inside floating Vexar® bags (44 cm wide x 88 cm long x 15 cm high) similar to those used in the culture of suspended oysters. Like in the laboratory experiments, the Vexar® bag trials used two different prey sizes separately. These experiments were intended to match laboratory preference trials but under less controlled field conditions (such as natural water temperature, salinity, diurnal cycle, and currents), and to prevent green crabs from potentially preying on alternative species (see bottom cage experiments). Six separate trials with ten replicates each were conducted (3 predator size treatments x 2 prey size treatments x 10 replicates). The second type of field experiment was held in inclusion cages constructed of plastic coated wire (40 cm x 40 cm x 75 cm high) with square mesh openings of 1.0 cm by 1.0 cm. These cages represent more natural conditions compared to the other two experiments. Cages were placed directly over the bottom (their sides inserted ~5-10 cm into the sediment to avoid crab escape), in the low part of the intertidal zone. The cages were placed ~5 m apart from each other and arranged in a line parallel to the low tide level. Cages were placed in areas without the presence of siphon holes from soft-shell clams, and other infaunal bivalves. Due to the very limited predation by small crabs and also very limited predation on the 25-35 mm SL bivalves in the laboratory and Vexar® bag experiments, cage trials used only one prey size: 15-25 mm SL and one size of predator: 35-45 mm CW. In addition to the 10 individuals from each bivalve species, green crabs were expected to have access to alternative prey within the sediment delimited by the cage or with the ability to enter the cages. Two separate trials with ten replicates were conducted (2 predator size treatments x 1 prey size treatments x 10 replicates).

### *3.4.5. Experimental procedure*

Once the 30 bivalves (10 of each species) of a given size were introduced in each experimental enclosure (laboratory tanks, field Vexar® floating bags or cages), they were allowed to acclimatize for approximately one hour (laboratory and Vexar® bag trials) or

24 hours (cages; to allow soft-shell clams to burrow in the sediment). Immediately after, an individual green crab of one of the sizes indicated above was introduced into the enclosures and the trial began. All the crabs used in these experiments were starved for 48 hours prior to the beginning of the trials in order to standardize hunger levels (e.g., Mascaro and Seed 2001b) and were used in only one occasion to avoid any risk of potential learning (Cunningham and Hughes 1984). All the trials lasted 72 hours in total, however, in order to determine potential differences in terms of timing or period of most intense foraging, bivalve mortality was monitored at different time intervals within the duration of the trials. Prey mortality per species in the laboratory trials was followed and recorded after 1, 2, 3, 24, 48, and 72 hours since the beginning of the trial. A similar approach was followed in both types of field experiments, but in those the trials were visually checked only after 24, 48, and 72 hours. For the cage field experiments, soft-shell clam mortality could only be checked after 72 hours as the clams were burrowed in the sediment and the siphonal holes in the sediment were not reliable enough to unambiguously account for density of clams alive. As checking bivalve mortality was visual and only required a short period of time, crab behaviour was not likely affected. At the end of the cage trials, once crabs, mussels and oysters were counted and removed, we carefully screened the first 5-10 cm of sediment until the 10 clams (or their remnants) were found. For each trial (i.e. for each crab size and prey size) a total of ten simultaneous replicates were conducted.

In order to account for alternative sources of prey mortality, preliminary 3-day trials without green crabs were run for both the laboratory and Vexar® bag experiments (n=10). Since the survival of the three prey species was 100%, no additional control trials were judged necessary. For the cage experiments, a similar 3-day control trial (without green crabs) was run simultaneously with the actual predation experiments (see Results). In cases where evidence of molting was observed during any stage of crab manipulation (including collection, starvation period, and feeding trial), the trial was disregarded and repeated with a new crab.

### *3.4.6. Shell thickness measurements*

In order to relate data on crab-related mortality with potential differences in species-specific shell thickness (used here as an indicator of shell strength), six different shell thickness measurements were taken from twenty individuals from each bivalve species and size (15-25 mm and 25-35 mm). Mastercraft® digital calipers fitted with a Shars® Digital Caliper Accessory Kit were used for taking accurate thickness measurements at three standard positions on both the right and left valves: at the center of each valve, towards the umbo edge and towards the siphonal edge (midpoint between the center and the actual edge of the shell along the main axis of the shell). Selection of these particular positions was based on the need to have standard measurement points, and on direct observations of green crabs breaking bivalve shells. Those observations suggested that green crabs frequently broke shells near the siphonal edge (in the case of blue mussels), near the umbo edge (in the case of oysters), or completely crushed the shell (in the case of clams).

### *3.4.7. Statistical analyses*

The assessment of prey-preference experiments as those presented here cannot be appropriately conducted with traditional one- or two-way ANOVAs due to the risk of incurring on pseudo-replication (cf. van der Meer 1992; Smallagange and van der Meer 2003). Therefore, a balanced three-way MANOVA model was used for the laboratory and field Vexar® bag experiments to compare the relative influence of predator size, prey size, time period and their interactions on the mortality levels of the three prey species measured throughout the three day period. Similarly, for the field cage experiments, a balanced one-way MANOVA model was used to compare the influence of crab size on prey mortality. In the balanced MANOVAs, the mortality levels of each bivalve species (oysters, mussels, and soft-shell clams) at each time period were the dependent variables. Since significant interaction terms were detected in preliminary runs of the analyses (for the laboratory and field Vexar® bag experiments), these "overall" MANOVAs were complemented with more specific balanced ANOVAs, serving as multiple comparisons. For both the laboratory and field Vexar® bag experiments, three separate three-way balanced ANOVA models were used to compare the influence of predator size, prey size, time period and their interactions on the mortality levels exhibited by each of the three prey species.

One-way ANOVAs were used to compare shell thickness among oysters, mussels, and clams. Separate comparisons were conducted at each of the three measurement-positions for each valve, and for the two size ranges. As a total of six measurements were conducted for each size of bivalve, a Bonferonni correction factor was applied to control for type I error ($\alpha=0.05/n$, for $n=6$). For all the analyses conducted, assumptions were properly tested using the Anderson-Darling normality test and Levene's test for equal variance, and in those cases where they failed to meet the assumptions, arcsine, logarithmic, or square root transformations were applied.

## 3.5. Results

### *3.5.1. Laboratory experiments*

The results of the balanced three-way MANOVA indicated that the all sources of variation identified and their interactions were significant: Crab size, Prey size, Time, Crab size x Prey size, Crab size x Time, Prey size x Time, and Crab size x Prey size x Time (all $P<0.001$; Table 3.1). Subsequent multiple comparisons were conducted with separate balanced three-way ANOVAs for each prey species. The results of these ANOVAs indicated that all sources of variation (Crab size, Prey size, and Time) and their interactions (Crab size x Prey size, Crab size x Time, Prey size x Time, and Crab size x Prey size x Time) were also significant ($P<0.001$; Table 3.2). In general, large green crabs exhibited the highest consumption rates and soft-shell clams were the most vulnerable to predation followed by mussels and then oysters (Fig. 3.2). For small prey (15-25 mm SL), small and medium sized green crabs caused higher mortality rates on soft-shell clams than on mussels and oysters, even during the first three hours of the trials (Fig. 3.2). Meanwhile, mussel mortality rates became noticeably higher than oyster mortality rates only after 72 and 24 hours of predation for small and medium green crabs, respectively. For large green crabs, soft-shell clam mortalities were always slightly higher than mussel mortalities (Fig. 3.2). Noticeable differences between mortality rates affecting mussels and oysters were present even during the first three hours of predation

Table 3.1. Results from three separate balanced MANOVAs examining the effects of crab size, prey size, time period and their interactions on mortality rates of oysters mussels and soft-shell clams measured in laboratory (tanks) and field (Vexar® bag and cage) experiments. Data underwent appropriate transformations (arcsine or square root), to meet MANOVA assumptions.

| Experiment | Source of variation | DF | Wilks' statistic | P-value |
|---|---|---|---|---|
| Laboratory tanks | Crab size (Cs) | 6, 644 | 0.63540 | <0.001 |
| | Prey Size (Ps) | 3, 322 | 0.48436 | <0.001 |
| | Time period (t) | 15, 889 | 0.28251 | <0.001 |
| | Cs x Ps | 6, 644 | 0.66860 | <0.001 |
| | Cs x t | 30, 945 | 0.76928 | <0.001 |
| | Ps x t | 15, 889 | 0.70691 | <0.001 |
| | Cs x Ps x t | 30, 945 | 0.74667 | <0.001 |
| Field Vexar bags | Crab size (Cs) | 6, 320 | 0.26573 | <0.001 |
| | Prey Size (Ps) | 3, 160 | 0.27164 | <0.001 |
| | Time period (t) | 6, 320 | 0.61169 | <0.001 |
| | Cs x Ps | 6, 320 | 0.44045 | <0.001 |
| | Cs x t | 12, 423 | 0.84803 | 0.009 |
| | Ps x t | 6, 320 | 0.97314 | 0.625 |
| | Cs x Ps x t | 12, 423 | 0.87301 | 0.038 |
| Field bottom cages | Crab size (Cs) | 3,16 | 0.84098 | 0.415 |

Table 3.2. Results from six separate three-way balanced ANOVAs, examining the effect of crab size, prey size, time period and the interactions for each of the three bivalve mortality rates in the laboratory and field (Vexar® bag) experiments. Data underwent appropriate transformations (arcsine or square root), to meet ANOVA assumptions.

| Experiment | Response | Source of variation | DF | SS | MS | P |
|---|---|---|---|---|---|---|
| Laboratory | Oysters | Crab size (Cs) | 2 | 0.85499 | 0.42750 | <0.001 |
| | | Prey Size (Ps) | 1 | 1.34039 | 1.34039 | <0.001 |
| | | Time period (t) | 5 | 1.25728 | 0.25146 | <0.001 |
| | | Cs x Ps | 2 | 0.85499 | 0.42750 | <0.001 |
| | | Cs x t | 10 | 0.95333 | 0.09533 | 0.001 |
| | | Ps x t | 5 | 1.25728 | 0.25146 | <0.001 |
| | | Cs x Ps x t | 10 | 0.95333 | 0.09533 | 0.001 |
| | | Error | 324 | 9.76759 | 0.03015 | |
| | Mussels | Crab size | 2 | 13.4201 | 6.7100 | <0.001 |
| | | Prey Size | 1 | 8.7785 | 8.7785 | <0.001 |
| | | Time period (t) | 5 | 14.8745 | 2.9749 | <0.001 |
| | | Cs x Ps | 2 | 2.9674 | 1.4837 | <0.001 |
| | | Cs x t | 10 | 6.5200 | 0.6520 | <0.001 |
| | | Ps x t | 5 | 4.6111 | 0.9222 | <0.001 |
| | | Cs x Ps x t | 10 | 2.1420 | 0.2142 | <0.001 |
| | | Error | 324 | 29.2086 | 0.0902 | 0.010 |
| | Clams | Crab size | 2 | 5.6856 | 2.8428 | <0.001 |
| | | Prey Size | 1 | 22.4788 | 22.4788 | <0.001 |
| | | Time period (t) | 5 | 54.6577 | 10.9315 | <0.001 |
| | | Cs x Ps | 2 | 4.9468 | 2.4734 | <0.001 |
| | | Cs x t | 10 | 1.5068 | 0.1507 | 0.022 |
| | | Ps x t | 5 | 6.1502 | 1.2300 | <0.001 |
| | | Cs x Ps x t | 10 | 1.8405 | 0.1840 | 0.005 |
| | | Error | 324 | 22.9625 | 0.0709 | |
| Field bags | Oysters | Crab size (Cs) | 2 | 5.06394 | 2.53197 | <0.001 |
| | | Prey Size (Ps) | 1 | 3.88600 | 3.88600 | <0.001 |
| | | Time period (t) | 2 | 0.23990 | 0.11995 | 0.020 |
| | | Cs x Ps | 2 | 2.39121 | 1.19561 | <0.001 |
| | | Cs x t | 4 | 0.13177 | 0.03294 | 0.356 |
| | | Ps x t | 2 | 0.00747 | 0.00374 | 0.882 |
| (continues | | Cs x Ps x t | 4 | 0.01349 | 0.00337 | 0.978 |
| next page) | | Error | 162 | 4.83196 | 0.02983 | |

| | | | | | | |
|---|---|---|---|---|---|---|
| (continued) | Mussels | Crab size | 2 | 8.8402 | 4.4201 | <0.001 |
| | | Prey Size | 1 | 12.5606 | 12.5606 | <0.001 |
| | | Time period (t) | 2 | 0.9246 | 0.4623 | <0.001 |
| | | Cs x Ps | 2 | 0.8643 | 0.4321 | <0.001 |
| | | Cs x t | 4 | 0.0677 | 0.0169 | 0.742 |
| | | Ps x t | 2 | 0.0712 | 0.0356 | 0.357 |
| | | Cs x Ps x t | 4 | 0.5832 | 0.1458 | 0.003 |
| | | Error | 162 | 5.5709 | 0.0344 | |
| | Clams | Crab size | 2 | 1.04220 | 0.52110 | <0.001 |
| | | Prey Size | 1 | 0.49642 | 0.49642 | <0.001 |
| | | Time period (t) | 2 | 0.70541 | 0.35270 | <0.001 |
| | | Cs x Ps | 2 | 0.52490 | 0.26245 | <0.001 |
| | | Cs x t | 4 | 0.16373 | 0.04093 | 0.002 |
| | | Ps x t | 2 | 0.01866 | 0.00933 | 0.363 |
| | | Cs x Ps x t | 4 | 0.03685 | 0.00921 | 0.406 |
| | | Error | 162 | 1.48223 | 0.00915 | |

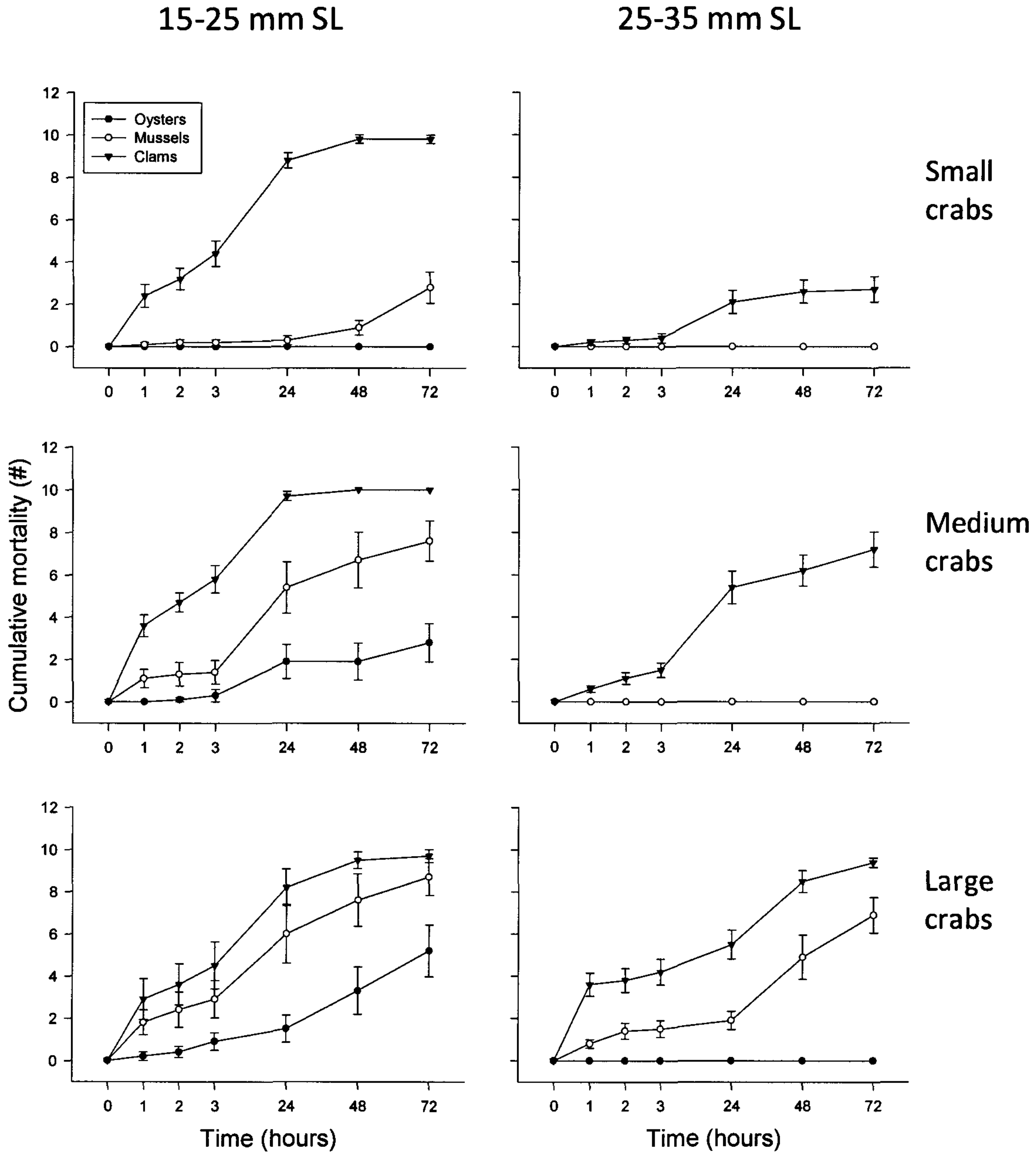

Figure 3.2. Mean (+/- SE) cumulative mortality of 15-25 and 25-35 mm SL soft-shell clams, blue mussels, and American oysters over time (hours) resulting from predation by small (35-45 mm carapace width), medium (45-55 mm), and large (55-75 mm) green crabs in multiple-choice laboratory experiments. For small and medium crabs with 25-35 mm SL bivalves, mussels and oysters follow identical curves. Therefore, mussel data also represents data on oyster mortality.

(Fig. 3.2). For larger prey (25-35 mm SL), small and medium sized green crabs preyed exclusively on soft-shell clams and most of the recorded mortality occurred within the first 24 hours (Fig. 3.2). Large green crabs preyed on both soft-shell clams and mussels since the very beginning of the experiments. Differences between mortality levels among the three species were apparent since the first couple of hours of experimentation (Fig. 3.2).

### *3.5.2. Field Vexar® bag experiments*

Results of the balanced three-way MANOVA indicated that all the sources of variation, and the main interaction term was significant (Crab size x Prey size x Time size; P=0.038 Table 3.1). Results of the separate balanced three-way ANOVAs for each prey species also indicated that all sources of variation (Crab size, Prey size, and Time) and some interactions (Oysters: Crab size x Prey size, Mussels: Crab size x Prey size and Crab size x Prey size x Time, Clams: Crab size x prey size and Crab size x time) were also significant (P<0.001) (Table 3.2).

For trials conducted with small prey, soft-shell clams (small crabs) or a combination of soft-shell clams and mussels (medium and large green crabs) generally exhibited higher mortality rates than oysters (Fig. 3.3). For trials conducted with larger prey, small green crabs preyed exclusively on soft-shell clams but at a lower rate than small soft-shell clams (near 40% less). Overall, medium and large green crabs preyed more on soft-shell clams, but exhibited at least some level of predation on mussels and oysters (Fig. 3.3).

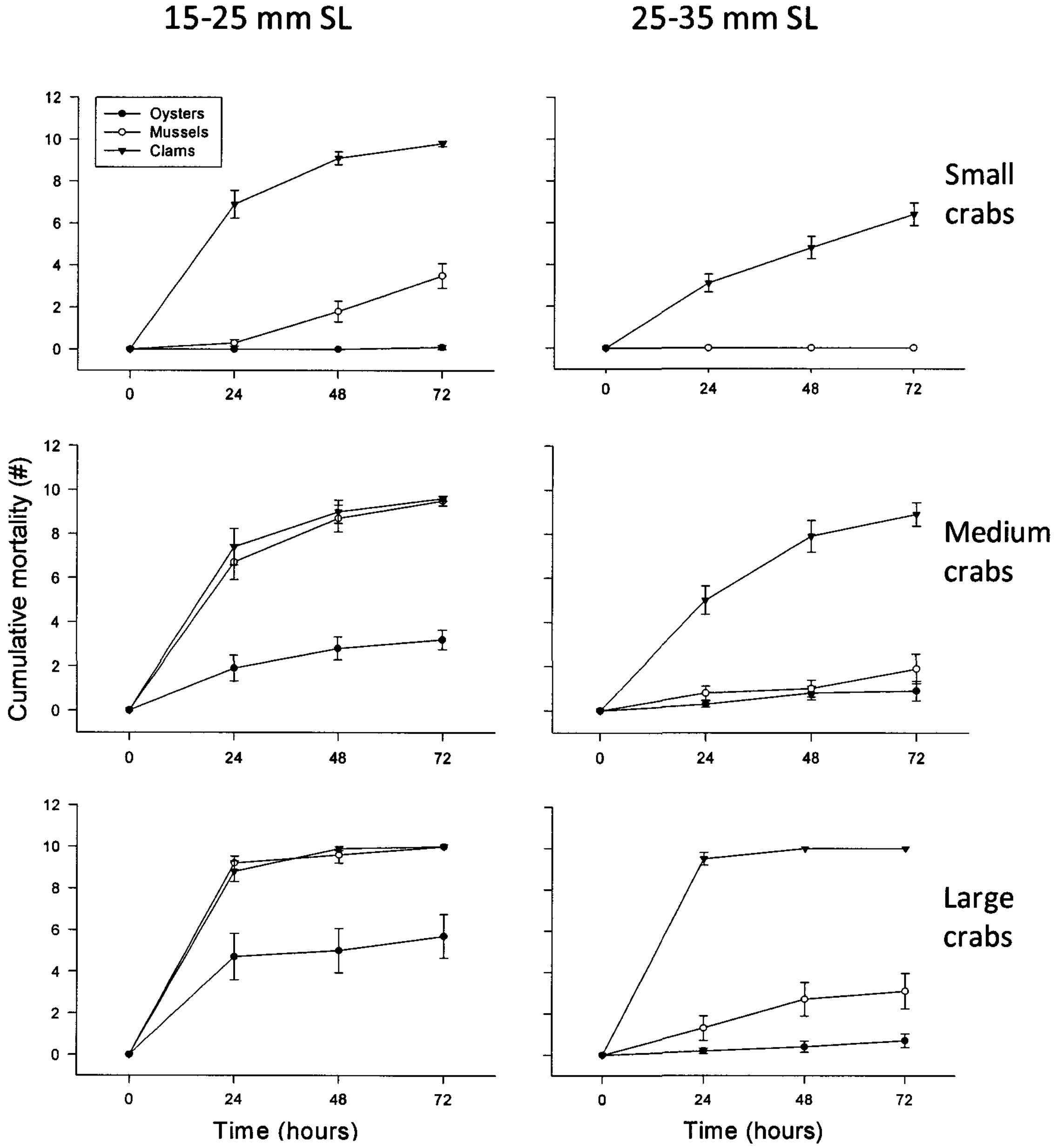

Figure 3.3. Mean (+/- SE) cumulative mortality of 15-25 and 25-35 mm SL soft-shell clams, blue mussels, and American oysters over time (hours) resulting from predation by small (35-45 mm carapace width), medium (45-55 mm), and large (55-75 mm) green crabs in multiple-choice field Vexar bag experiments. For small crabs with 25-35 mm SL bivalves, mussels and oysters follow identical curves. Therefore, mussel data also represents data on oyster mortality.

### *3.5.3. Cage experiments*

Results of the balanced one-way MANOVA indicated that the main source of variation (Crab size) was not significant (P=0.415). Medium and large green crabs were able to feed on all three prey species (Fig. 3.4). In the first two days of the trials, when we were unable to properly estimate soft-shell clam mortality (due to burrowing in the sediment), mussel mortality was consistently higher than oyster mortality since the first day. By the third day, clams were found to have a similar mortality level than mussels, both well above the mortality observed in oysters (Fig. 3.4). A control trial consisting on the inclusion of bivalves but not green crabs showed null mussel and oyster mortality (100% survival). As in the previous trials, soft-shell clam mortality was measured after 72 hours and reached 2.5 (+/- 0.9) individuals.

### *3.5.4. Shell thickness measurements*

For both prey-size groups, shell thickness was similar for the right and left valves at each of the three measured positions (Fig. 3.5). The results of 12 separate one-way ANOVAs indicated that there were significant differences (significance level was adjusted using Bonferonni correction, $\alpha$=0.0083) among prey (for each corresponding measurement separately; P<0.001 in all the comparisons; Table 3.3). Tukey multiple comparisons indicated that clams had significantly thinner shells at every position in the shell where we measured. Similarly, in most comparisons mussel shells were significantly thinner than oyster shells.

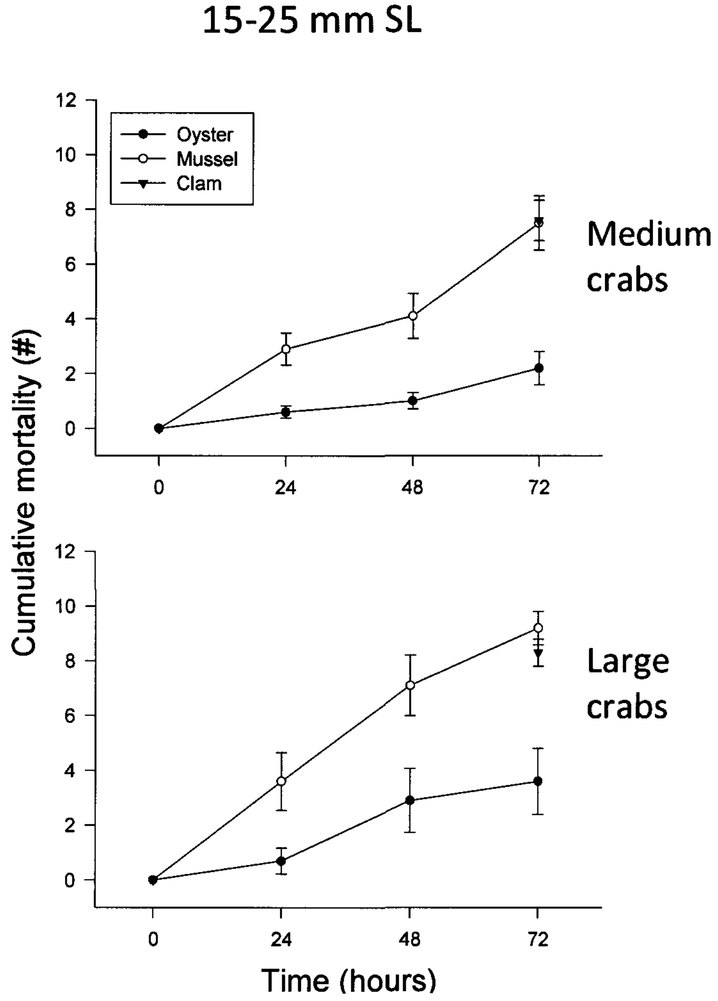

Figure 3.4. Mean (+/- SE) cumulative mortality of 15-25 mm SL soft-shell clams, blue mussels, and American oysters over time (hours) resulting from predation by medium (45-55 mm carapace width), and large (55-75 mm) green crabs in multiple-choice field wire cage experiments. Soft-shell clam mortality was recorded at 72 hours only.

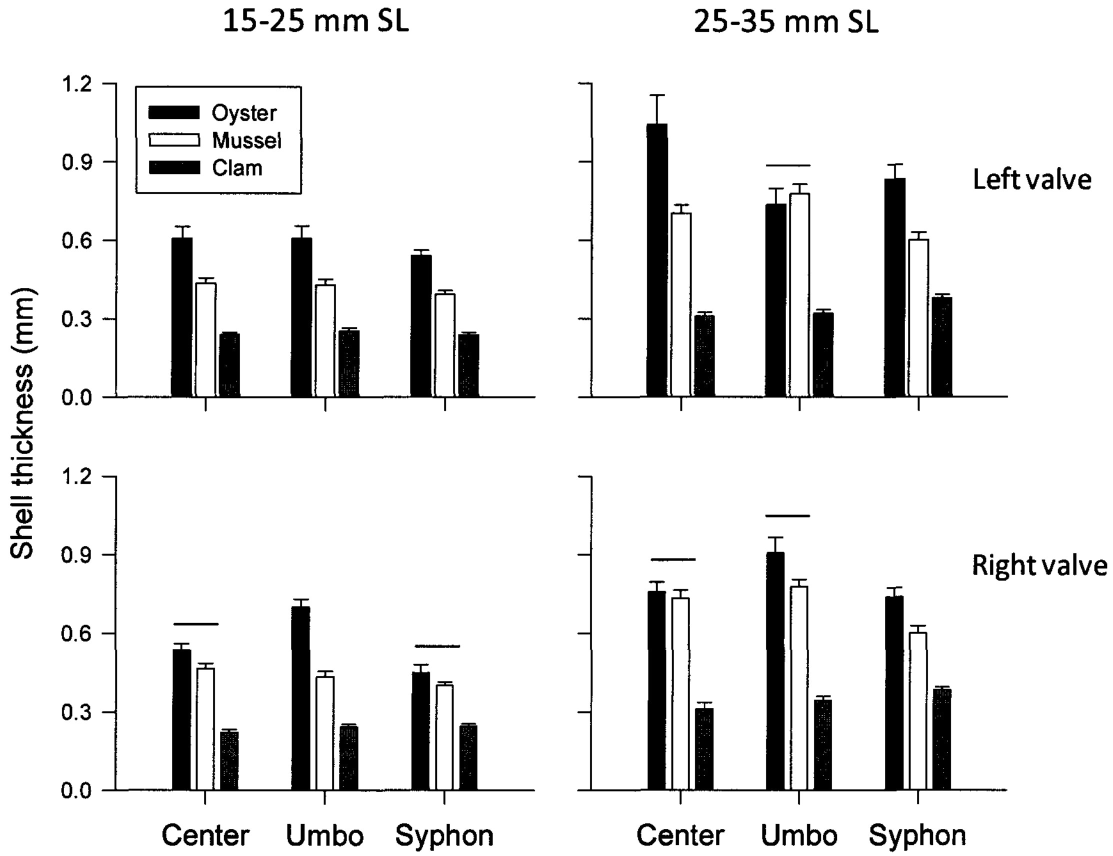

Figure 3.5. Mean (+ SE) shell thickness measured at three standard positions (center, and near umbo and siphon edges) on the left and right valves of 15-25 and 25-35 mm SL soft-shell clams, blue mussels, and American oysters. Lines over bars identify non-significant differences between species.

Table 3.3. Results from12 separate ANOVAs examining the effect of bivalve species on shell thickness at three uniform locations (near the center, umbo, and siphon) on the left and right valve of 15-24 and 25-34 mm SL bivalves. Bivalves measured were soft-shell clams, blue mussel, and American oyster. Data underwent appropriate transformation (square root or logarithm) to meet ANOVA assumptions. Significance level was adjusted using Bonferonni correction, α=0.05/n where n=6, α=0.0083).

| Size | Valve | Position | Source of Variation | DF | SS | MS | P |
|---|---|---|---|---|---|---|---|
| 15-25<br>mm SL | Left | Center | Bivalve Species | 2 | 1.56699 | 0.78350 | <0.001 |
| | | | Error | 57 | 0.72010 | 0.01263 | |
| | | Umbo | Bivalve Species | 2 | 0.70935 | 0.35468 | <0.001 |
| | | | Error | 57 | 0.50006 | 0.00877 | |
| | | Siphon | Bivalve Species | 2 | 0.61521 | 0.30730 | <0.001 |
| | | | Error | 57 | 0.17372 | 0.00305 | |
| | Right | Center | Bivalve Species | 2 | 0.76465 | 0.38232 | <0.001 |
| | | | Error | 57 | 0.23296 | 0.00409 | |
| | | Umbo | Bivalve Species | 2 | 1.17721 | 0.58860 | <0.001 |
| | | | Error | 57 | 0.25703 | 0.00451 | |
| | | Siphon | Bivalve Species | 2 | 0.33485 | 0.16743 | <0.001 |
| | | | Error | 57 | 0.28322 | 0.00497 | |
| 25-35<br>mm SL | Left | Center | Bivalve Species | 2 | 2.6163 | 1.3082 | <0.001 |
| | | | Error | 57 | 1.0765 | 0.0189 | |
| | | Umbo | Bivalve Species | 2 | 1.75265 | 0.87633 | <0.001 |
| | | | Error | 57 | 0.70687 | 0.01240 | |
| | | Siphon | Bivalve Species | 2 | 1.04264 | 0.52132 | <0.001 |
| | | | Error | 57 | 0.83223 | 0.01460 | |
| | Right: | Center | Bivalve Species | 2 | 1.22961 | 0.61480 | <0.001 |
| | | | Error | 57 | 0.35215 | 0.00618 | |
| | | Umbo | Bivalve Species | 2 | 2.0208 | 1.0104 | <0.001 |
| | | | Error | 57 | 0.5994 | 0.0105 | |
| | | Siphon | Bivalve Species | 2 | 0.80771 | 0.40385 | <0.001 |
| | | | Error | 57 | 0.36087 | 0.00633 | |

### 3.6. Discussion

Our results did not support our null hypothesis. Green crabs exhibited strong prey preferences when given a choice among various bivalve species of comparable size, and those preferences changed in the course of the few days it takes to run a feeding trial. Whereas prey preferences have been reported elsewhere in the literature (Cohen et al. 1995; Mascaro and Seed 2001b; Palacios and Ferraro 2003), we struggled to find studies explicitly addressing the changes faced by prey between 0 and 3 days of predator manipulation. Indeed, most studies rely only on the final outcome of prey preference trials and, as our results indicate, this may prevent researchers from perceiving key short term changes in prey availability or predator behaviour. Such changes are relevant considering two arguments. First, all the green crab sizes studied here were found capable of consuming various amounts of soft-shell clams, mussels, and/or oysters. Second, this non-indigenous species continues to spread to new un-invaded habitats threatening to decimate populations of similar species.

Given that consumed bivalves were not replaced during our feeding trials, we consider changes in prey availability to be intimately related to the changes in prey preferences observed during the course of the three day feeding trials. Elner and Hughes (1978) examined the size-selectivity of green crabs feeding on various sizes of blue mussels in experiments with and without prey replacement. In those trials where replacement of consumed prey took place, these authors found that green crabs continued to forage on the most optimal size of mussel. However, in trials similar to ours, where prey were not replaced, green crabs switched to less optimal sized mussels as soon as the most preferred size began to diminish (Elner and Hughes 1978). Both types of experiments may reflect to some extent, natural conditions. For instance, replacement experiments may reflect temporary scenarios when prey items are very abundant and predators are not yet numerous or effective as foragers. In contrast, experiments without replacement reflect conditions where prey abundance is limited or become quickly limited and/or predators are fairly abundant. Without disregarding the natural occurrence of the first scenario, our experiments intended to reflect the latter scenario which we consider far more common. Green crab populations grow fast and have been held responsible for several large scale declines in bivalve populations (e.g., Ropes 1968; Ritchie 1976; Grosholz et al. 2000). The aftermath of those prey collapses has not been an abrupt decline or disappearance of green crab population, but rather, the persistence and further spread of the species (e.g., Audet et al. 2003; Grosholz et al. 2000). Those phenomena cannot be explained without the existence of a switch to alternative preys as shown at a much smaller scale by all our experiments.

Our study focused solely on multiple-choice experiments where green crabs were given a choice among three different prey species. Had we conducted single-choice experiments, our results could have been somewhat different. For example, when comparing the predation rates of rock crabs (*Cancer irroratus*) and green crabs in single and multiple-choice experiments, Miron et al. (2005) reported that rock crabs were not as efficient while foraging on multiple prey species compared to foraging on a single species. Also, in comparison to multiple-choice experiments, green crabs in single-choice experiments appeared to have higher predation rates on individual species and foraged on larger prey sizes. Miron et al. (2005) also suggested that green crabs spend less time searching for prey species and exhibit a more opportunistic behaviour compared to rock crabs. Both types of experiments may represent natural conditions found in the field: multiple-choice experiments may reflect wild beds while single-choice experiments may reflect aquaculture sites or leases, where one species is overly abundant.

### *3.6.1. Laboratory and field Vexar® bag experiments*

In general, there was little difference between the feeding experiments conducted in the laboratory tanks and the field Vexar® bags. In both, and for all sizes of crabs, soft-shell clams were consistently the most preferred prey followed by mussels, and then oysters. These preferences are different from those reported by Miron et al. (2005), who found that mussels were the most preferred, followed by oysters, and then clams. However, those authors worked only with cage experiments similar to those discussed below, where soft-shell clams had the ability to burrow until a refuge depth into the sediment. Our laboratory and Vexar® bag experiments were designed to remove such variable and allow us to measure green crab preferences and feeding rates at optimal conditions for the predator. In these conditions and as expected, large crabs preyed on more species and had the highest predation rates. As reported for this and several other crab species, larger individuals have higher nutritional requirements, greater crushing strength (e.g., Eggleston 1990), and larger chela gape (the overall distance the chela can open; see Boulding 1984). Consistently, small green crabs were less efficient as consumers, particularly on mussels and oysters, likely because their small size may have imposed physical limitations for the crushing of the thicker shells of these species (e.g., Boulding 1984). The higher vulnerability of soft-shell clams to predation by small green crabs may also be related to their exposed siphons and pedal gapes. Exposed gapes facilitate the crab's ability to reach the prey body tissues, improving chela handling and manipulation, and enhancing predation rates regardless of prey size. In feeding experiments similar to ours, Boulding (1984) found the butter clam (*Saxidomus gianteus*) to be more vulnerable to predation from the red rock crab (*Cancer productus*) than Pacific little necked clams (*Protothaca staminea*) of comparable size and shell thickness. Similarly, Brousseau et al. (2001) reported small Asian shore crabs (*Hemigrapsus sanguineus*) feeding on soft-shell clams by pulling body tissues through the siphonal gapes rather than breaking into the shell.

Chela size limitations may also explain the lack of preference exhibited by small and medium sized crabs on the larger mussels that, consequently, appeared to gain a refuge in size when entering the 25-35 mm SL category. Miron et al. (2005) reported a similar refuge in size but for green crabs in general (all sizes). Although the size of the large green crabs used in their study was similar to ours, in our study large green crabs were able to cause considerable mortality on mussels >25 mm SL. In this aspect, our results better match those of Dare et al. (1983), who reported that large green crab predation was substantially reduced only once mussels reached ~40 mm SL. Soft-shell clams did not reach such size refuge, not even for small green crabs. This contradicts the results reported by Floyd and Williams (2004) but is consistent with an early study by Ropes (1968) who reported that green crabs were even capable of preying on soft-shell clams larger than their own carapace width. Regardless of size differences, our laboratory and Vexar® bag experiments show solid evidence that green crabs prefer certain species but can quickly switch (in the course of 24 to 48 hours) to alternative prey in the absence or decline of their preferred prey.

### *3.6.2. Field cage experiments*

These trials took place directly on the bottom of the lower intertidal zone, to reflect more natural, less controlled conditions than the ones described above. Green crabs were able to feed on all species and sizes of prey, and after 72 hours of predation, clams and mussels appeared to be equally preferred. In comparison to our previous experiments, these results are closer to those reported by Miron et al. (2005), although those authors found stronger preference for mussels and then oysters, both above soft-shell clams. As expected, soft-shell clams did indeed burrow into the sediment seeking refuge against crab predation (Boulding 1984; Palacios and Ferraro 2003; Dudas et al. 2005; Miron et al. 2005) and effectively reducing predator-prey encounter rates. Differences in burrowing depth are not likely responsible for such differences. In both Miron et al.'s (2005) and our experiments, soft-shell clams were allowed to acclimatize (and burrow) for 24 hours prior to the introduction of predators. Furthermore, in both experiments, sediment depth should not have been limiting to burial deoth for the sizes of soft-shell clams used as our bottom cage experiments were held in the field and Miron et al. (2005) provided 10 cm in laboratory tanks.

Changes in preference have been shown already for other prey species of green crabs. For instance, Palacios and Ferraro (2003) reported that green crabs prefer Olympia oysters (*Ostrea conchaphila*) over California soft-shell clams (*Cryptomya californica*) and those ones over bent-nosed macoma clams (*Macoma nasuta*). These authors related such order of preference to the corresponding increase in burial depth reached by each clam species. Our results, however, are not fully explained by the ability of soft-shell clams to burrow into the sediment. In fact, soft-shell clams gained only partial refuge from predation. We cannot ignore that green crabs are highly skilled predators (Elner and Hughes 1978; Cohen et al. 1995) that use both tactile and chemosensory stimuli to detect prey and are capable of digging as deep as 15 cm under the sediment surface (Ropes 1968). In addition, burrowing may not be as beneficial when other factors play a role in prey preference. For example, in feeding experiments on the west coast of North America, green crabs showed a marked preference for the burrowing Asian clam (*Potamocorbula ameruensis)* while disregarding mussels clustered on the surface (Cohen et al. 1995). Similarly, in experiments involving the Asian shore crab (*Hemigrapsus sanguineus*), Brousseau et al. (2001) found that buried soft-shelled clams were heavily preferred over two other bivalves living in the surface.

In addition to burrowing, several factors may have prevented a more effective consumption of soft-shell clams. Green crabs could have foraged on an array of alternative preys (cf. Ropes 1968; Elner 1981; Baeta et al. 2006) that may have entered or been already in the bottom areas that were enclosed by the cages. Among them, the periwinkle (*Littorina littorea*) was able to pass through the cage mesh and indeed shell remnants were detected in parallel single-choice experiments done in identical cages (P. Quijon, pers. comm.). Alternatively, predators like the moon snail (*Euspira heros*) may have been inside the cages and contributed to the fraction of clam mortality that was unrelated to crab predation. However, even when moon snails are important shellfish predators (cf. Quijon et al. 2007), they feed at a much slower pace and leave distinctive perforations in the shell, none of which was observed in our experiments. From a different perspective, the soft-shell clams used in our experiments appeared healthy and, as expected, burrowed into the sediment immediately after setting up the cages, to a depth of ~5-10 cm in control trials. However, unsuitable environmental conditions that we are unaware of may be responsible for the slight level of mortality detected in the control trial and may have also deterred green crabs from further consumption in the experimental cages. Finally, we cannot ignore that artifact effects related to the deployment of cages in a sedimentary bottom (cf. Hulberg and Oliver 1980; McGuinness 1997) may have somehow affected the behaviour of the crabs. However, the short duration of the experiments, the lack of sediment accumulation within the cages, the removal of seaweeds eelgrass or other material stranded in the cages, and the daily monitoring of the cages (for estimations of mussel and oyster mortality) do not suggest that this was an issue. Without disregarding the potential influence of these or other factors that we may have unintentionally overlooked, predation rates on soft-shell clams were considerably high. We interpret that has further evidence of a strong preference for this species that is therefore consistent with the outcome of the other two types of experiments.

### *3.6.3. Shell thickness measurements*

As reported in some studies elsewhere (e.g., White and Wilson 1996; Wheaton et al. 2008) soft-shell clams consistently had the thinnest shell whereas oysters had the thickest. If we assume that shell thickness is inversely related to prey vulnerability (Zuschin and Stanton 2001), the bulk of our results consistently suggest that prey preference in green crabs is driven by differences in shell thickness. This is coincident, for example, with studies of predator preference for thin-shelled morphs of the Pacific little neck clam (*P. staminea*) by the red rock crab (*C. productus*) (Boulding 1984).

Although other factors such as shell shape, width, and the presence of drill holes affect overall shell strength, shell thickness is considered the best predictor of compressive shell strength (Elner 1978; Zuschin and Stanton 2001) and the ability of bivalves to withstand larger compressive loads (Boulding 1984; Leonard et al. 1999). For example, Newell et al. (2007) found that the Suminoe oyster (*Crassostrea ariakensis*) was more susceptible to predation by several species of mud crab (*Rhithropanopeus harrissi, Eurypanopeus depressus, Dyspanopeus sayi, Panopeus herbstii*) and the blue crab (*Callinectes sapidus*) than the American oyster, and attributed the differences in vulnerability to their differences in compressive strength.

Although most foraging theory studies investigate crabs feeding on various sizes of a single bivalve species, the preference for thinner shelled bivalves observed in our study may be also easily explained by the maximization of energy intake associated to the reduction in handling times (Elner and Hughes 1978). As compressive strength increases with shell thickness, predators require chela with greater crushing forces and often are required to apply more compressive pulses (Elner 1978; Boulding 1984). Since handling time increases with greater shell strength, the energetic cost of foraging on the prey increases as well. As crabs are expected to select the most profitable prey item (Hughes 1980), it is not surprising that thinner shelled bivalves demanding less handling time from the predators are the preferred prey.

Clearly, other factors besides the handling time required to break a shell affect energy maximization while foraging. Several studies have reported that within a same prey species green crabs consistently select smaller than optimal sized prey (Juanes 1992; Smallagange and van der Meer 2003; Smallagange et al. 2008). This is not unusual among bivalve predators: Rutten et al. (2006) demonstrated that oystercatchers (*Haematopus ostralegus*) generally select smaller, less profitable, bivalves as well. These authors suggested that predators prefer smaller, thinner shelled bivalves over more profitable ones to prevent bill (oystercatchers) or claw (crabs) wear and damage. As claw damage can have severe impacts on the mating success, foraging ability, and overall fitness of green crabs, risk of claw damage in some cases may play a more prominent role on prey preferences than energy maximization (Smallagange and van der Meer 2003). Moreover, by reducing the risk of claw damage, green crabs may actually be maximizing their long term net energy gain by avoiding subsequent limitations in foraging ability (Smallagange et al. 2008).

### *3.6.4. Summary and implications*

Our results suggest that green crabs exhibit strong prey preferences when given a choice among three ecologically and commercially important bivalve species. In general, soft-shell clams were preferred over mussels, while mussels were preferred over oysters, and such order of preference corresponds with the increase in bivalve shell thickness reported here. Knowledge on green crab prey preferences in areas of high shellfish productivity is critical in order to forecast impacts and prepare mitigation strategies. Our study identified consistent prey preferences among three prominent bivalve species, which should help managers and the shellfish industry to prioritize future research and management efforts. Indirectly, our study also sheds light on the most vulnerable prey sizes, information that may allow managers and harvesters to target more specifically the measures of protection against green crab predation, at least until the bivalves reach larger, less preferred sizes. As green crabs continue to spread in the Gulf of St. Lawrence and Newfoundland, its current northernmost limit of distribution for the region, new productive areas are likely to become invaded by this species. Although the overall population effects of selective predation are not fully understood, an increase in the number of green crabs has been shown to increase predation rates on its preferred preys and size range (e.g., Seed and Brown 1975; Floyd and Williams 2004). Therefore, concerns regarding the sustainability of bivalve populations, particularly those with relatively thin shells, such as soft-shell clams, are well justified.

### 3.7. Acknowledgements

Thanks to Kristen Murray, Luke Poirier, Melanie Rossong, and Daniel McNeill (UPEI) for field and laboratory assistance. Thanks also to Erica Watson (Department of Fisheries and Oceans Canada - Gulf Division), the Shellfish Research Group (AVC-UPEI) and the Biology Department (UPEI) for the use of facilities, equipment, and vehicles. Finally, I thank Tim Barrett (UNB) for his advice with statistical analyses. This project was funded by the PEI Shellfish Association and the Atlantic Shrimp Corporation through an Aquaculture and Fisheries Research Initiative granted to P. Quijon and J. Davidson. T. Pickering also acknowledges graduate support from the National Science and Engineering Research Council (NSERC) and UPEI'S Duffy Graduate Scholarship in Science.

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# Chapter 4. INCREASING NUMBERS OF GREEN CRAB AS A THREAT FOR OYSTER BED SUSTAINABILITY: ASSESSING PREDATOR SIZE AND PREY SIZE VULNERABILITY

Pickering, T., Quijon, P.A., Davdison, J., McKenna, S. (in prep.) Increasing numbers of green crab as a threat for oyster bed sustainability: assessing predator size and prey size vulnerability.

## 4.1. Abstract

Non-indigenous green crabs (*Carcinus maenas*) are emerging as important predators of American oysters (*Crassostrea virginica*) throughout coastal areas of Atlantic Canada and the eastern seaboard of the United States. To document their potential population growth and impact, we carried out trapping surveys in seven coastal sites during 2008, 2009, and 2010 and conducted a series of predator-prey (crab-oyster) manipulations. The trapping surveys confirmed that there is an ongoing spread of green crabs into new oyster habitats while rapidly increasing in previously established areas. We utilized three types of experiments in the laboratory and the field to assess predation rates exhibited by small b(35-45 mm carapace width), medium (45-55 mm), and large (55-75 mm) green crabs feeding on small (5-15 mm shell length), medium (15-25 mm), large (25-35 mm), and extra-large (35-50 mm) oysters. All experiments lasted three to five days but oyster mortality was assessed on a daily basis. Overall, the outcome of green crab-oyster predator-prey interactions was heavily dependent on both oyster size and crab size. While almost no predation occurred on extra-large oysters, large and medium green crabs preyed heavily on all other sizes, usually in the first three days of manipulation. Small and medium oysters were the most vulnerable to predation but reached a partial size refuge at ~35 mm SL. Under that size threshold, oysters in areas invaded or likely to be

invaded remain highly vulnerable and require management measures in order to secure the sustainability of this shellfish resource.

## 4.2. Keywords

American oyster, *Crassotrea virginica,* European green crab, *Carcinus maenas*, predator-prey interactions; size vulnerability; crab spread and establishment, shellfish sustainability

## 4.3. Introduction

In most bivalve aquaculture industries, predation on various life stages of clams, mussels or oysters represents a substantial source of mortality and a limiting factor for their productivity and sustainability (e.g., Bisker and Castagna 1987; Flimlin and Beal 1993). The American oyster (*Cassostrea virginica*) fishery, one of the most traditional industries along the eastern seaboard of the United States and Atlantic Canada, is no exception (e.g., Glude 1955; Elner and Lavoie 1983; Miron et al. 2005). Although in recent years there has been a growing trend towards off-bottom oyster aquaculture in the region, in many areas this industry still relies on the harvesting of wild beds and on benthic grow-out conditions for at least part of the life cycle of the oysters (PEI DFARD 2007). In these instances, small oysters (seed) may remain on the bottom or are intentionally placed on the bottom and become vulnerable prey to a wide variety of predators. Gastropods, sea-stars, predatory fish species, and crustaceans such as crabs and lobsters are among the most prominent predators of oysters (Flimlin and Beal 1993). Although the role played by some of these predators has been studied in the past (Elner and Lavoie 1983; Harding et al. 2007; Kennedy et al. 2009), our ability to predict the outcome of their individual predator-prey interactions remains limited. Among other reasons, this is due to the lack of studies that systematically focus on two or more life stages (sizes) of the predator and, simultaneously, also focus on the vulnerability of different life stages of the prey.

Invasions by predatory species such as the European green crab (*Carcinus maenas*) have made the analysis of predator-induced bivalve mortality even more difficult. Green crabs are voracious, generalist predators with the ability to diminish prey populations in virtually every coastal habitat where they have been studied (Cohen et al. 1995; Mascaro and Seed 2000a). As bivalves make up a substantial portion of the green crab's diet (Elner 1981; Baeta et al. 2006), it is not surprising that most impacts reported in the literature relate directly to shellfish resources. For example, in their European home range green crabs are known to forage on a wide variety of commercially harvested and cultured bivalves, such as blue mussels (*Mytilus edulis*) (Dare and Edwards 1976), Pacific oysters (*Crassostrea gigas*) (Walne and Davies 1977), and hard clams (*Mercenaria mercenaria*) (Walne and Dean 1972). Meanwhile, in their expanded range green crabs have been linked to severe collapses in bivalve populations throughout many regions. For example, on the west coast of North America, the green crab invasion has been linked to substantial declines of two native clam species, *Nutricola tantilla* and *Nutricola confuse* (Grosholz et al. 2000). Similarly, on the east coast, green crabs are known predators of blue mussels, soft-shell clams (*Mya arenaria*), and American oysters, all of which are commercially exploited species (Miron et al. 2005). One of the most notable cases from this region is the New England soft-shell clam fishery in which clam abundance declined by 50% within 4 years after the arrival of the green crab (Glude 1955). Experimental evidence also suggests that green crabs will become detrimental to vernerid clam (*Katelysia scalarina)* populations in Tasmania, as their predation rates on these clams are much higher than those estimated for native predators (Walton et al. 2002).

The green crab was first confirmed in the southern Gulf of St. Lawrence and Prince Edward Island (PEI) in 1997 (Gillis et al. 2000; Audet et al. 2003). Since the initial invasion, green crab populations continue to grow and spread (Audet et al. 2008) and are gradually establishing in many oyster habitats. Some of the richest oyster harvesting and culture habitats in the region are located in southern PEI, an area that accounts for ~80% of the total oyster production in Atlantic Canada (PEI DFARD 2007). Green crabs have recently reached those habitats and are already emerging as one of their most prominent predators (Miron et al. 2005), becoming a concern for the oyster aquaculture industry. As with other invasive species, the potential impact of this predatory crab is linked to the build up of large, well established populations. Therefore, documenting green crab population numbers and assessing predation rates exhibited by representative crab sizes are among the most basic steps to forecast impacts and develop suitable mitigation strategies. In this study we report trapping surveys carried out at seven coastal sites located in two important oyster areas in PEI during 2008, 2009, and 2010. We also report the assessment of their predation potential with a systematic series of predator-prey (crab-oyster) manipulations that aimed to measure green crab feeding rates on an array of oyster sizes. Specifically, in both field and laboratory settings, we manipulated three distinctive crab size ranges preying upon four distinctive sizes of prey. Our null hypothesis was that prey mortality levels are similar and unrelated to predator size and oyster size. However, based on the literature available (e.g., Elner and Hughes 1978; Boulding 1984), we expected to find increasing prey mortality rates with the increase in crab size and decreasing mortality rates with the increase in oyster size.

## 4.4. Materials and methods

### *4.4.1. Study area and green crab abundance*

Bedeque Bay and North River are shallow estuarine systems located in the south shore of PEI (Fig. 4.1). Bedeque Bay includes the estuarine portion of Wilmot River and Dunk River whereas North River is embedded into the Hillsborough River system and drains towards Hillsborough Bay. Both systems are characterized by extensive oyster beds and, in fact, sustain a substantial proportion of the wild oyster harvesting activity in PEI and the Southern Gulf of St. Lawrence. In order to characterize green crab abundances, trapping surveys were conducted at seven sites during the fall seasons of 2008, 2009 and 2010: three sites were located in North River and four sites in Bedeque Bay (two in Wilmot River and two in Dunk River; Fig. 4.1). Green crab abundances were estimated by 24 h deployment of 8-12 multispecies Fukui traps (60 cm x 45 cm x 20 cm high, with a 40 cm opening at each end) per site. Each trap was baited with ~100 g of Atlantic mackerel (*Scomber scrombus*) and properly cleaned after use to avoid unintentional transport of invasive species between the two main sampling areas. All the field experiments reported below were conducted in Stewart Cove, Stratford, a site located adjacent (~3 km away) the Lower Site in North River (Fig. 4.1).

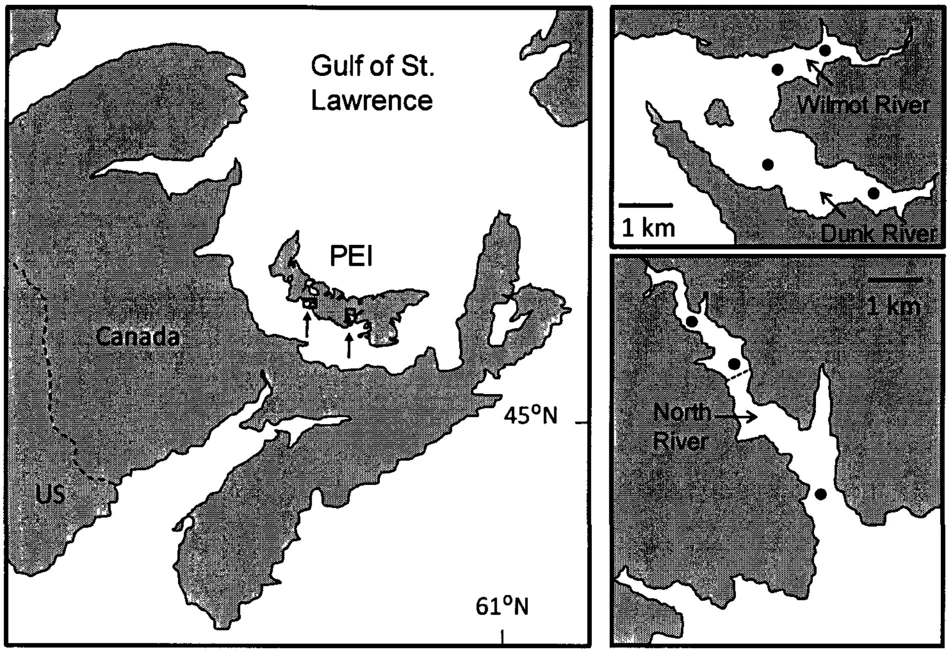

Figure 4.1. Map of Prince Edward Island (PEI) within the Canadian Maritimes, with the approximate location of Bedeque Bay and North River (inserts). The map also shows the approximate location of the sampling sites in Bedeque Bay (upper and lower sites in Wilmot River and Dunk River) and upper, middle and lower sites in North River.

### *4.4.2. Collection of experimental animals: green crabs and oysters*

Green crabs were collected from the seven sites identified above (Fig. 4.1) and from two alternate sites located ~70 km away: Basin Head and Souris River. To reduce variability associated with morphology and gender only intact male green crabs were collected and kept for the experiments (e.g., Smallagange and van der Meer 2003). They were classified into three size categories based on the size structure from the sampling surveys: small (35-45 mm carapace width; CW), medium (45-55 mm CW), and large green crabs (55-75 mm CW). All the crabs used in the experiments were starved for 48 hours prior to the beginning of the trials in order to standardize hunger levels (e.g., Mascaro and Seed 2001), and used only once in order to avoid potential learning after repetitive trials (Cunningham and Hughes 1984). At the time of collection, water temperature at these locations ranged from 18-22°C. American oysters were obtained from a private oyster grower in PEI and were classified into four size ranges based on values reported in the literature (e.g., Miron et al. 2005),: small (5-15 mm shell length (SL)), medium (15-25 mm SL), large (25-35 mm SL), and extra-large (35-50 mm SL).

### *4.4.3. Feeding experiments in Vexar® bags*

Green crab predation rates were measured in single-choice field trials conducted off-bottom in individual Vexar® floating bags (44 cm x 88 cm x 15 cm high) similar to those used in the region for culturing oysters. Thirty oysters of a given size (small, medium, large or extra-large) were placed into each Vexar® bag and then an individual green crab was added. Separate trials were run for each size of oyster and each size of green crab (12 replicated combinations in total).

### *4.4.4 Laboratory experiments*

In the laboratory, single-choice feeding trials were held in glass tanks (21.6 cm x 41 cm x 25 cm high) filled with prepared seawater (18-22 ppt; 18-20°C) and covered by a hood to avoid crab escape. Air stones were placed in each tank and the sides were carefully covered to increase darkness and avoid external visual stimuli that may alter green crab behaviour (e.g., Palacios and Ferraro 2003). Photoperiod was maintained at 12 hours of light and 12 hours of darkness. The laboratory trials were intended to match the field trials but under more rigorously controlled conditions to conduct direct observations of crab feeding. Because the outcome of the trials conducted in the Vexar® bags indicated near 100% mortality of small oysters and near 0% mortality of extra-large oysters (see Results), the laboratory experiments were conducted with medium and large oysters only (15-25 and 25-35 mm SL, respectively). Additional multiple-choice laboratory trials measured green crab feeding rates when presented with two different sizes of oysters (15 medium and 15 large), simultaneously. For those experiments, individual green crabs of medium and large sizes were used separately as predators.

### *4.4.5. Cage inclusion experiments*

Single-choice feeding trials were also held directly on the bottom using inclusion cages constructed of plastic coated wire (40 cm x 40 cm x 75 cm high) with square mesh openings of 1 by 1 cm. Cages had open bottoms and were inserted 5-10 cm into the sediments of the lower intertidal zone to avoid crab escape and minimize potential desiccation due to low tide exposure. In comparison to the previous trials, the cage experiments intended to measure feeding rates under less controlled conditions: in addition to the oysters provided, green crabs were in direct contact with the seafloor and therefore had access to other potential prey, mainly the common periwinkle (*Littorina littorea*) which was abundant near the site with the cages. At the time the cages were placed, relatively large (visible) epibenthic organisms (such as *L. littorea*) were removed by hand but sediments were not excavated and/or sieved to remove smaller infaunal organisms. Like in the laboratory experiments, only medium and large oysters were used as prey. In addition, only medium and large green crabs were used due to the minimal effect green crabs of the small size had on oyster of the sizes described (see Results). Cages were checked daily in order to remove stranded eelgrass or seaweeds and to check for potential accumulation of fine sediments.

#### *4.4.6. Experimental procedure*

Oysters placed in Vexar® bags, laboratory tanks or inclusion cages were allowed to acclimatize for approximately one hour before the inclusion of an individual crab of a given size. All the trials lasted 5 days with the exception of the first set of laboratory trials (which lasted 3 days). In order to identify the time period of most intense foraging, oyster mortality was recorded on a daily basis for all these experiments. As the daily checking of oyster mortality was done visually and required only a few minutes, it is unlikely that crab behaviour was severely affected. All the trials conducted in Vexar® bags and laboratory tanks (i.e. for each crab size and oyster size combination) were replicated (n=10). Due to logistic limitations, cage inclusion experiments were conducted with a lower level of replication (n=6) and only two sizes of predators: medium (45-55 mm CW) and large (55-75 mm CW) crabs.

In order to account for alternative sources of prey mortality, preliminary 5 day trials without green crabs were run for all the experiments conducted in the field and in the laboratory (n=10). Since the survival of oyster size was 100% in all the trials, no additional control trials were judged necessary.

### *4.4.7. Statistical analysis*

A two-way ANOVA model was used for the predation experiments (laboratory tanks, field Vexar® bags, field cages) to compare the relative influence of predator size, prey size, and their interaction on the mortality levels measured at the end of the 3 or 5 day period. Since significant interaction terms were expected to occur, these overall ANOVAs were complemented with one-way ANOVAs comparing mortality rates among oyster sizes (for each trial and time) for each day separately. The sole purpose of these additional ANOVAs was to detect when predation took place and when between-size oyster mortalities become significantly different. In those cases where significant differences were detected, the Tukey's a posteriori test was used to identify significant differences among oyster size. In those cases where only two oyster sizes were compared, two-sample t-tests were used for comparing mortality rates among oyster sizes (for each trial and time) separately.

For the laboratory experiments where green crabs were given a choice between 15-25 and 25-35 mm SL oysters (simultaneously), a balanced one-way MANOVA model was used to compare the relative influence of the predator size on the mortality of each size of oyster. Since significant interaction terms were detected in preliminary runs of the analysis, this "overall" MANOVA was complemented with more specific balanced

ANOVAs, serving as multiple comparisons. Two separate one-way balanced ANOVA models were used to compare the influence of predator size on the mortality levels exhibited by each of the oyster sizes. For all these analyses, assumptions were properly tested using the Anderson-Darling normality test and the Levene's test for equal variance, and in those cases where they failed to meet the assumptions, arcsine or square root transformations were applied.

## 4.5. Results

### *4.5.1. Green crab abundance*

The trapping surveys showed an increase and/or an establishment of green crab abundances at all seven sampling sites from 2008 to 2010 (Fig. 4.2; see Appendix for full data set). Of the four sampling sites located in Bedeque Bay, in 2008 green crabs were only found at the Upper Wilmot site and in low numbers (<0.5 crab trap$^{-1}$ day$^{-1}$). In 2009 and 2010, green crabs were found at all four sites although no clear increase in abundance was seen between those two years. In both years, trapping abundances averaged between 0 and ~10 crabs trap$^{-1}$ day$^{-1}$, depending on date and site (Fig. 4.2). At the three sites in North River, a small increase in trapping abundance was observed between 2008 and 2009 (~0-5 and then ~0-10 crabs trap$^{-1}$ day$^{-1}$ in 2008 and 2009, respectively). However, in 2010 a large increase at all three sites was detected, with trapping averages ranging from ~10-60 crabs trap$^{-1}$ day$^{-1}$ (Fig. 4.2).

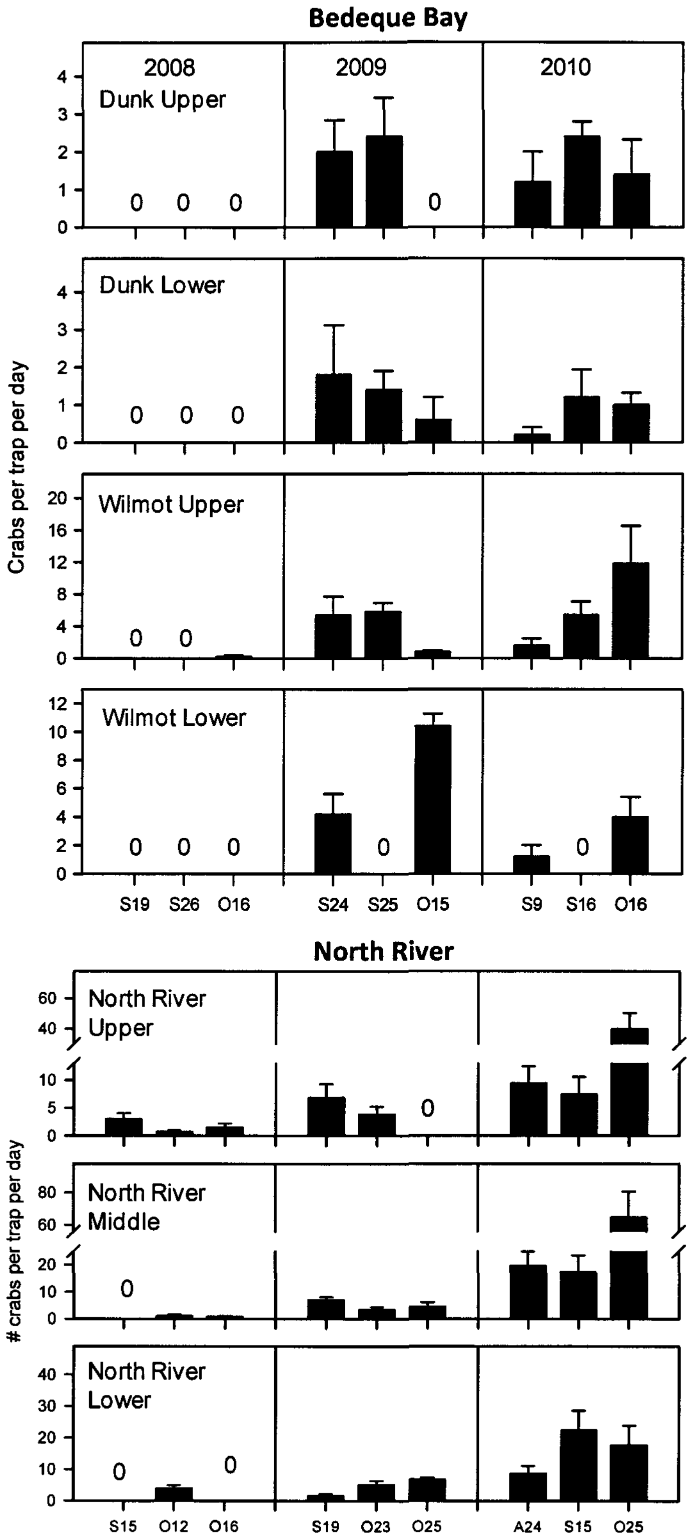

Figure 4.2. Mean (+ SE) crabs per trap per day collected in three representative dates of the fall seasons of 2008-2010 in each of the sites identified in Figure 1. Letters and numbers identify months and days. A: August, S: September, O: October.

### *4.5.2. Field Vexar® bags experiments*

For the field Vexar bag predation experiments, the results of the two-way ANOVA indicated that both sources of variation (crab size and oyster size) and their interaction had a significant effect on oyster mortality ($p<0.001$; Table 4.1). The results of additional one-way ANOVA comparisons and the post-hoc tests are summarized with the use of asterisks in Fig. 4.3. In all cases, small oysters were the most vulnerable to predation whereas extra-large oysters were the least vulnerable (Fig. 4.3). Mortality levels generally decreased with increasing oyster size. Small green crabs only caused noticeable mortality on the smallest size of oyster (5-15 mm SL), while causing almost no mortality on the three larger size classes. Predation by medium sized green crabs on small oysters was significantly higher than their predation rates on all other oyster sizes (Fig. 4.3). Large green crabs caused 100% mortality on the smallest size of oyster after one day and almost no mortality on the extra-large oysters, even after five days of predation. Significant differences were found between all size groups at all time periods except between large and extra-large oysters after the first and second day of the trials (Fig. 4.3).

### *4.5.3. Laboratory experiments*

The two-way ANOVA indicated that both sources of variation (crab size and oyster size) and their interaction had a significant influence on oyster mortality ($p<0.001$; Table 4.1). Comparisons of mortality rates among different oyster sizes at each time period are summarized with the use of asterisks in Fig. 4.4. In general, small crabs foraged only slightly on medium sized oysters and did not cause any mortality on the large oysters; significant differences in mortality between the two sizes were only found on the third

Table 4.1. Results from three separate two-way ANOVAs examining the effect of crab size (Cs), oyster size (Os), and their interaction on bivalve mortality rates measured in off-bottom Vexar ® bags, laboratory tanks, and inclusion cages. Data underwent appropriate transformation (arcsine or square root) to meet ANOVA assumptions.

| Experiment | Source of variation | DF | SS | MS | P |
|---|---|---|---|---|---|
| Field Vexar® bags | Crab size (Cs) | 2 | 5.3567 | 2.6783 | <0.001 |
| | Oyster size (Os) | 3 | 21.7923 | 7.2641 | <0.001 |
| | Cs x Os | 6 | 3.5789 | 0.5965 | <0.001 |
| | Error | 108 | 1.9554 | 0.0181 | |
| Laboratory trials | Crab size (Cs) | 2 | 4.0643 | 2.0321 | <0.001 |
| | Oyster size (Os) | 1 | 3.0761 | 3.0761 | <0.001 |
| | Cs x Os | 2 | 0.6494 | 0.3247 | <0.001 |
| | Error | 54 | 1.9622 | 0.0368 | |
| Field wire cages | Crab size (Cs) | 1 | 0.33041 | 0.33041 | 0.002 |
| | Oyster size (Os) | 1 | 0.76030 | 0.76030 | <0.001 |
| | Cs x Os | 1 | 0.00001 | 0.00001 | 0.988 |
| | Error | 20 | 0.49201 | 0.02460 | |

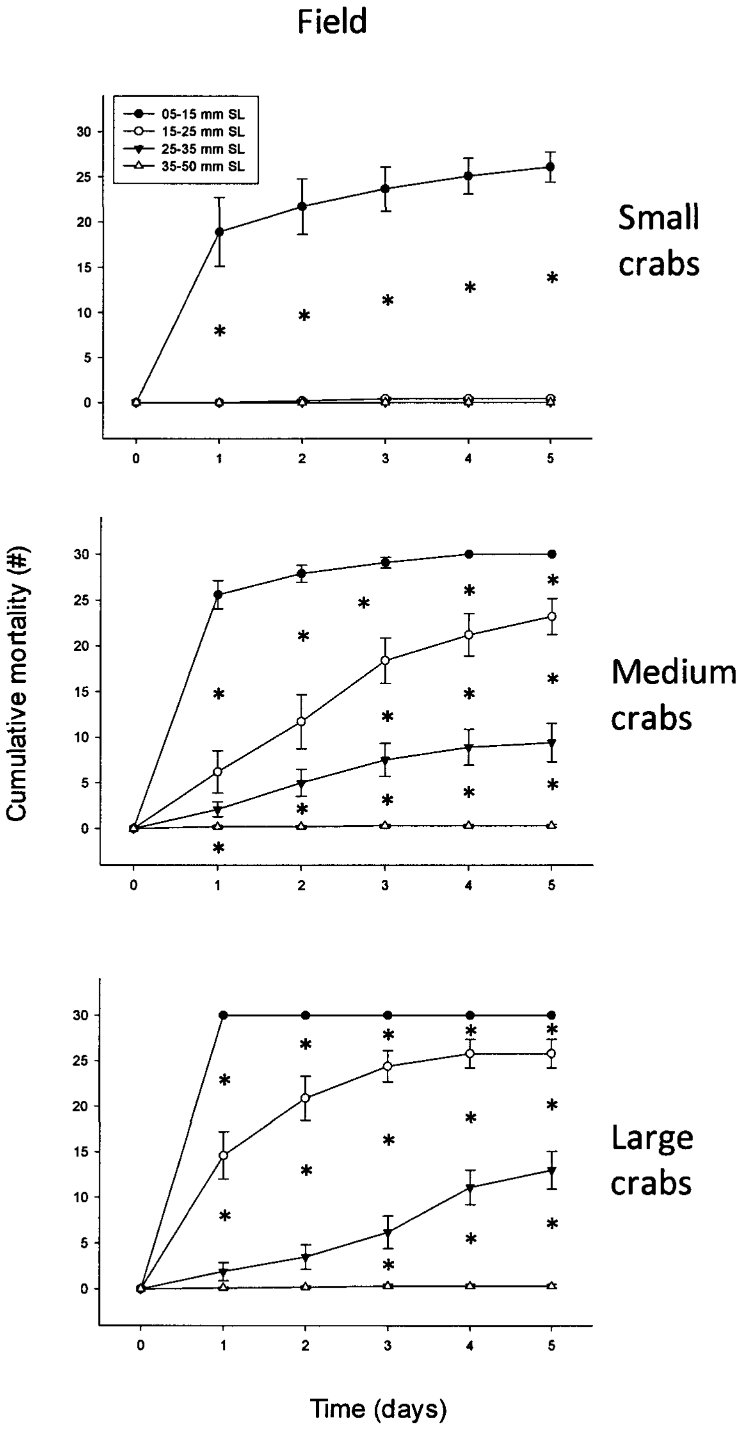

Figure 4.3. Mean (+/- SE) cumulative mortality of small (5-15 mm SL), medium (15-25 mm), large (25-35 mm), and extra-large (35-50 mm) American oysters over time (days) resulting from predation by small (35-45 mm CW), medium (45-55 mm), and large (55-75 mm) green crabs in single-choice field Vexar® bag experiments. Asterisks identify significant differences between oyster size mortality levels at each time period.

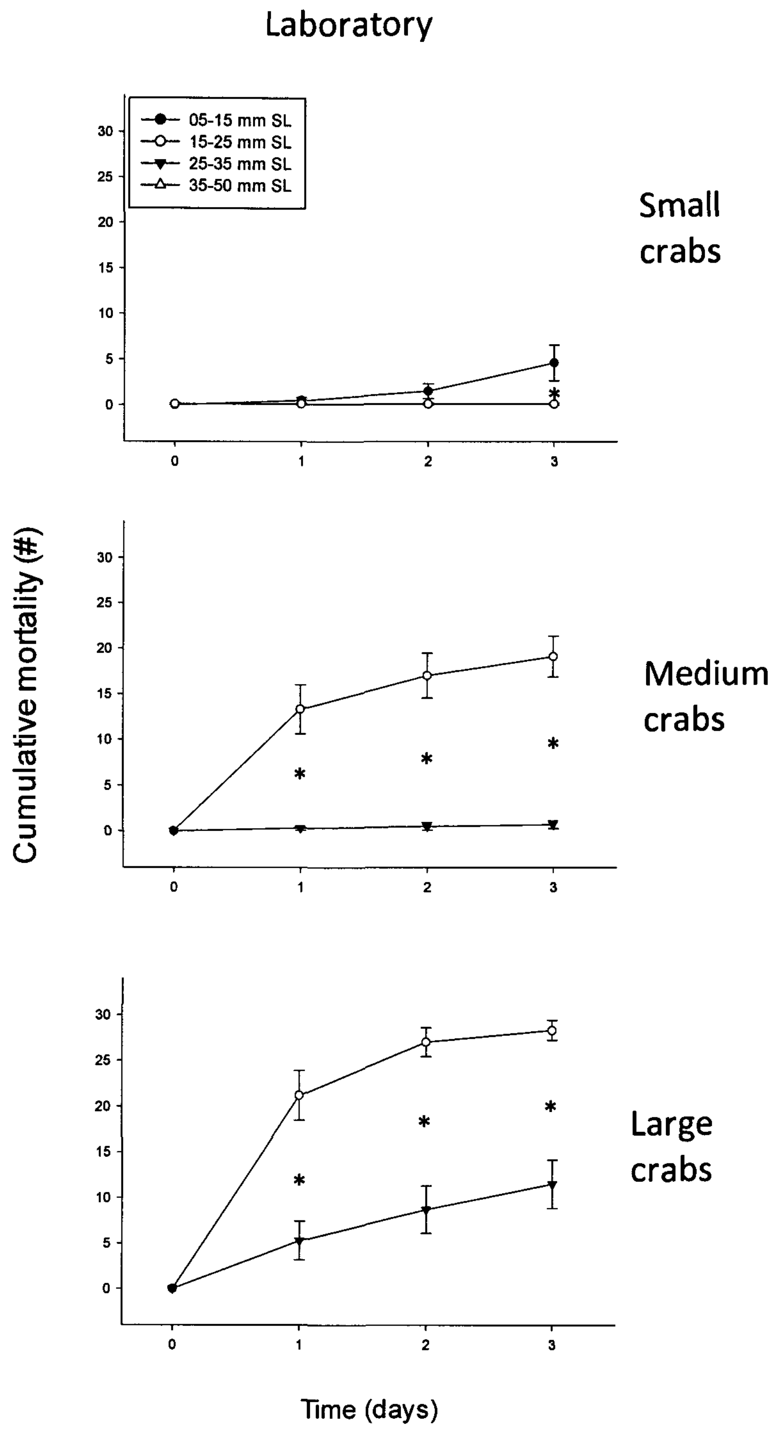

Figure 4.4. Mean (+/- SE) cumulative mortality of medium (15-25 mm) and large (25-35 mm) American oysters over time (days) resulting from predation by small (35-45 mm CW), medium (45-55 mm), and large (55-75 mm) green crabs in single-choice laboratory experiments. Asterisks identify significant differences between oyster size mortality levels at each time period.

day of the trial (Fig. 4.4). Medium crabs caused substantial mortality on the medium sized oysters but almost no mortality on the large oysters, a difference that was evident since day 1 of the trials. Large crabs were able to forage on both oyster sizes, and their predation rates (Fig. 4.4) were fairly similar to those observed in the field Vexar® bag experiments described above.

In the laboratory trials that used a combination of medium and large oysters, the results of the balanced one-way MANOVA indicated that the source of variation identified (crab size) was significant ($p=0.001$; Table 4.2). Subsequent multiple comparisons were conducted with separate balanced one-way ANOVAs for each prey size. The results of these ANOVAs indicated that the source of variation (Crab size) was significant for both the 15-25 and 25-35 mm SL ($p<0.001$ and $p=0.002$, respectively; Table 4.3).When given a choice between the two oyster sizes, medium green crabs caused a lower than expected level of mortality: they only fed on medium oysters during the first day. No signs of molting or poor health conditions were detected in these crabs. In contrast, large green crabs followed the pattern observed in the previous experiments and caused substantial mortality on both sizes of oysters, particularly on medium sized oysters (Fig. 4.5).

### *4.5.4. Cage inclusion experiments*

The results of the two-way ANOVA indicated that both sources of variation (crab size and oyster size) were significant ($p=0.002$ and $p<0.001$, respectively) but not their interaction term ($p=0.988$). Additional comparisons of mortality rates among different oyster sizes are summarized with the use of asterisks in Fig. 4.6. Medium green crabs

Table 4.2. Results from a balanced MANOVA examining the effects of crab size on the mortality rates of 15-25and 25-35 mm SL oysters in multiple-choice laboratory (tanks) experiments (green crabs were able to forage on both sizes of oysters simultaneously). Data underwent appropriate transformations (arcsine), to meet MANOVA assumptions.

| Experiment | Source of variation | DF | Wilks' | P-value |
|---|---|---|---|---|
| Laboratory choice | Crab size (Cs) | 2, 17 | 0.43032 | 0.001 |

Table 4.3. Results from two separate balanced ANOVAs, examining the effect of crab size on the mortality rates of 15-25 and 25-35 mm SL oyster in multiple-choice laboratory (tanks) experiments (green crabs were able to forage on both sizes of oysters simultaneously).. Data underwent appropriate transformations (arcsine), to meet ANOVA assumptions.

| Experiment | Response | Source of variation | DF | SS | MS | P |
|---|---|---|---|---|---|---|
| Laboratory choice | 15-25 mm SL | Crab size (Cs) | 1 | 4.4855 | 4.4855 | <0.001 |
| | | Error | 18 | 3.4025 | 0.1890 | |
| | 25-35 mm SL | Crab Size (Cs) | 1 | 110.45 | 110.45 | 0.002 |
| | | Error | 18 | 146.50 | 8.14 | |

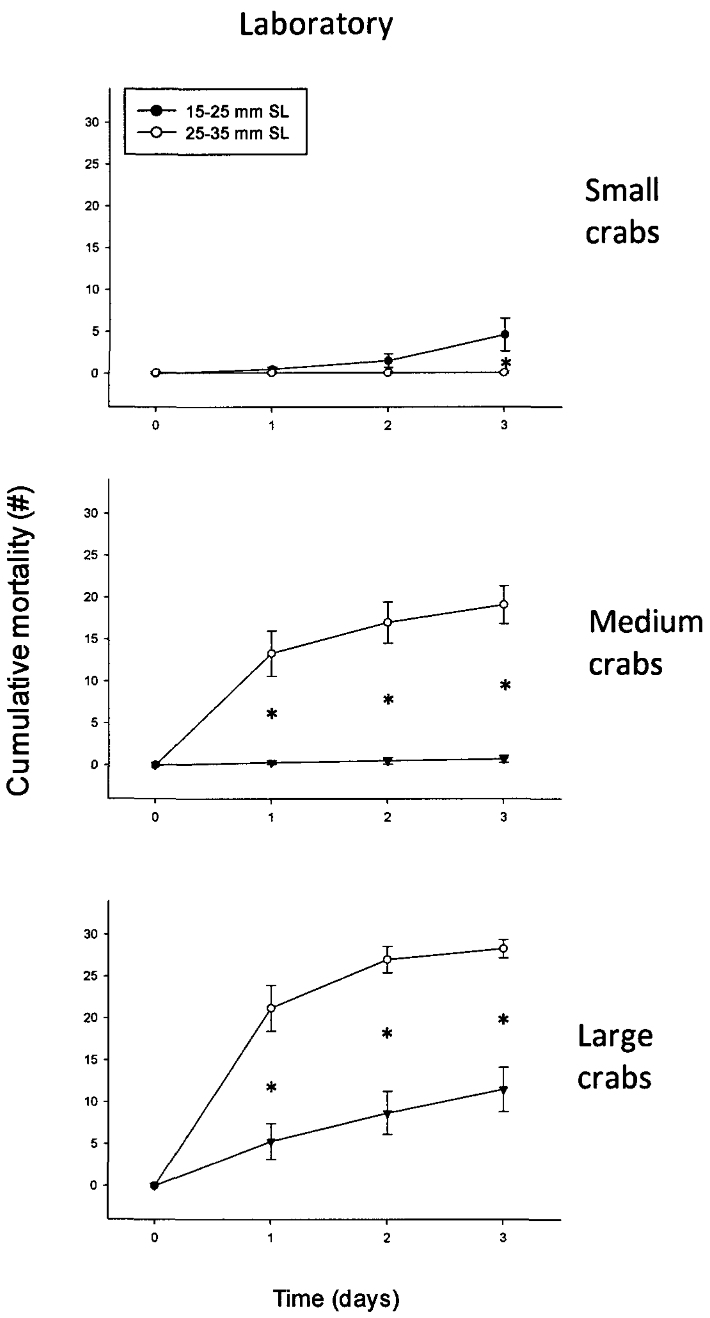

Figure 4.5. Mean (+/- SE) cumulative mortality of medium (15-25 mm SL) and large (25-35 mm) American oysters over time (days) resulting from predation by medium (45-55 mm CW) and large (55-75 mm) green crabs in multiple-choice laboratory experiments (green crabs were allowed to forage on both sizes of oysters simultaneously). Asterisks identify significant differences between oyster size mortality levels at each time period.

preyed on medium sized oysters and only minimally on large oysters; the difference in mortality rates between these sizes became significant only after 5 days (Fig. 4.6). Large green crabs also preyed on both medium and large oysters but caused higher mortality rates on the medium oysters and in general fed more than medium sized crabs. Incidentally, quantifiable evidence of predation on the common periwinkle (*Littorina littorea*) was obtained from, several cages (not shown in Fig. 4.6). At the end of the five day trial, medium crabs feeding on 15-25 mm SL oysters caused a mean mortality of 0.11 (± 0.10) periwinkles while medium crabs feeding on 25-35 mm SL oysters caused a mean mortality of 0.10 (± 0.10). Large crabs feeding on 15-25 mm SL and 25-35 mm SL oysters caused a mean mortality of 6.25 (± 4.13), and 1.00 (±0.68) periwinkles, respectively.

## 4.6. Discussion

Overall, the largest green crabs were the most detrimental for oysters of all sizes whereas the smallest oysters were by far the most vulnerable to predation. This is consistent with what we know about most crab species: larger individuals have higher nutritional requirements, greater crushing strength (e.g. Eggleston 1990), and larger chela gape (e.g., Boulding 1984), and therefore have the potential to generate the most severe impacts. In contrast, smaller crabs face physical limitations that restrict their consumption on relatively large prey (Boulding 1984). Less expected, however, was the impact of medium sized green crabs which caused considerable levels of mortality and also represent a threat that should be carefully monitored in light of the growing population sizes reported here. In the feeding experiments, foraging intensity appeared to be greatest

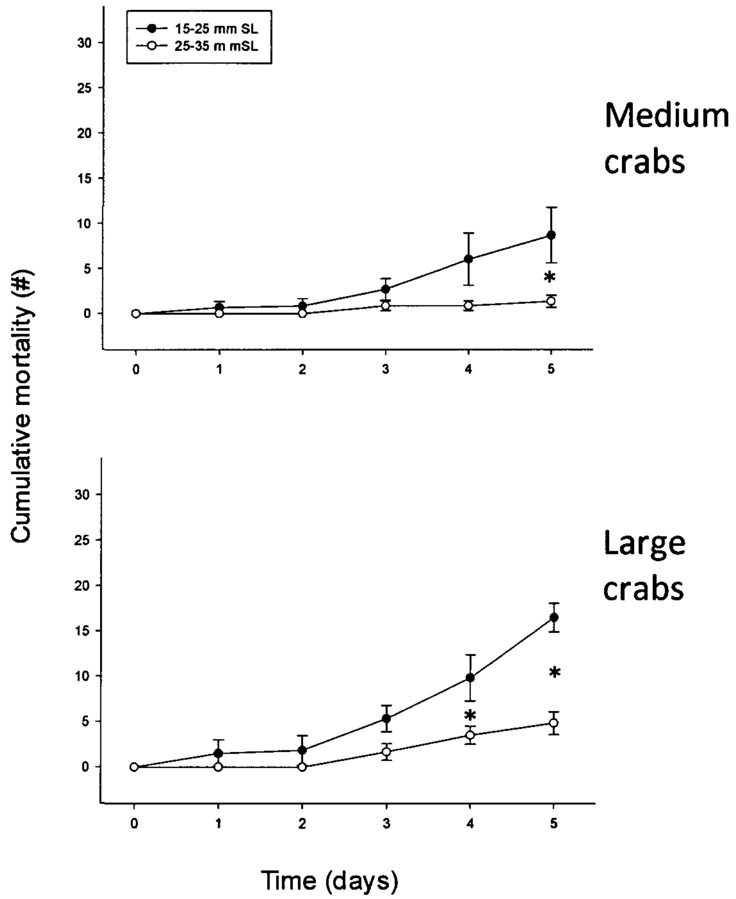

Figure 4.6. Mean (+/- SE) cumulative mortality of medium (15-25 mm SL) and large (25-35 mm) American oysters over time (days) resulting from predation by medium (45-55 mm CW) and large (55-75 mm) green crabs in single-choice field caged experiments. Asterisks identify significant differences between oyster size mortality levels at each time period.

during the first three days of the trials, with predation still occurring, although to a lesser extent, up to the fifth and final day of the trials. These early, most intense foraging periods may be partially explained by issues associated with prey depletion (in some cases). Also, as the green crabs started to feed on the oysters, their hunger levels, and ultimately their foraging rates, may have gradually decreased (Murray et al. 2007). The spread to sites previously un-invaded in Bedeque Bay and the sharp increase in green crab densities observed in sites already invaded for a few years (North River), suggest an ongoing process of population growth that requires monitoring.

### *4.6.1. Field Vexar® bag and laboratory predation experiments*

The majority of our results in Vexar® bags and in the laboratory suggest that green crabs prefer smaller sized oysters over larger ones, which is consistent with most other studies on green crab prey size preferences (Floyd and Williams 2004; Miron et al. 2005; Murray et al. 2007). For example, Murray et al. (2007) demonstrated that green crab predation on mussels exponentially decreases with increasing mussel shell length. Juanes and Hartwick (1990) offered an explanation for this: crabs choose smaller prey as repeatedly attempting to open larger prey can cause chelal damage and wear, reducing their overall foraging ability. Mascaro and Seed (2000b) however showed that green crabs select intermediate sizes of blue mussels as opposed to smaller or larger individuals. The authors explained this preference by suggesting that larger items were too difficult to open whereas smaller items were less likely to be encountered and more frequently dropped. Based on our results, younger, smaller sized individuals are most likely to be the most affected by a further green crab invasion. A potential decimation of young bivalve size classes will then cause steep population declines once the older, larger individuals begin to die off and are not replaced (Floyd and Williams 2004).

Our results differ from those reported by Mascaro and Seed (2000b) for green crab predation on flat oysters (*Ostrea edulis*) and Pacific oysters (*Crassostrea gigas*). These authors reported a complete lack of prey size preference, and concluded that all size classes were equally vulnerable to green crab predation. The results by Mascaro and Seed (2000b) are unusual when compared to the study by Miron et al. (2005) in this region, our own study, and most studies elsewhere. Evidence of strong size preferences by green crabs or other comparable crab species are indeed abundant in the literature and are typically related to distinctive levels of profitability (e.g., Elner and Hughes 1978; Hughes 1980; Smallegange and van der Meer 2003; Smallegange et al. 2008). Although our trials are more similar to those conducted by Miron et al. (2005) in terms of evidence of prey size preferences, predation rates measured in our study were much higher than those estimated from their single and multiple choice experiments using the same predators and preys. As a result of that, the refuge size reported by Miron et al. (2005; 25 mm SL) is considerably smaller than the one our results suggest: 35 mm SL. In our experiments, oyster in the 25-35 mm SL range were affected by substantial mortality due to predation by medium and large sized crabs. One potential explanation for the difference between both studies is a slight difference in the experimental protocol. While most of our experiments exposed all size classes of oysters to predation separately, Miron et al. (2005) combined oysters of different sizes in the same trial. Thus, in their study the size refuge may be driven more by prey preferences for small oysters than by the intrinsic ability of the crabs to forage up to certain size.

The oyster size refuge measured in this study were comparable to those measured for native predators along the east coast of North America. For example, Eggleston (1990) reported that most blue crabs (*Callinectes sapidus*) along the eastern seaboard of the United States can only forage on American oysters up to 35 mm SL. Similarly, in Atlantic Canada, Elner and Lavoie (1993) reported a size refuge of 30-35 mm SL against predation from rock crabs (*Cancer irroratus*). Miron et al. (2005), however, reported a smaller size refuge against rock crabs at 25 mm SL, but again this difference may be attributed to differences in experimental procedure. Given that the evidence available suggests that at ~35 mm SL oysters reach a refuge from both native and invasive crabs, larger size classes of oysters should not be particularly affected by a further green crab invasion. However, the intense predation rates on smaller oysters and the establishment and growth of large green crab populations remain to be serious concerns for the oyster industry.

### *4.6.3. Wire cage predation experiments*

The wire cage experiments were conducted directly on the sediment and were designed to reflect more natural, less controlled conditions compared to the experiments discussed above. As expected, predation rates were generally lower but the size preferences remained evident and consistent with the previous experiments. Green crabs could easily forage on many alternative prey species (cf. Ropes, 1968; Elner, 1981; Baeta et al. 2006) and some of them may have entered through the mesh of the cages or may have already been present when the cages were placed in the sediment. The common periwinkle (*Littorina littorea*) was able to pass through the cage mesh, and green crab did indeed forage on them: periwinkle shell remnants indicate that predation rates on these organisms were as high as 6.25 ± 4.13 individuals by the fifth and final day of the trial, which may likely explain the lower predation rates on oysters. Other prey species such as soft-shell clams (*Mya arenaria*), quahogs (*Mercenaria mercenaria*) and a variety of large polychaetes could have been also present in the sediment and are typically found in oyster beds and aquaculture leases. Green crabs would likely exhibit a preference for these alternative preys (cf. Mascaro and Seed 2000a; Mascaro and Seed 2001, Miron et al. 2005; Pickering and Quijon submitted) but this would not prevent them from consuming oysters. Parallel experiments indicate that as the abundance of alternative prey items diminish, green crabs quickly turn to oysters as a main food source (Pickering and Quijon submitted).

Alternatively predators known to feed on oysters, such as the moon snail (*Euspira heros*) (Miron et al. 2005), may have been present inside the cages and may have contributed to oyster mortality and, therefore, created a bias in our results. We consider that scenario very unlikely though. Moon snails are important shellfish predators (Quijon et al. 2007) but feed at a much slower pace and leave distinctive perforations in the shells that were never detected in the oyster remnants. Furthermore, in the control trials conducted without green crabs, no mortality was observed within the cages, which suggests that alternative predators and other sources of mortality were negligible.

### *4.6.4. Implications*

Since the initial invasion of green crabs to the region, populations have gradually become established in many oyster habitats in the region. Data on oyster size vulnerability and feeding rates is critical in order to forecast impacts and prepare mitigation strategies for this aquaculture industry. Our results suggest that American oysters up to ~35 mm SL are vulnerable to green crab predation, and that smaller sized individuals are by far the most preferred. Therefore, protection measures such as fencing or off-bottom culturing should target this fraction of the oyster population. Seafloor seeding efforts aiming to repopulate oyster grounds should rely and apply these results as well. The use of protective fencing and growing oysters with off-bottom culturing methods until they reach larger sizes will likely increase production costs for lease managers. However, seeding with unprotected oyster sizes smaller than 35 mm SL would be largely ineffective in areas invaded or likely to be invaded by populations of green crab that, as our results indicate, continue to spread and grow.

### 4.7. Acknowledgements

I would like to thank Kristen Murray, Luke Poirier, Melanie Rossong, and Daniel McNeill of the University of Prince Edward Island (UPEI) for field and laboratory assistance. I also thank Erica Watson (Department of Fisheries and Oceans Canada - Gulf Division), the Biology Department and the Shellfish Research Group (UPEI) for the use of facilities, equipment, and vehicles. This project was funded by the PEI Shellfish Association and the Atlantic Shrimp Corporation through an Aquaculture and Fisheries Research Initiative granted to P. Qujon and J. Davidson. T. Pickering also acknowledges graduate support from the National Science and Engineering Research Council and UPEI'S Duffy Graduate Scholarship in Science.

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# Chapter 5. SUMMARY, IMPLICATIONS, AND FUTURE RESEARCH

Given the observed effects of green crabs elsewhere and the ecological and economic importance of these bivalves to the region, concerns regarding the green crab invasion are well justified. As ecological knowledge on the predator-prey interactions between green crabs and bivalves native to this region is insufficient, assessing these interactions represents a critical step towards understanding the impacts associated with green crab invasions. Furthermore, knowledge on the vulnerability of bivalve populations to green crab predation is essential for the identification of appropriate mitigation strategies, and for improving our preparedness to future invasions. The research reported in this thesis aimed to address two critical gaps in the knowledge on predator-prey green-crab bivalve interactions for the region: green crab prey-preference and green crab-oyster predation effects and vulnerability. This thesis may also provide a better understanding of the potential impacts green crab have on the region's bivalve populations.

## 5.1 Summary

All objectives outlined for this study were met with the appropriate methods. The first research section of this thesis (Chapter 3) investigated prey preferences in a coastal predator-prey system. Specifically the chapter assessed green crab feeding rates among three commercially important bivalve species to the region, *Mytilus edulis*, *Crassotrea virginica*, and *Mya arenaria*. The feeding rates were assessed by running a series of feeding trials in both laboratory (tanks) and field (Vexar® bags and bottom cages) experiments. In these experiments, green crabs exhibited strong prey preferences.

Overall, *M. areanaria* was the most preferred, followed by *M. edulis*, then *C. virginica*. Potential short-term variations in prey preferences occurring within the time frame of the feeding trials were also identified. Green crabs showed an early preference for *M. arenaria* and only as they declined in numbers, a switch towards *M. edulis*, and subsequently towards *C. virginica* was observed. Differences associated with predator and prey size were also identified by running the feeding trials separately with three sizes of crabs and two sizes of bivalves. The multiple sizes of predators and prey used in the experiments confirmed that the largest sizes of crabs are the most detrimental to bivalve populations while the smallest sizes of bivalves are the most vulnerable. Finally, the differences in prey preferences observed in the results were related to differences in bivalve shell thickness, a main predictor of compressive shell strength (Elner 1978; Zuschin and Stanton 2001). The shell thickness measurements determined *M. arenaria*, the most preferred bivalve species, consistently had the thinnest, therefore potentially weakest shell. Similarly, *C. virginica*, the least preferred species, in almost all cases had thicker shell measurements compared to *M. edulis*.

As the *C. virginica* industry is believed to be at risk from the green crab invasion (Gillis et al. 2000), the objectives for the second area of research (Chapter 4) focused solely on green crab-*C. virginica* predator prey interactions. Specifically, the objectives for this chapter were met by measuring green crab feeding rates while foraging on various sizes of *C. virginica* in both field (Vexar® bag and bottom cages) and laboratory (tank) experiments. In this chapter, potential differences in green crab feeding rates associated to predator and prey size were identified by running the feeding trials with multiple sizes predators and multiple sizes of prey. Although *C. virginica* was the least preferred in the prey preference experiments, all sizes of green crabs were able to forage and cause considerable mortality on at least the smallest sized individuals. Medium and large sized green crabs were also able to cause considerable mortality on *C. virgincia* up to approximately 35 mm SL, an apparent size refuge from green crab predation. The period of most intense foraging during the course of the feeding trials was also identified. Foraging intensity appeared to be greatest during the first three days of the trials, with predation still occurring, although to a lesser extent, up to the fifth and final day of the trials. These early, most intense foraging periods may be partially explained by issues associated with prey depletion (in some cases). Also, as the green crabs started to feed on the oysters, their hunger levels, and ultimately their foraging rates, may have gradually decreased (Murray et al. 2007).

Related to the results obtained in Chapters 3 and 4, is the identification of potential mitigation strategies against green crab predation. Such mitigation strategies were reviewed in detail in the last part of the Literature Review (Chapter 2). In that review, the benefits and disadvantages of a wide arrange of mitigation strategies were discussed. Finally, several of these strategies including those potentially suitable for PEI and the southern Gulf of St. Lawrence are discussed in the paragraphs that follow.

### 5.2 Potential mitigation strategies

Throughout the native and expanded range of the green crab many mitigation strategies have been developed and tested in an attempt to reduce their impacts on wild and cultured bivalve beds (Flimlin and Beal 1993; Lafferty and Kuris 1996; Thresher et al. 2000). The results of this study aimed to address the critical gaps in our knowledge regarding predator-prey green crab-bivalve interactions for this region and should prove valuable information for the identification and development of practical, cost effective mitigation strategies. While some of the strategies proposed elsewhere may be applicable for this region, others may be considered unsuitable. For example, mitigation strategies that involve chemical and biological control agents are not likely appropriate for the region due to undesired environmental effects. For example, applying chemical agents, such as pesticides, directly on the water or soaked in bait may reduce green grab populations (Hanks 1961; Feldman et al. 2000). However, the effects of such a measure may extend well beyond green crab populations and have an impact on other organisms, especially (but not limited to) eelgrass beds (Feldman et al. 2000). Similarly, proposed biological control agents such as the rhizocephalon barnacle, *Sacculina carcini* (Lafferty and Kuris 2000; Thresher et al. 2000; Goddard et al. 2005) and the nemertean egg predator, *Carcinonemertes epialti* (Torchin et al. 1996) may prove to be useful against controlling green crab populations. However, the degree of host specificity in these organisms remains uncertain and may also affect other species of crabs (Torchin et al. 1996; Thresher et al. 2000; Goddard et al. 2005).

Trapping programs, such as subsidized fisheries, may prove suitable for the region and have been previously discussed as a potential mitigation strategy in the area (Miron et al. 2005). However, most trapping programs have not shown conclusive evidence that the complete eradication of a green crab population is possible and, regardless, there is always the risk of re-introduction (Gillis et al. 2000). The development of a commercial fishery is also unlikely as the crabs' meat is low in yield (Cohen et al. 1995; Lafferty and Kuris 1996), dark in colour, and considered low quality by North American standards (Gillis et al. 2000). Furthermore, subsidized fisheries may not completely control the green crab populations in the long-term as participation in the fishery would likely decrease once green crab abundances became diminished (Klassen and Locke 2007).

Other, more adaptive measures suggested for mitigating green crab impacts on bivalve beds may prove more useful. These methods include using protective nets and fencing, spreading bivalves at certain sizes and densities, and changing culturing practices to off-bottom methods (Flimlin and Beal 1993). For example, a common method used for the bivalve fishery and aquaculture industries in the northeastern United States involves laying protective mesh covers over seed beds (Walne and Davies 1977; Beal and Kraus 2002). These protective nets allow good water flow while excluding green crabs and other predators, and may prove valuable for burrowing bivalves such as soft-shell clams (*Mya arenaria*) and hard clams (*Mercanaria mercanaria*) (Walne and Davies 1977). Methods such as these however are not well suited for bivalves that grow directly on top of the substrate, such as oysters.

For these types of bivalves, the use of protective fencing may be more suitable. Plastic mesh fences can be constructed around areas of cultured shellfish and physically exclude green crabs and other predators (Davies et al. 1980; Beal and Krause 2002). During the course of this study, a simple mitigation experiment designed to replicate protective fencing was conducted. In this experiment, circular wire mesh cages (diameter = 21.5 cm) were placed inside larger cages (same as those cages described in Chapters 3 and 4) to protect oysters (15 individuals per cage). The smaller circular cages were sunk 2 cm into the sediment and held in place by 3 metal spikes. Green crabs could only access oysters by burrowing under the protective enclosure as the tops were also covered. We ran these mitigation experiments with one and two green crabs to simulate different levels of invasion. With both predator densities, and in all replicates (n=10 for each), no oyster mortality was recorded and green crabs were not observed to burrow under the inner cage during the entire five day feeding trial. Although this was a rather simple, small-scale design, these results suggest that protective fencing may work as an effective mitigation strategy to reduce green crab predation on oyster beds or leases. However, the ability to develop practical, cost-effective fencing that is suitable for the oyster industry in the region remains to be determined and could be an area for future research. As green crabs were observed to climb the sides of the larger caged enclosures, a covering over the top of the protective fencing will likely be required, and further add to the difficulty of achieving practicality for the oyster industry.

The results reported in this thesis on prey preference and size vulnerability are also useful in determining suitable mitigation strategies. Several authors have reported that culturists and managers may reduce green crab predation by spreading bivalve seed at certain sizes and densities (Sponaugle and Lawton 1990; Murray et al. 2007). In the prey preference experiments, *C. virginica* and *M. edulis* mortality from green crab predation was greatly reduced once above 25 mm SL in both field and laboratory experiments. Consistent with other studies (Ropes 1968; Floyd and Williams 2004), no such refuge was reported for *M. arenaria*. In single choice experiments, however, substantial predation on 25-35 mm SL *C. virginica* was observed even by medium sized 45-55 mm CW green crabs. In these single choice experiments, *C. virginica* did not appear to reach a size refuge against predation until ~35-40 mm SL. These results suggest that culturists and managers should protect *C. virginica* seed through methods such as protective fencing and off-bottom culturing techniques until this size refuge is reached to reduce green crab predation. However, the limitations associated to fencing or netting, particularly at spatial scales that are relevant for lease management, may decrease the practicality or suitability of this option for the oyster industry. As the size at which oyster spat is currently spread on lease bottoms may vary among culturists, the main recommendations of this thesis consititute the the seeding of oyster "spat" at sizes of ~35-40 mm SL, as described above.

The use (spread) of different densities of bivalve seed may also influence green crab predation rates. However, the evidence so far is unclear, and its applicability to aquaculture settings is not straightforward. For example, Murray (2009) suggested it would be beneficial to spread *C. virginica* seed at high densities on aquaculture leases as green crab predation is proportionally lower when prey density is high. On the contrary, Sponaugle and Lawton (1990) demonstrated that several portunid crab species foraged less efficiently on hard clams (*M. mercanaria*) at relatively low densities. And yet another study by Kamermans et al. (2009) found that spreading *M. edulis* seed at high or low densities had no overall effect on green crab predation rates.

As the results presented in this thesis indicate, *C. virginica* is not the most preferred prey of green crabs, and therefore, the availability of other prey species may naturally reduce or "hold" predation rates on *C. virginica*. Several species co-exist with oysters so culturists and managers could expect that predation rates, at least in the short term will not be as high as those reported in Chapter 4. However, as indicated in Chapter 3, once the abundance of other (preferred) prey items begin to diminish, green crabs may turn to *C. virginica* as a main food source. A more adaptive measure is the switching to off-bottom growing methods or raising existing off-bottom methods further in the water column (Gillis et al. 2000). The *M. edulis* aquaculture industry in this region currently relies solely on off-bottom culturing methods (Ramsay 2008), that seems to prevent a substantial predation from green crabs and other species. Although there is a growing trend towards off-bottom *C. virginica* culture in areas like New Bruunswick, the PEI industry still relies on harvesting wild beds and seeding unprotected lease bottoms (Aaron Ramsay, PEI Department of Fisheries, Aquaculture, and Rural Development, Pers. Comm.). The off-bottom culture combined with the seeding of bottoms at appropriate oyster sizes (~35 mm SL) may help ensure the sustainability of the industry and alleviate the threats posed by invasive predatory species such as green crabs.

However, the implementation of such mitigation strategies has a cost  Protective nets and fencing require additional equipment and increased labour costs. Trapping programs, even if conducted solely by culturers on their own leases, would also require the purchase of traps and increase labour costs. Growing seed oysters in nursery stages for longer periods of times will no doubt require extra equipment such as floating Vexar® bags, additional off-bottom leases, and increased labour costs linked to management practices oysters. In an ideal mitigation strategy, the benefit of reducing green crab predation on seed oysters however, should however off-set any of the additional costs of implementation.

## 5.3 Suggestions for future research

As green crabs continue to spread throughout Prince Edward Island and the Gulf of St. Lawrence (Audet et al. 2008) much research still needs to be conducted. The experiments presented in this thesis took place in relatively small enclosures with a limited number of predators and preys. Therefore, the next logical step is to investigate these predator-prey interactions in scenarios that include variable numbers of green crabs, for example, as green crab foraging may be altered in the presence of a conspecific (see Bélair and Miron 2009a,b). Similarly, adding heterospecific predators, native to the region such as rock crabs (*Cancer irroratus*), mud crabs (*Dyspanopeus sayi* and *Rhithropanopeus harrisii*), and American lobsters (*Homarus americanus*) may also influence green crab foraging to a level that is not yet well known (but see Bélair and Miron 2009a,b; Rossong et al. 2006; Williams et al. 2006). The addition of these predators to feeding trials, especially in larger experimental enclosures, may reflect more natural conditions and give a better understanding of the true impact green crabs may impose.

Additionally, these experiments looked solely at green crab predation on three commercially important species of bivalves. Other bivalves such as razor clams (*Ensis directus*) and hard clams (*Mercenaria mercenaria*) are commonly found throughout coastal estuaries in PEI and the southern Gulf of St. Lawrence. Including these bivalves in future prey preference experiments may be beneficial as they are also reported, although to a lesser extent, in the diet of green crabs (Elner 1981; Miron et al. 2005). While bivalves account for a large portion of the green crab's diet, other prey items are naturally abundant in PEI and the southern Gulf of St. Lawrence and include gastropods, rock crabs, barnacles, amphipods, polychaetes (*Nereis* spp.), and sea stars (*Asterias vulgaris*) (Elner 1981). Prey preference experiments that incorporate some of these organisms along with bivalves may also prove useful and add to the general understanding of green crab predator-prey interactions.

Another relevant venue is the examination of the actual economic costs associated to the invasion of green crabs in PEI and the Atlantic Canadian region. Such type of research would allow the people involved in the bivalve industries to better understand the costs associated with this invasion and determine how much of their budget should be spent on mitigation strategies. For example, in Wales, green crabs have been estimated to reduce the production of cultured mussels by 10% in some areas (Murray et al. 2007). If values such as this were reported for the bivalve industries in Atlantic Canada, the development of cost-effective mitigation strategies would be much easier.

The green crab is not the only invasive species creating a concern for the oyster industry. The invasion of the oyster thief (*Codium fragile* ssp. *tomentosoides*) (Garbary et al. 1997) and the recent expansion of the Atlantic oyster drill (*Urosalpinx cinerea*) (PEIDFARD 2006) both represent also threats for the wild harvest and culture of *C. virginica* in the province and elsewhere. The further spread of the green crab into rich oyster grounds poises the question of what type of interactions this species will have with both the oyster thief and the oyster drill. The continued monitoring of these species, the further assessment of their individual and combined roles, and the study and implementation of rapid response initiatives to initial invasions, are all important to effectively minimize future impacts and prepare for future invasions (Locke and Hanson 2009).

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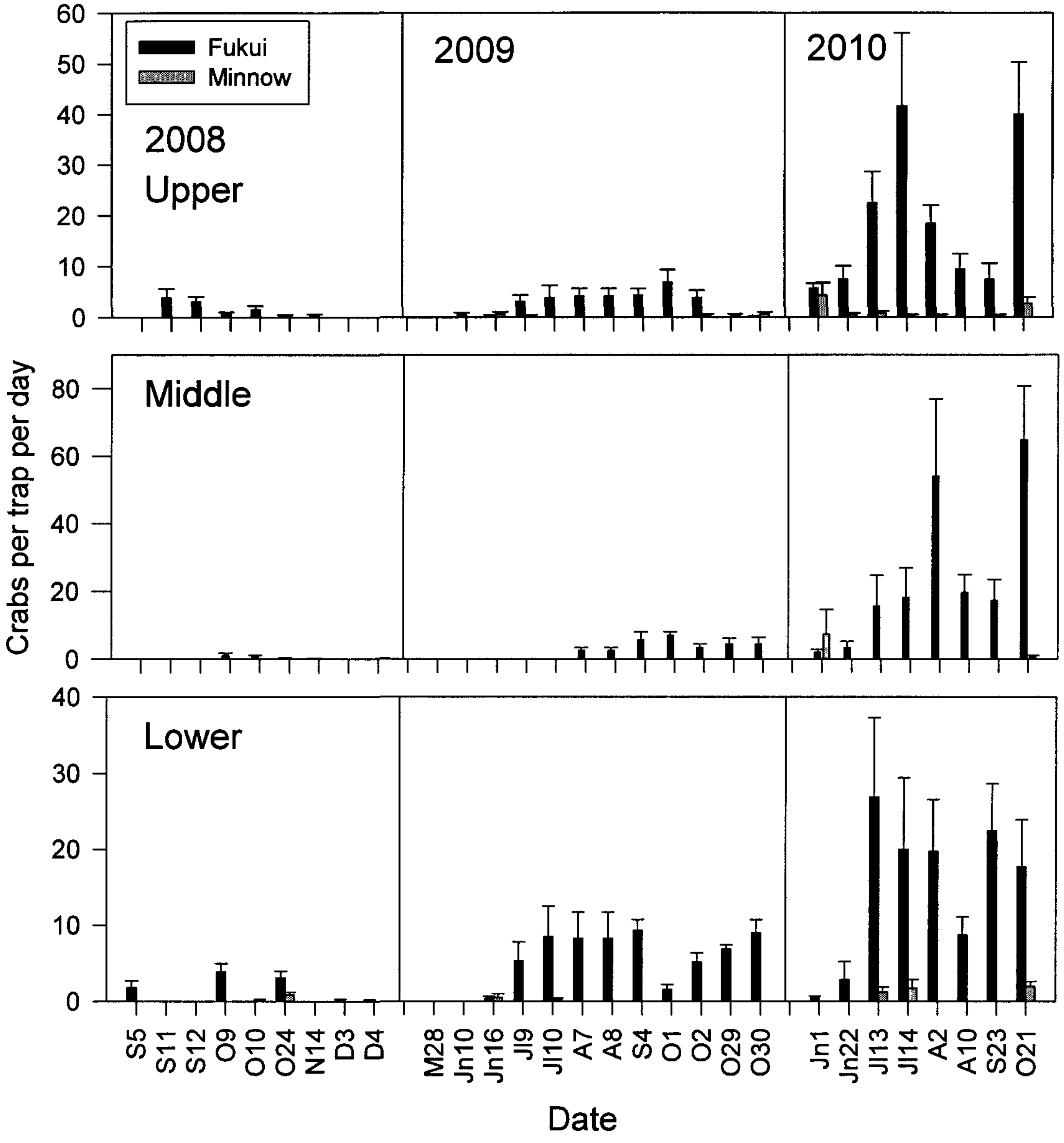
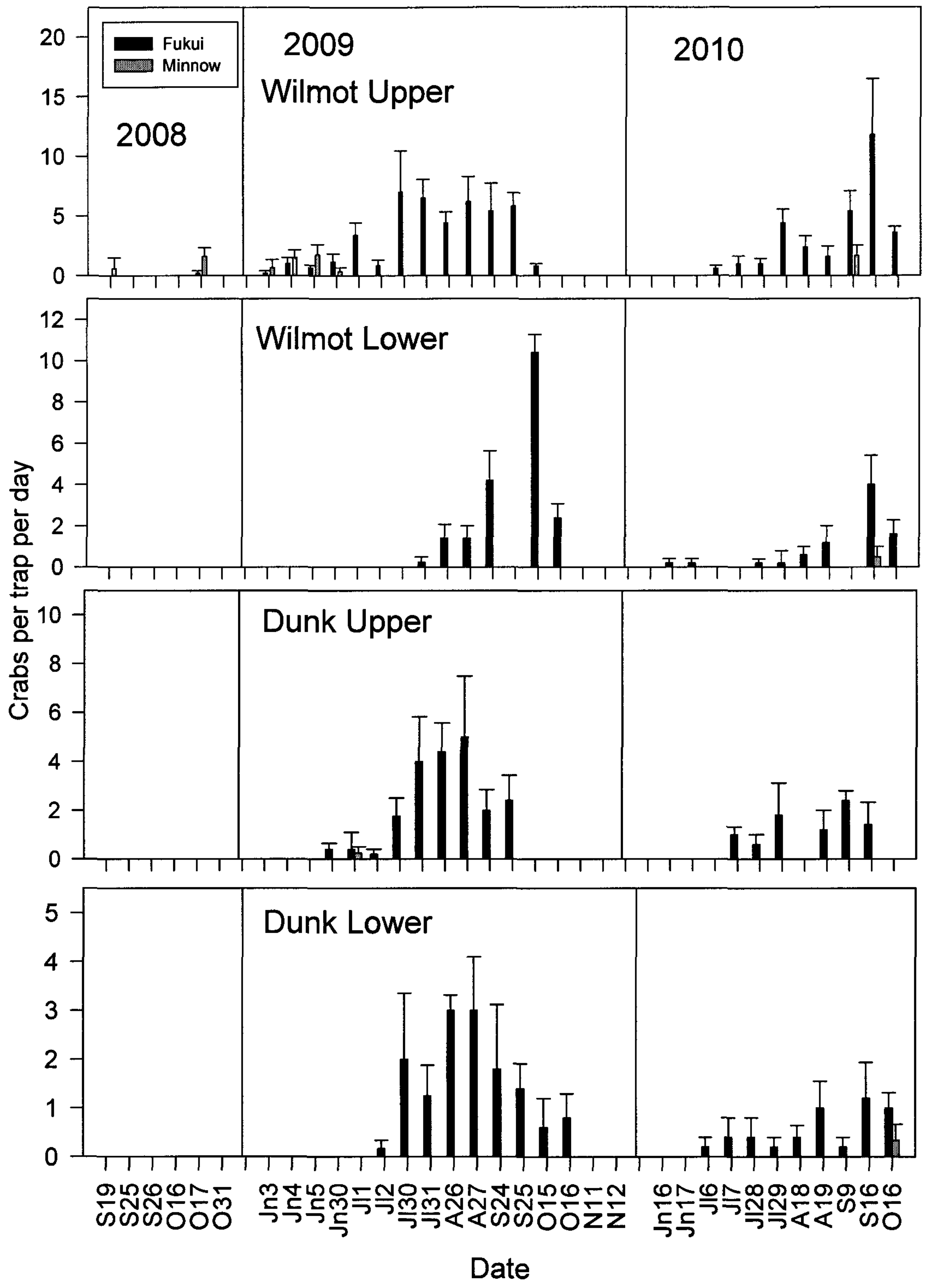
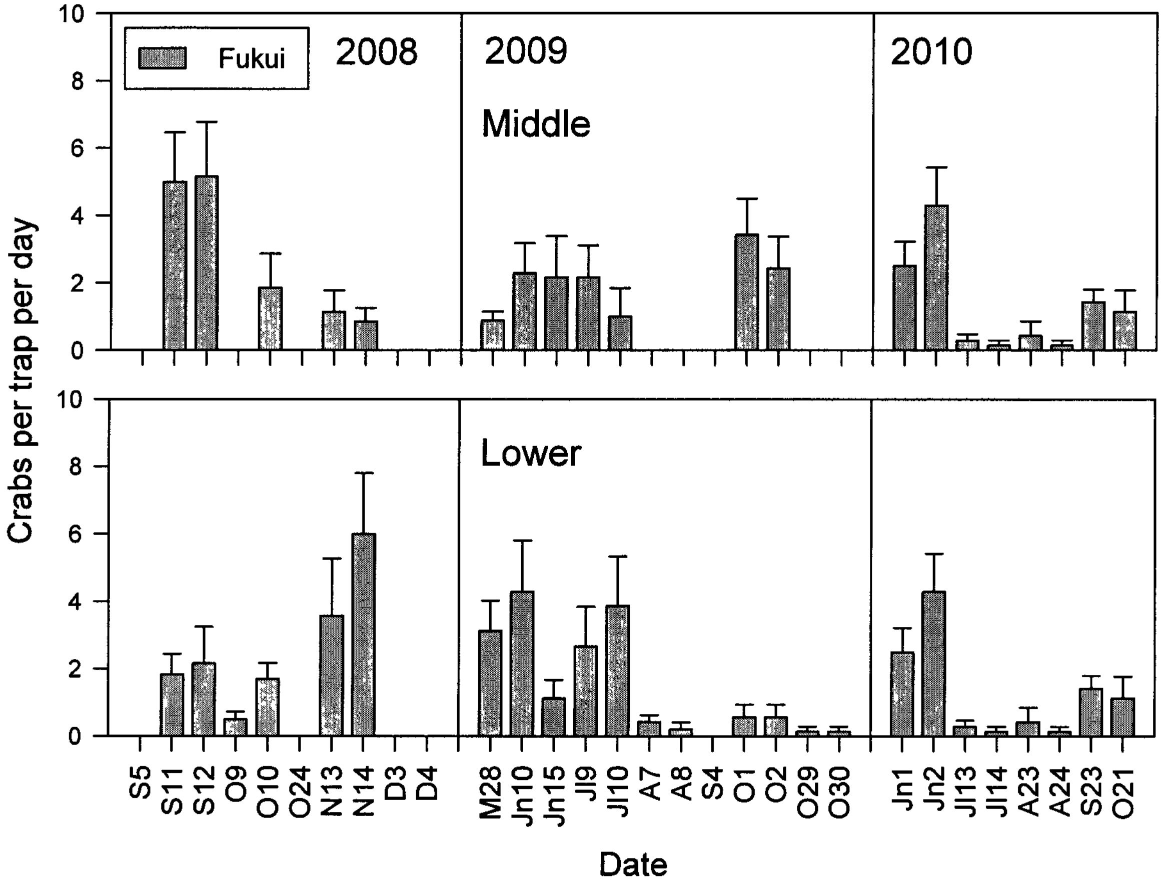
# APPENDIX



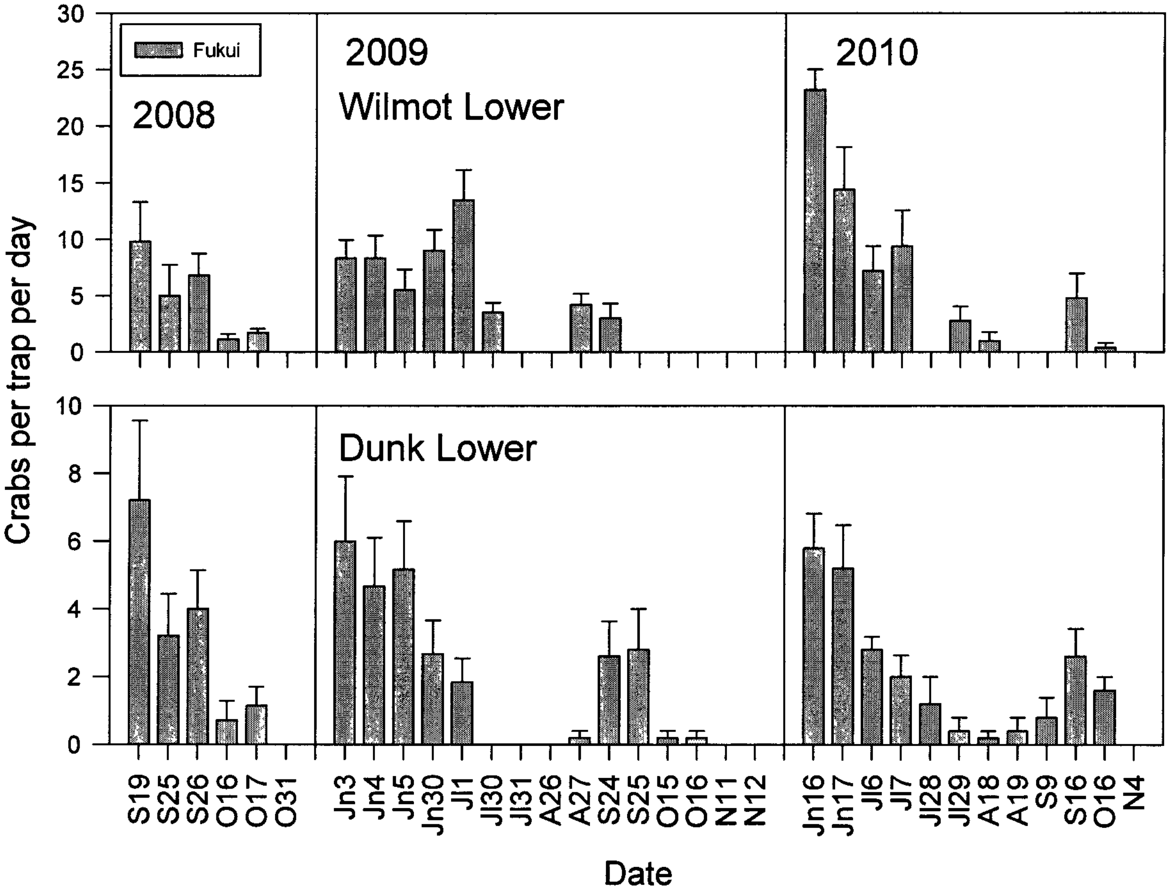
Appendix Fig. 1. Mean (+ SE) trapping abundances of green crabs from Fukui and minnow traps at each site in North River during different sampling dates during 2008, 2009, and 2010. Letters and numbers indicate month and day of the year.



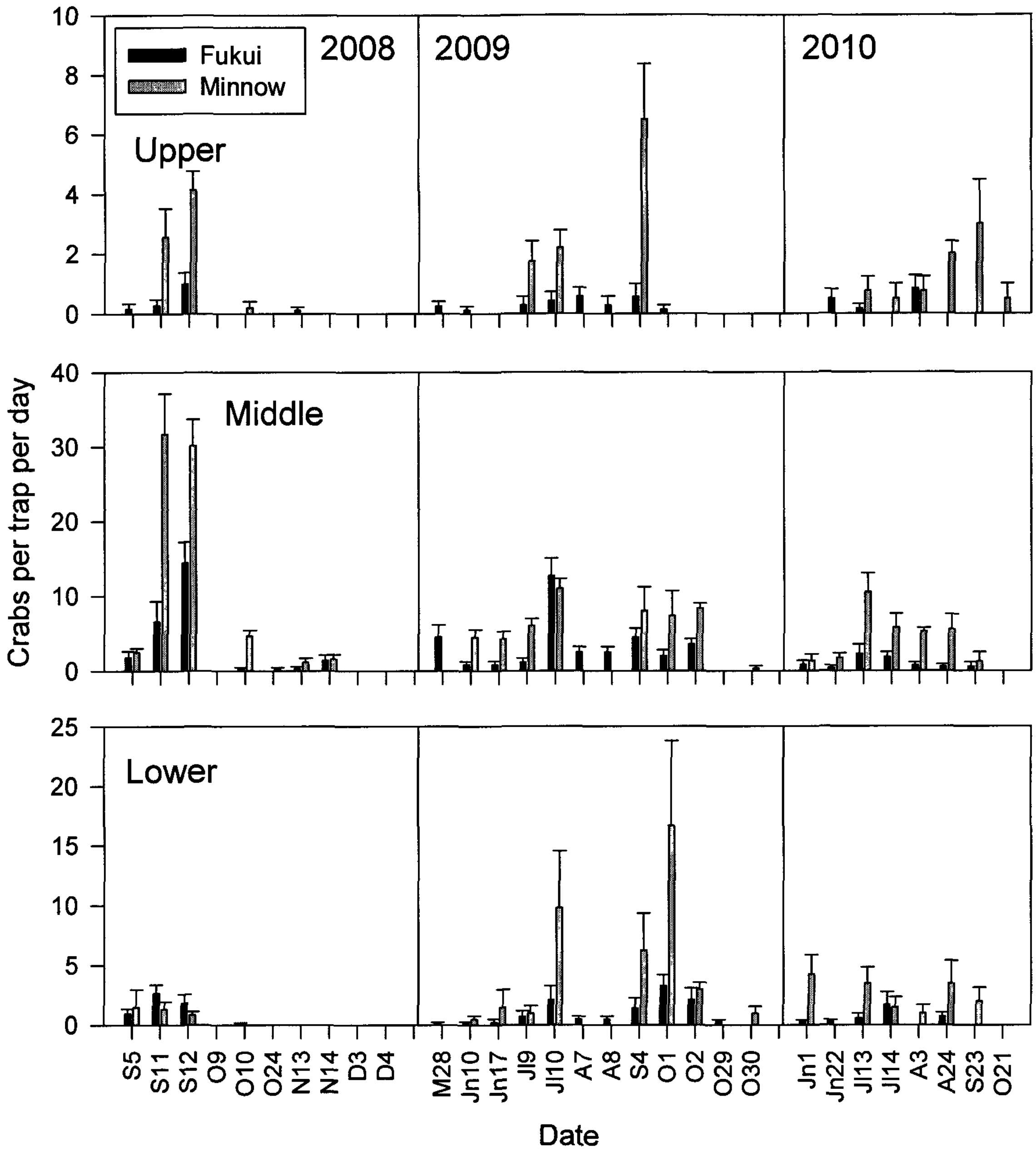
Appendix Fig. 2. Mean (+ SE) trapping abundances of green crabs from Fukui and minnow traps at each site in Bedeque Bay during different sampling dates in 2008, 2009, and 2010. Letters and numbers indicate month and day of the year.



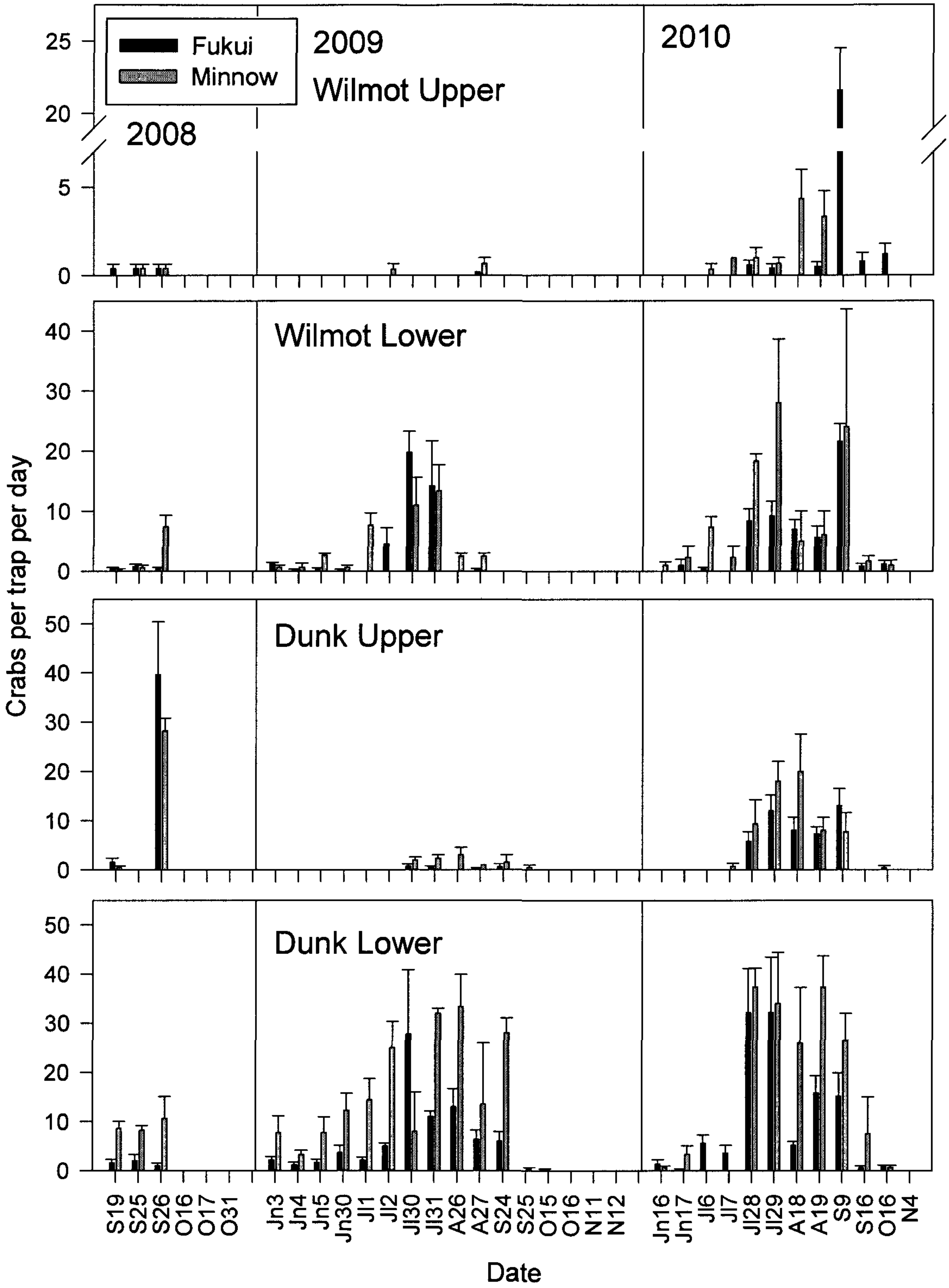
Appendix Fig. 3. Mean (+ SE) trapping abundances of rock crabs from Fukui traps for two sites in North River during different sampling dates in 2008, 2009, and 2010. No rock crabs were caught in minnow traps or at the upper site in any of the years. Letters and numbers indicate month and day of the year.



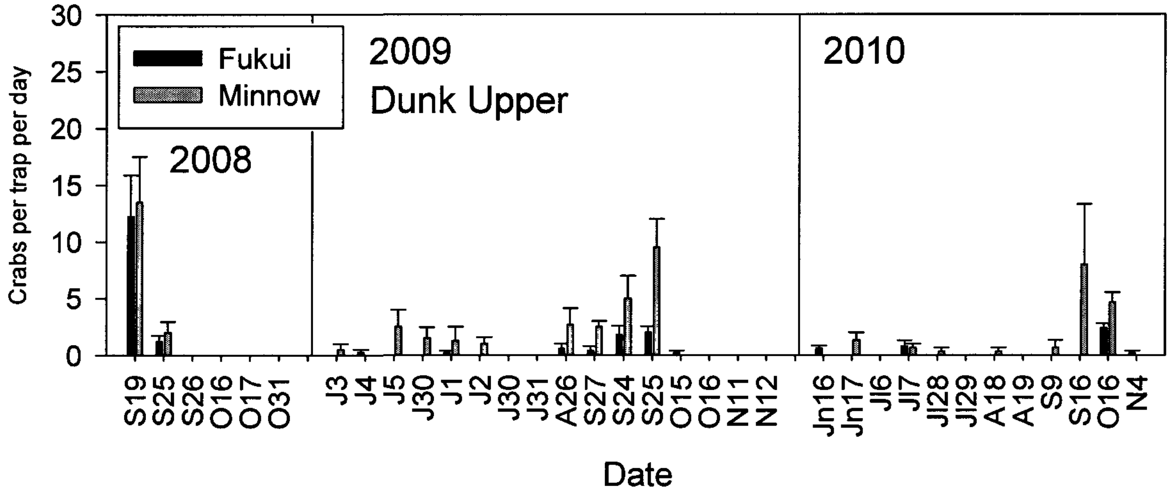
Appendix Fig. 4. Mean (+ SE) trapping abundances of rock crabs from Fukui traps for each site in Bedeque Bay during different sampling dates during 2008, 2009, and 2010. No rock crabs were caught in minnow traps or at the upper sites in the Wilmot and Dunk Rivers in any of the years. Letters and numbers indicate month and day of the year.



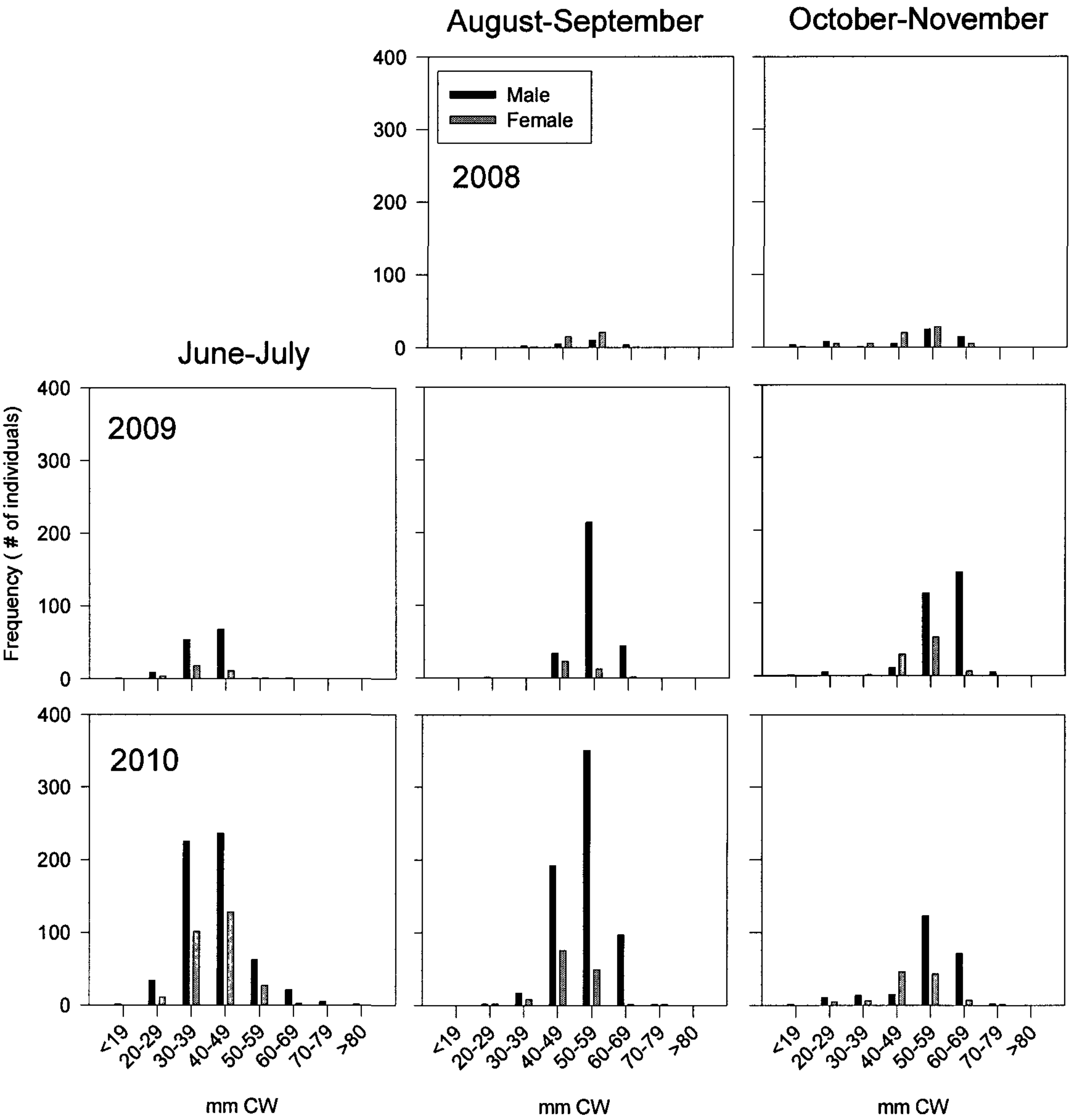
Appendix Fig. 5. Mean (+ SE) trapping abundances of black fingered mud crabs from Fukui and minnow traps at each site in North River during different sampling dates in 2008, 2009, and 2010. Letters and numbers indicate month and day of the year.



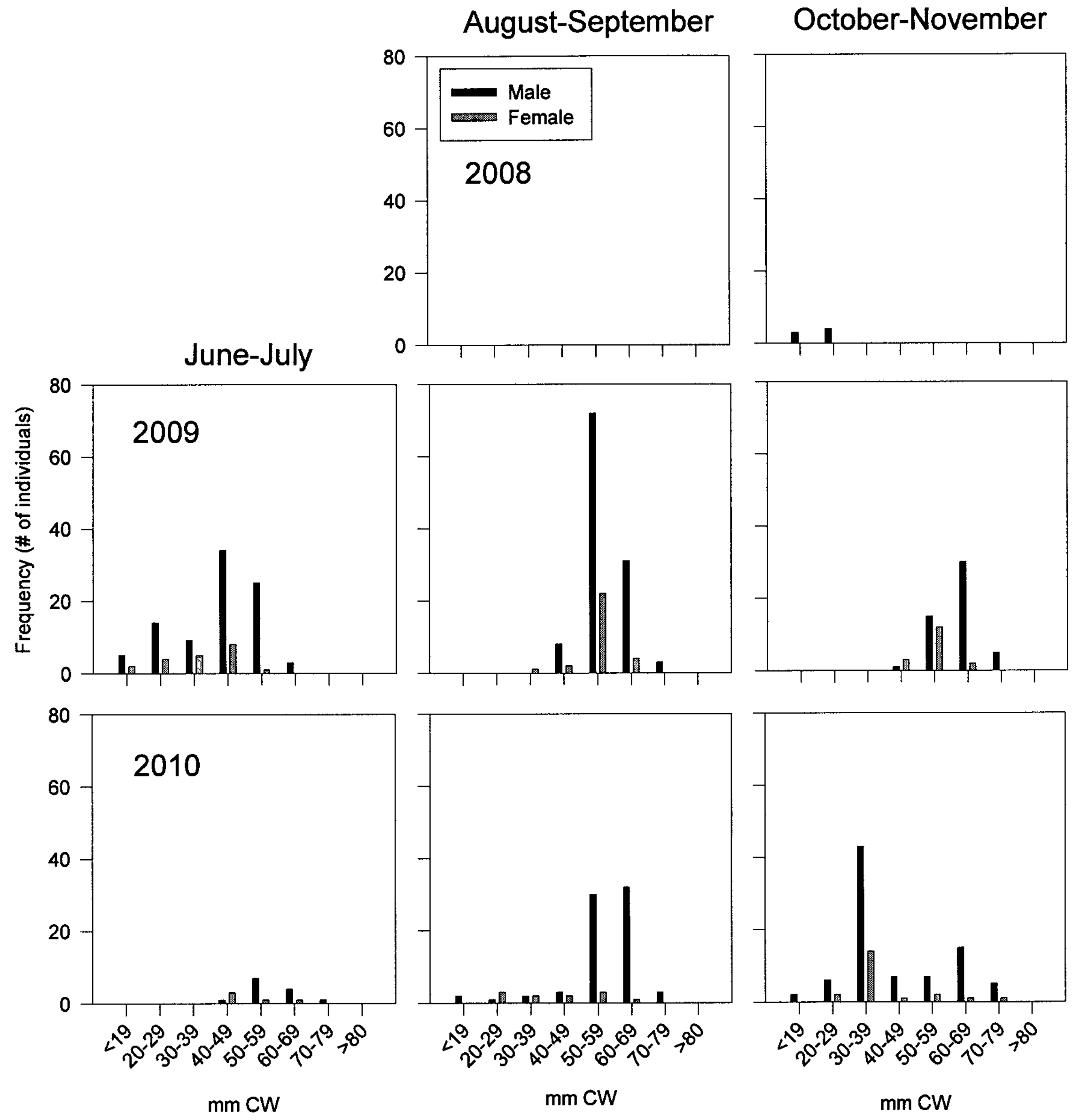
Appendix Fig, 6. Mean (+ SE) trapping abundances of black fingered mud crabs from Fukui and minnow traps at each site in Bedeque Bay during different sampling dates in 2008, 2009, and 2010. Letters and numbers indicate month and day of the year.



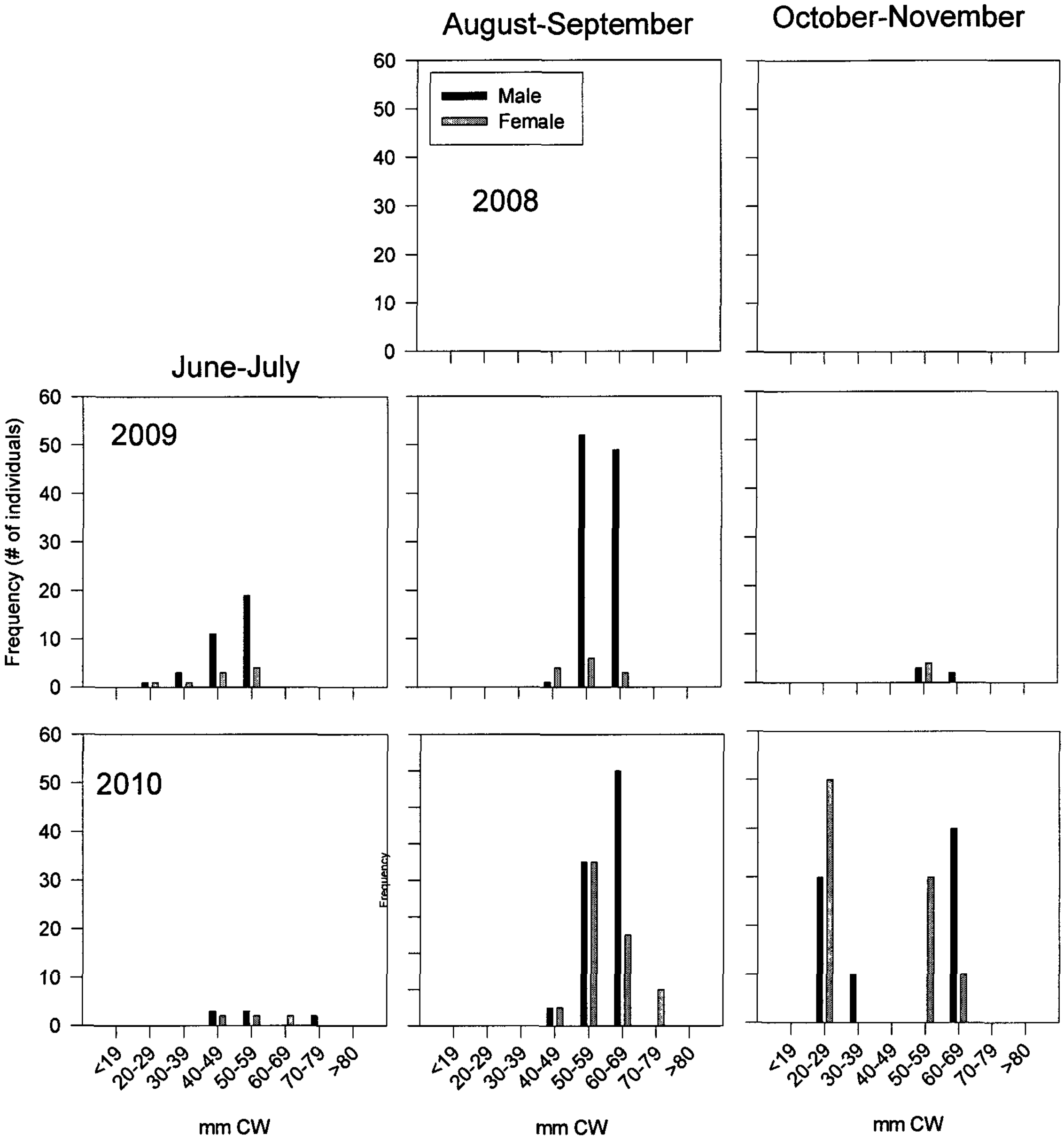
Appendix Fig. 7. Mean (+ SE) trapping abundances of white fingered mud crabs from Fukui and minnow traps at one site in Bedeque Bay during different sampling dates in 2008, 2009, and 2010. White finger mud crabs were not caught at any other site in Bedeque Bay or North River in any of the years. Letters and numbers indicate month and day of the year.



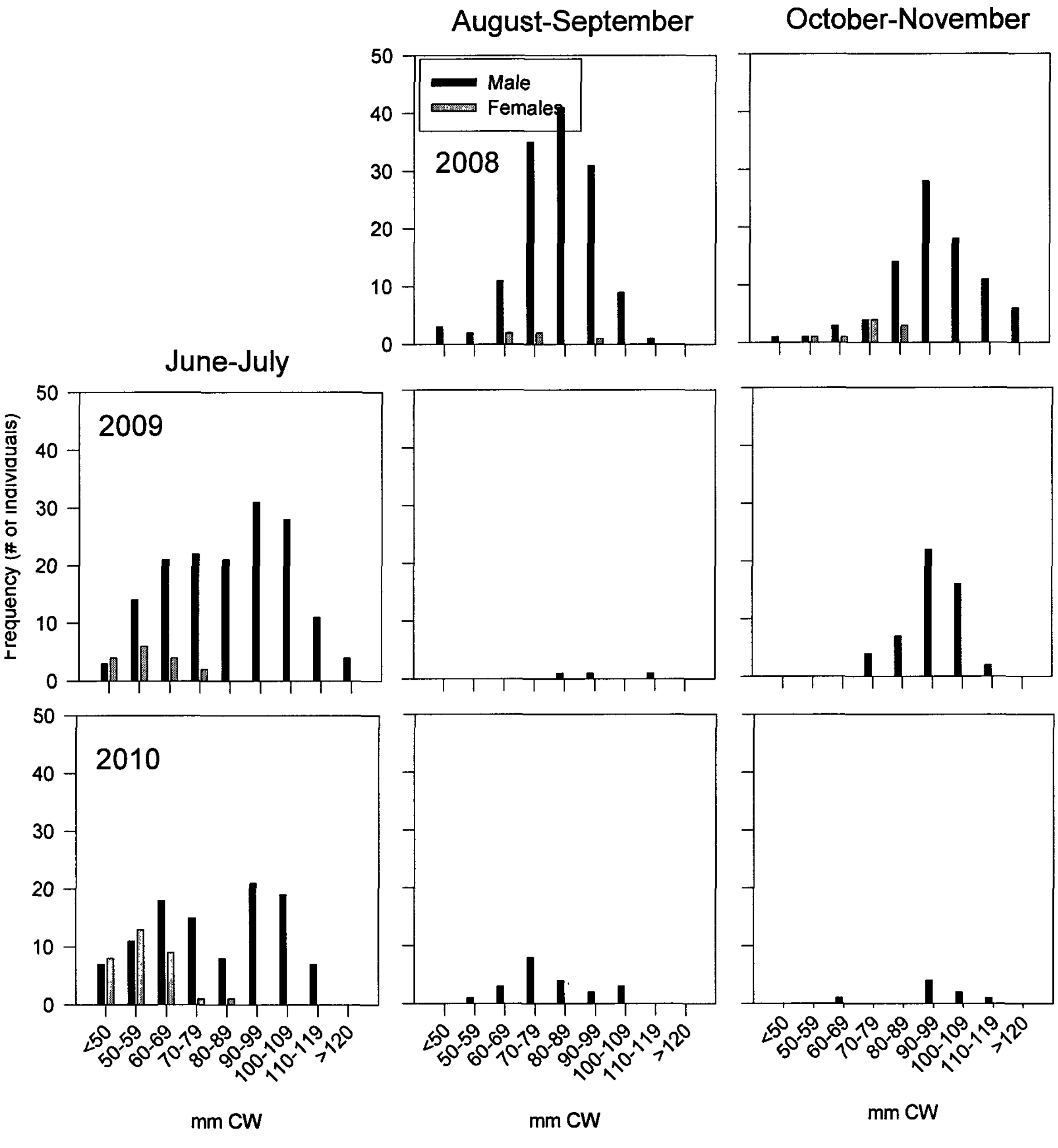
Appendix Fig. 8. Histograms for carapace width of male and female green crabs caught at all sites in North River during different months in 2008, 2009, and 2010.



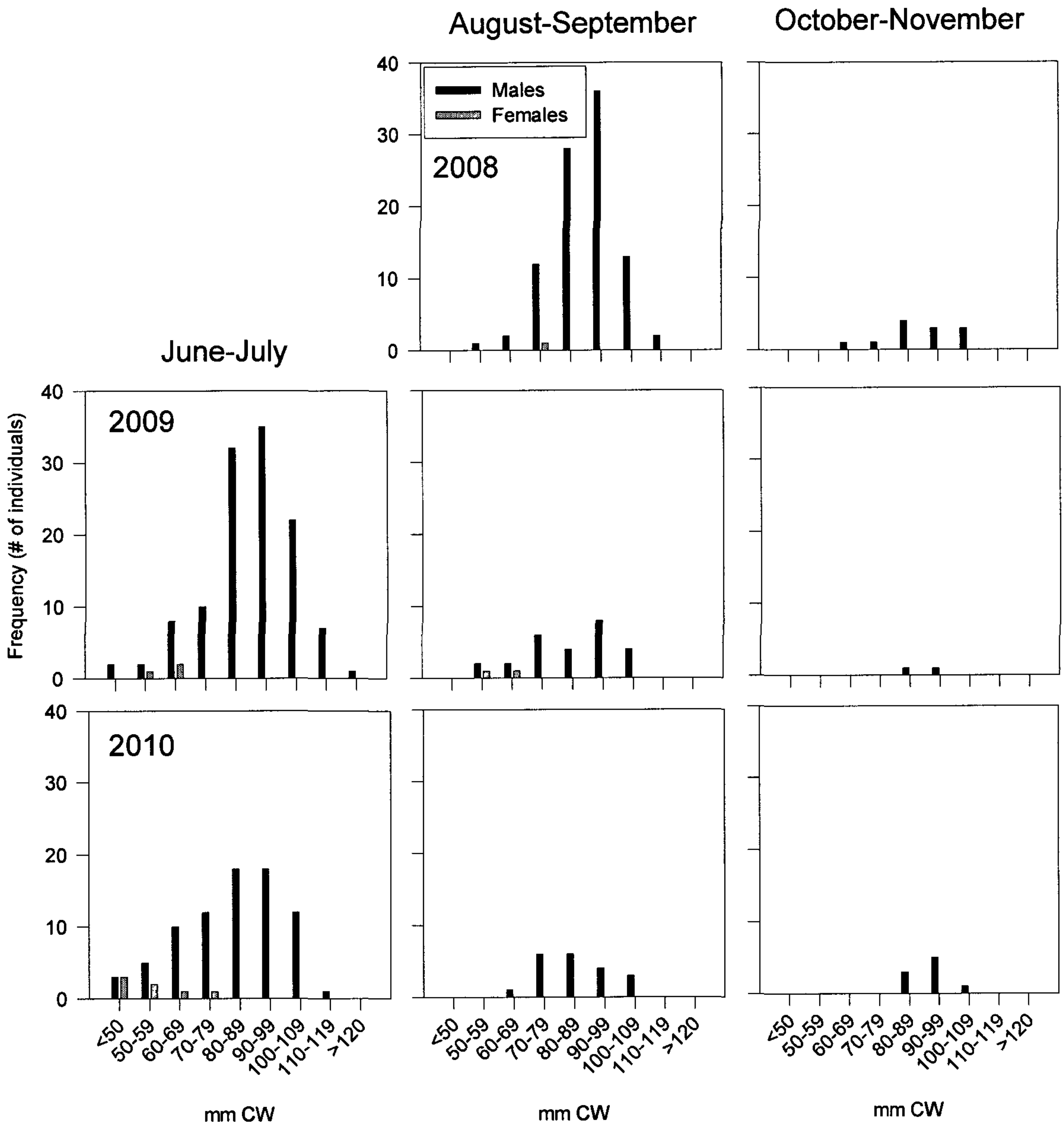
Appendix Fig. 9. Histograms for carapace width of male and female green crabs caught at both sites in Wilmot River, Bedeque Bay during different months in 2008, 2009, and 2010.



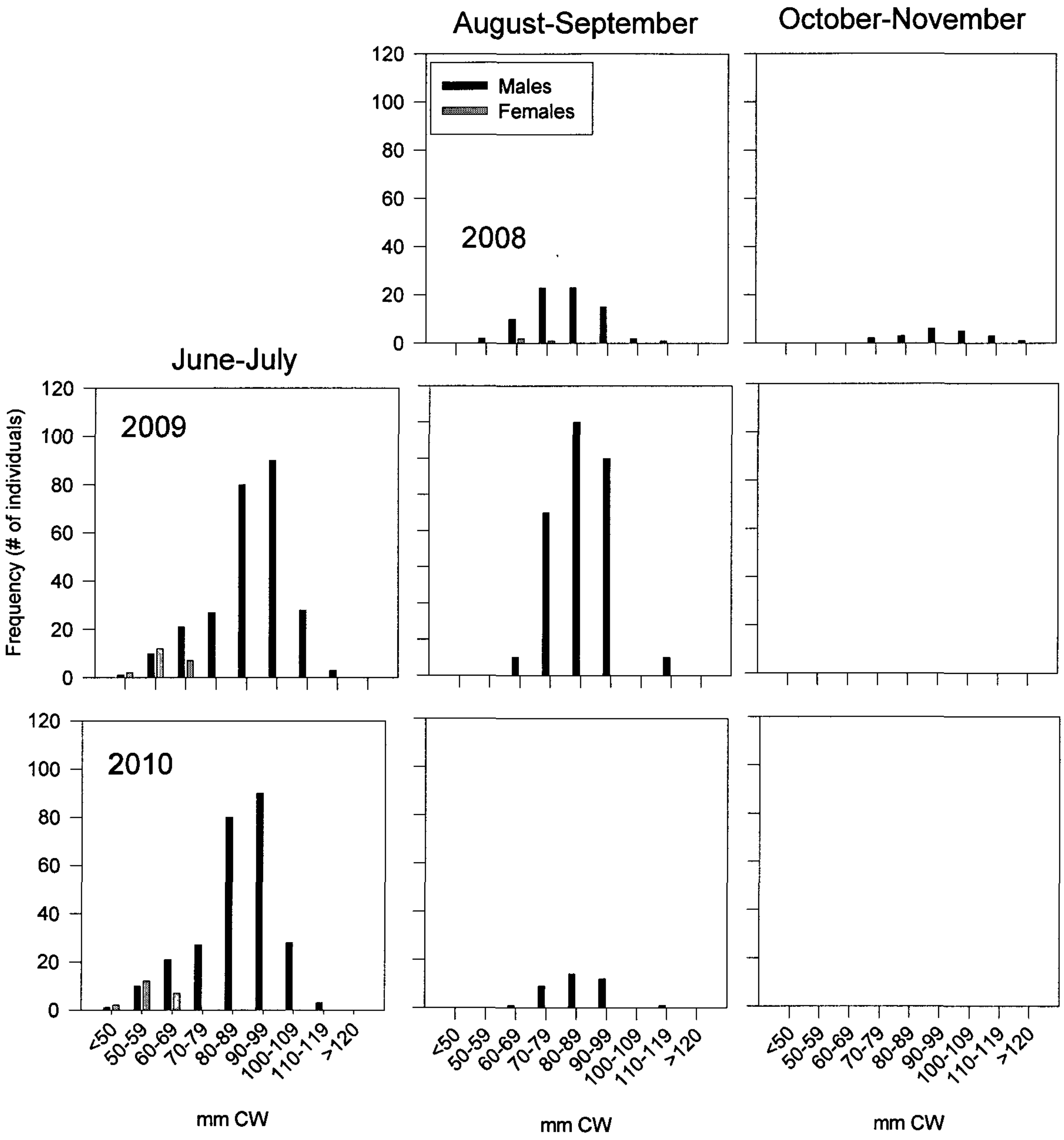
Appendix Fig. 10. Histograms for carapace width of male and female green crabs caught at both sites in Dunk River, Bedeque Bay during different months in 2008, 2009, and 2010.



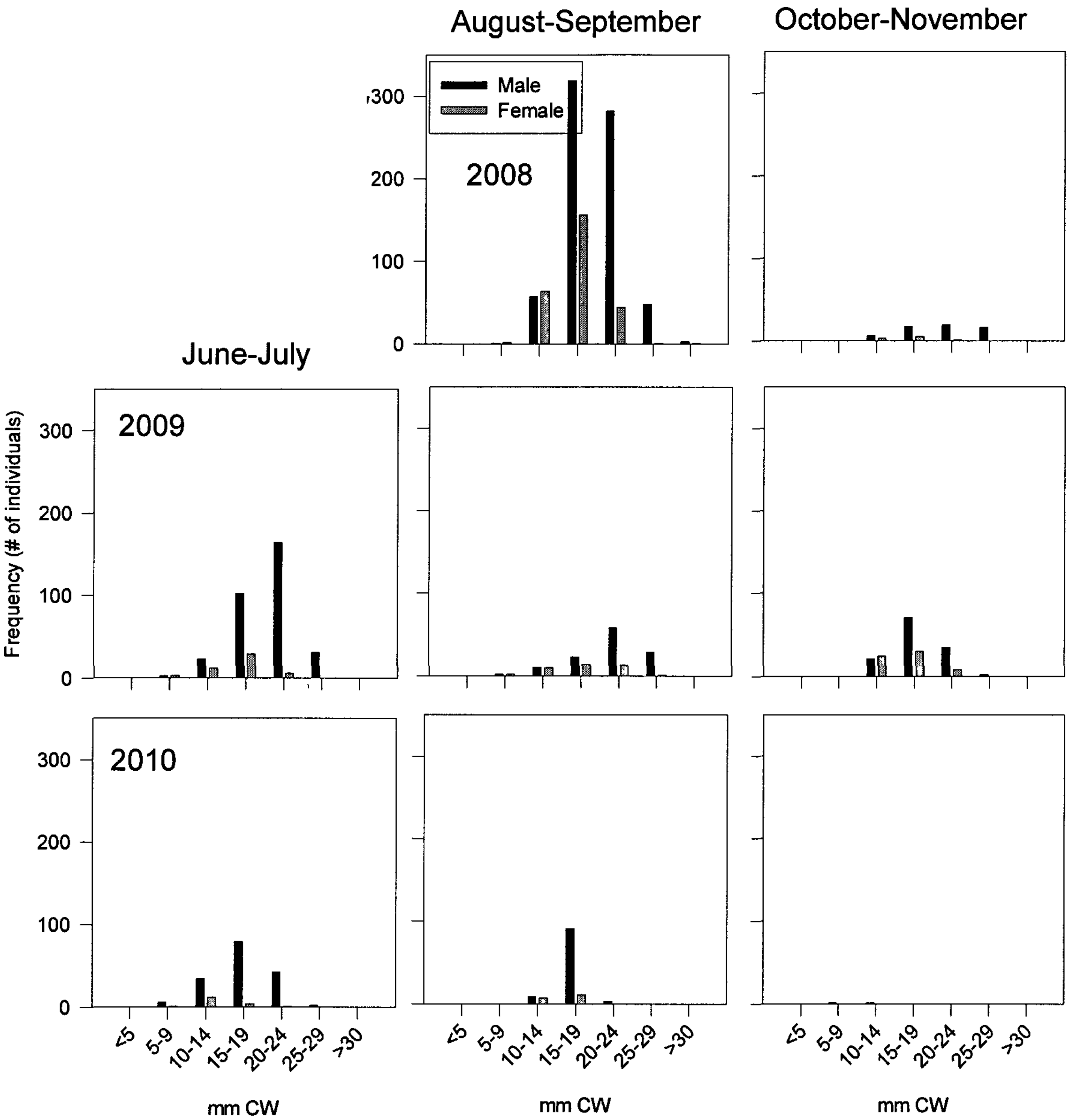
Appendix Fig. 11. Histograms for carapace width of male and female rock grabs caught at all sites in North River during different months in 2008, 2009, and 2010.



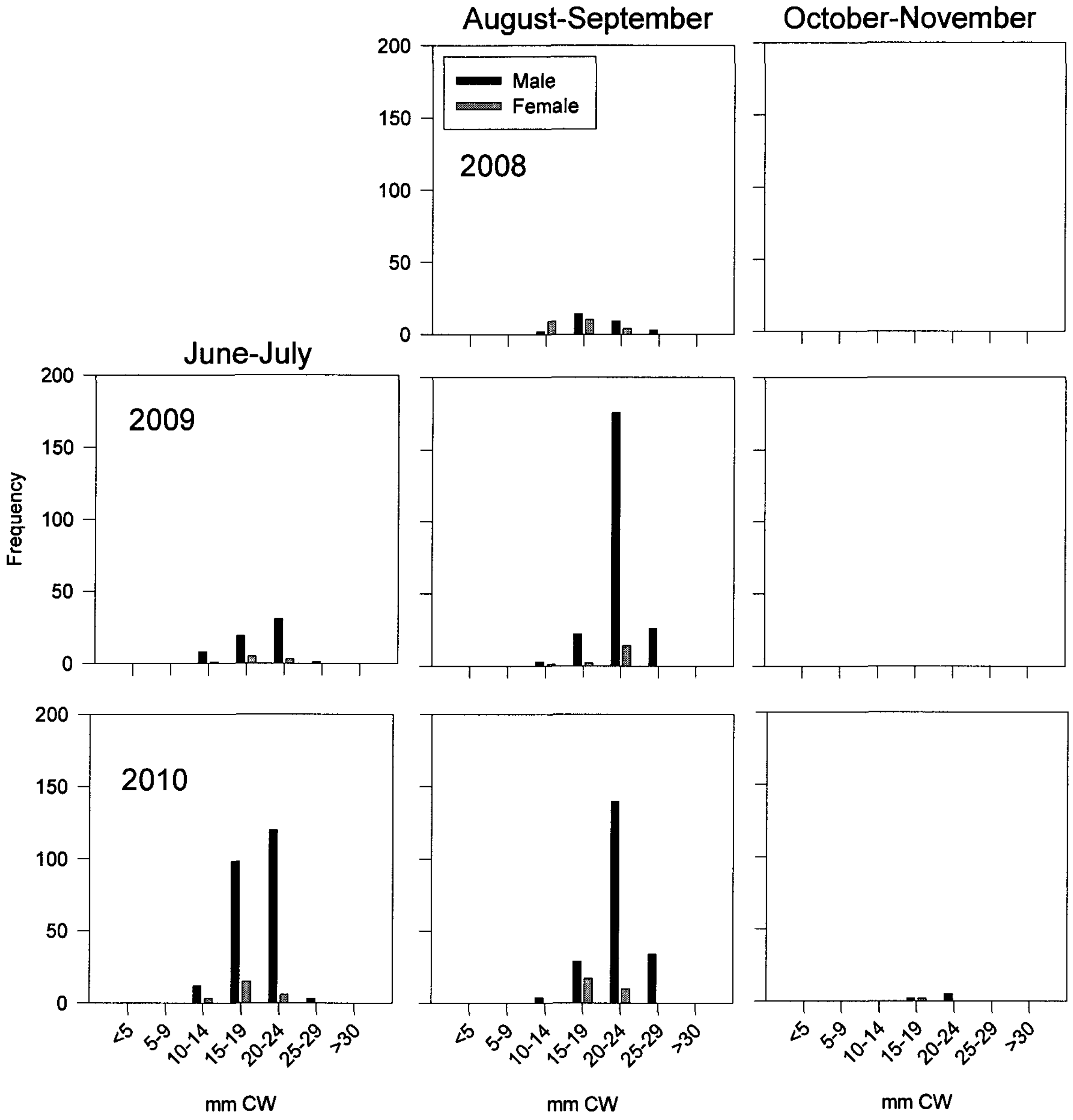
Appendix Fig. 12. Histograms for carapace width of male and female rock grabs caught at both sites in Wilmot River, Bedeque Bay during different months in 2008, 2009, and 2010.



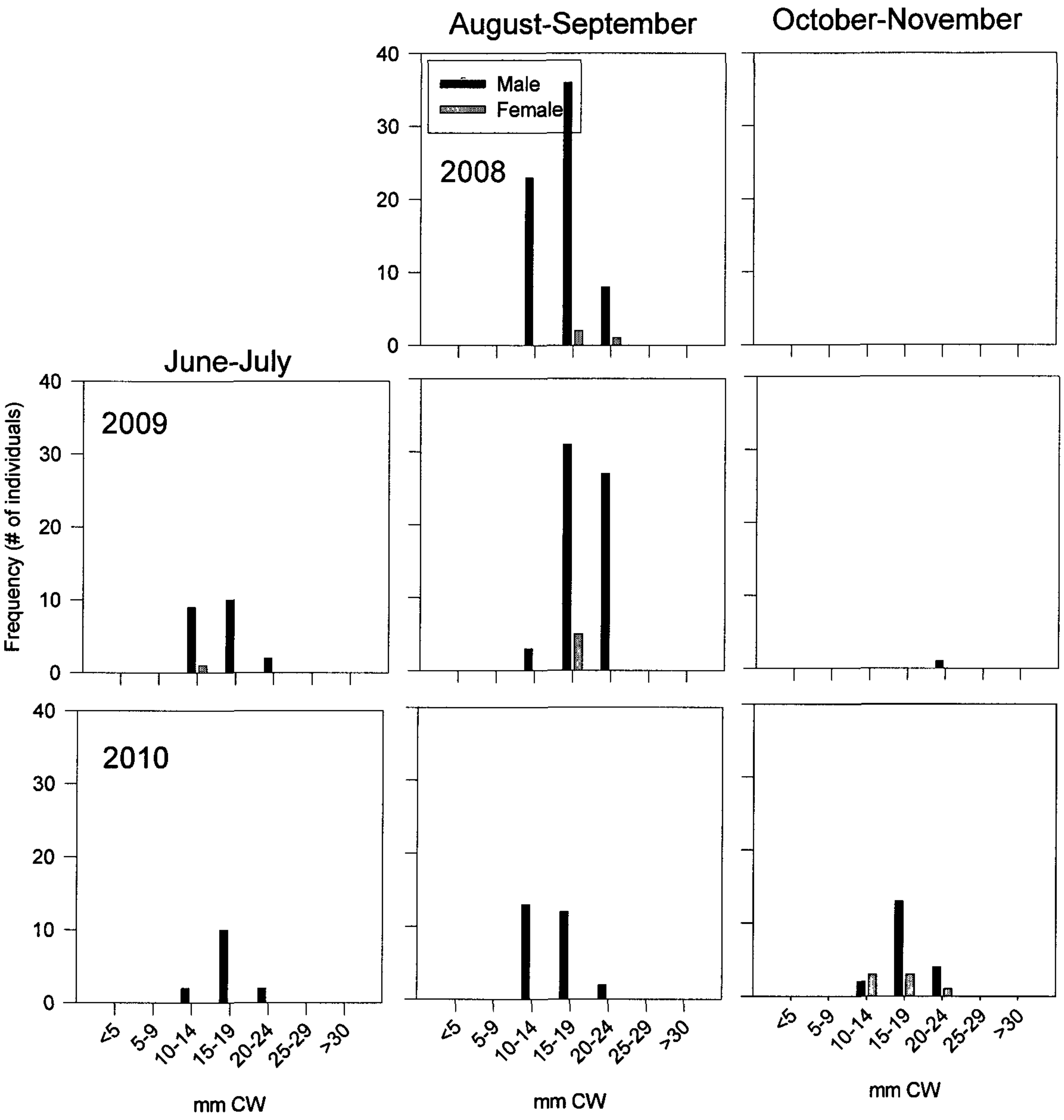
Appendix Fig. 13. Histograms for carapace width of male and female rock grabs caught at both sites in Dunk River, Bedeque Bay during different months in 2008, 2009, and 2010.



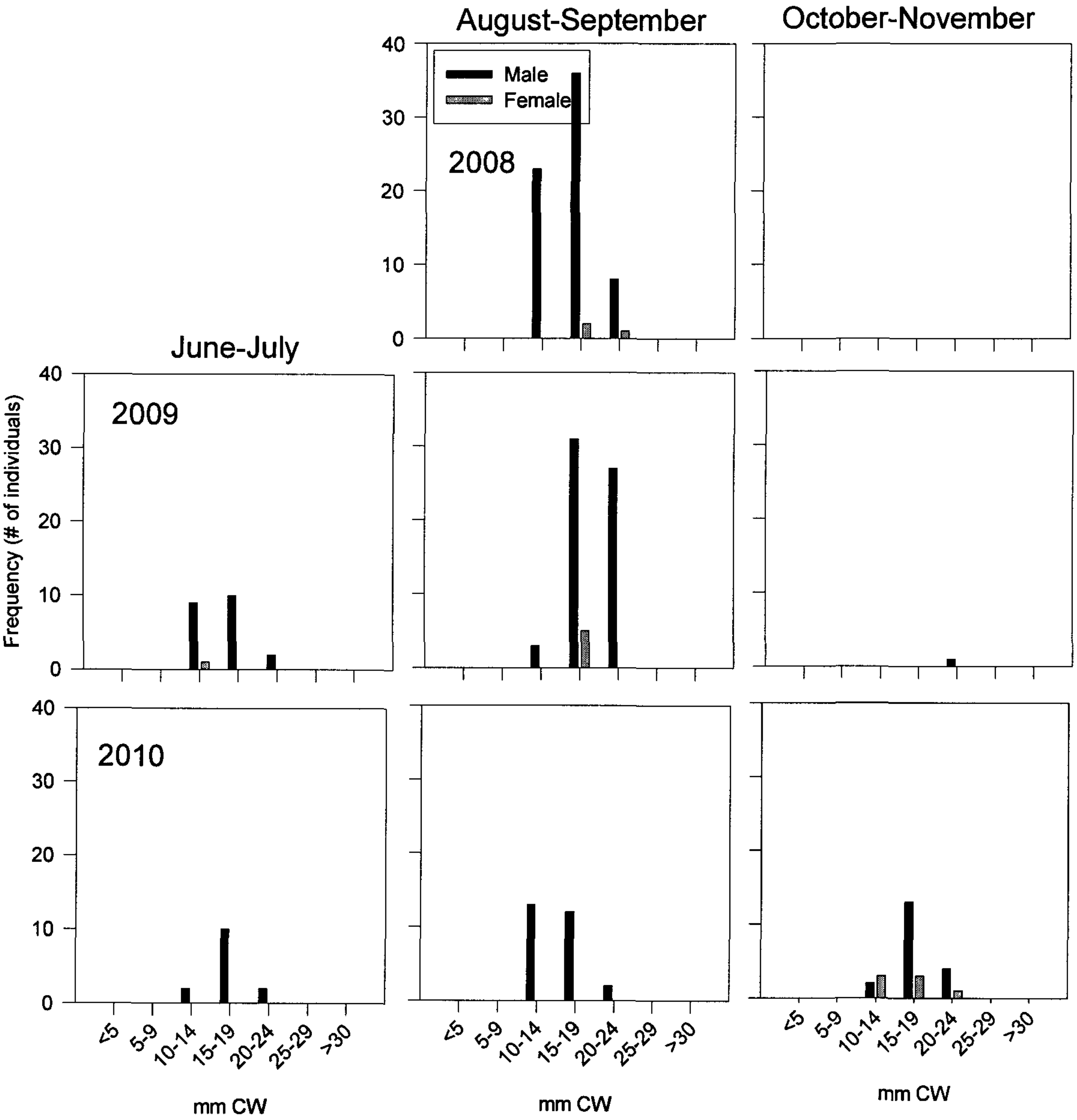
Appendix Fig. 15. Histograms for carapace width of male and female black fingered mud crabs caught at all sites in North River during different months in 2008, 2009, and 2010.



Appendix Fig. 16. Histograms for carapace width of male and female black fingered mud crabs caught at all sites in Wilmot River, Bedeque Bay during different months in 2008, 2009, and 2010.



Appendix Fig. 17. Histograms for carapace width of male and female black fingered mud crabs caught at all sites in Dunk River, Bedeque Bay during different months in 2008, 2009, and 2010.



Appendix Fig. 18. Histograms for carapace width of male and female white fingered mud crabs caught at all sites in Dunk River, Bedeque Bay during different months in 2008, 2009, and 2010. White fingered mud crabs were not caught at any site in North River or Wilmot River.

Appendix Table 1. Minimum and maximum carapace width (mm) for male and female green crabs caught in each sampling month for North, Wilmot, and Dunk River during 2008, 2009, and 2010.

| | | **Minimum and maximum carapace widths (mm CW)** | | | | | |
|---|---|---|---|---|---|---|---|
| | | **North River** | | **Wilmot River** | | **Dunk River** | |
| **Year** | **Month** | **Males** | **Females** | **Males** | **Females** | **Males** | **Females** |
| 2008 | September | 38-63 | 38-61 | - | - | - | - |
| | October | 16-68 | 15-63 | 16-24 | - | - | - |
| | November | 25-62 | 22-22 | - | - | - | - |
| | December | 48 | - | - | - | - | - |
| 2009 | June | 16-34 | 26-33 | 15-42 | 17-42 | 31-38 | - |
| | July | 25-65 | 23-57 | 35-61 | 33-50 | 25-59 | 21-55 |
| | August | 21-66 | 40-54 | 46-70 | 46-60 | 5-65 | 42-64 |
| | September | 43-69 | 41-64 | 50-73 | 32-63 | 50-78 | 46-55 |
| | October | 16-72 | 39-67 | 44-75 | 43-60 | 52-58 | 50-55 |
| | November | - | - | - | - | 61-66 | - |
| 2010 | June | 19-95 | 26-59 | - | 64-64 | - | - |
| | July | 21-76 | 22-66 | 49-73 | 41-54 | 43-70 | 43-61 |
| | August | 30-69 | 27-58 | 38-68 | 35-52 | 46-67 | 42-58 |
| | September | 25-75 | 38-71 | 14-73 | 24-64 | 50-67 | 55-73 |
| | October | 19-73 | 24-70 | 18-77 | 36-74 | 27-68 | 21-61 |
| | November | - | - | 27-64 | 30-32 | 28-29 | 28-29 |

Appendix Table 2. Minimum and maximum carapace width (mm) for male and female rock crabs caught in each sampling month for North, Wilmot, and Dunk River during 2008, 2009, and 2010.

| | | Minimum and maximum carapace width (mm CW) | | | | | |
|---|---|---|---|---|---|---|---|
| | | North River | | Wilmot River | | Dunk River | |
| **Year** | **Month** | **Males** | **Females** | **Males** | **Females** | **Males** | **Females** |
| 2008 | September | 14-108 | 77-90 | 57-119 | 66-70 | 51-67 | 72 |
| | October | 47-120 | 55-86 | 76-122 | - | 67-104 | - |
| | November | 69-141 | 68-72 | - | - | - | - |
| | December | - | - | - | - | - | - |
| 2009 | May | 60-126 | - | | | | |
| | June | 44-120 | 47-54 | 48-114 | 40-60 | 45-121 | 56-62 |
| | July | 46-116 | 44-75 | 55-109 | - | 63-106 | - |
| | August | 85-110 | - | - | - | - | 68 |
| | September | - | - | 67-11 | | 56-109 | 51 |
| | October | 72-116 | - | - | - | - | - |
| | November | - | - | - | - | - | - |
| 2010 | | | | | | | |
| | June | 16-118 | 34-82 | 58-118 | - | 42-109 | 33-64 |
| | July | 48-113 | 48-68 | 53-107 | - | 42-112 | 49-72 |
| | August | 75-83 | - | 65-95 | - | 77-96 | - |
| | September | 51-104 | - | 64-106 | - | 69-104 | - |
| | October | 68-115 | - | 106 | 82 | 84-108 | - |
| | November | - | - | - | - | | |

Appendix Table 3. Minimum and maximum carapace width (mm) for male and female black fingered mud crabs caught in each sampling month for North, Wilmot, and Dunk River during 2008, 2009, and 2010.

| | | **Minimum and maximum carapace width (mm CW)** | | | | | |
|---|---|---|---|---|---|---|---|
| | | **North River** | | **Wilmot River** | | **Dunk River** | |
| **Year** | **Month** | **Males** | **Females** | **Males** | **Females** | **Males** | **Females** |
| 2008 | September | 9-30 | 9-25 | 12-26 | 10-22 | 10-32 | 8-24 |
| | October | 11-24 | 14-17 | - | - | - | - |
| | November | 18-29 | 12-20 | - | - | - | - |
| | December | 24 | - | - | - | - | - |
| 2009 | May | 12-17 | 11-19 | - | - | - | - |
| | June | 10-28 | 13-17 | 12-28 | 11-22 | 7-25 | 11-20 |
| | July | 7-28 | 7-22 | 14-23 | 22 | 12-28 | 13-20 |
| | August | 8-29 | 9-21 | 12-29 | 8-24 | 11-29 | 14-23 |
| | September | 9-29 | 9-26 | 14-23 | 14-15 | 13-24 | 14-20 |
| | October | 12-25 | 11-22 | - | - | 21 | 17 |
| | November | - | - | - | - | - | - |
| 2010 | June | 12-24 | 12-18 | 13-23 | - | 11-20 | 18 |
| | July | 6-26 | 8-20 | 12-27 | 13-23 | 11-27 | 12-22 |
| | August | 13-27 | 13-17 | 16-29 | 17-23 | 14-28 | 12-26 |
| | September | 15-22 | 16-18 | 12-28 | 16-22 | 12-27 | 16-28 |
| | October | 9-11 | - | 18-24 | 16-18 | 14-24 | 18 |
| | November | - | - | - | - | - | - |

Appendix Table 4. Minimum and maximum carapace width (mm) for male and female white fingered mud crabs caught in each sampling month for North River, Wilmot River, and Dunk River during 2008, 2009, and 2010.

| | | **Minimum and maximum carapace width (mm CW)** | | | | | |
|---|---|---|---|---|---|---|---|
| | | **North River** | | **Wilmot River** | | **Dunk River** | |
| **Year** | **Month** | **Males** | **Females** | **Males** | **Females** | **Males** | **Females** |
| 2008 | September | - | - | - | - | 10-24 | 15-22 |
| | October | - | - | - | - | - | - |
| | November | - | - | - | - | - | - |
| | December | - | - | - | - | - | - |
| 2009 | May | | | | | | |
| | June | - | - | - | - | 10-19 | - |
| | July | - | - | - | - | 13-21 | 12 |
| | August | - | - | - | - | 12-21 | - |
| | September | | | | | 13-23 | 17-19 |
| | October | - | - | - | - | - | - |
| | November | - | - | - | - | - | - |
| 2010 | June | - | - | - | - | 15-21 | 14 |
| | July | - | - | - | - | 13-18 | 18 |
| | August | - | - | - | - | 16 | - |
| | September | - | - | - | - | 12-21 | - |
| | October | - | - | - | - | 13-22 | 13-22 |
| | November | - | - | - | - | - | 19 |