The behavioural interactions between the American lobster (*Homarus americanus*) and the invasive green crab (*Carcinus maenas*)

by

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Abstract

The American lobster (*Homarus americanus*) is the most commercially important decapod species in Newfoundland. Since the 1990s, fishery landings in Placentia Bay, Newfoundland have been steadily decreasing. The invasive green crab (*Carcinus maenas*) was first recorded in North Harbour (Placentia Bay) most likely in 2002, and shortly after this, lobster landings decreased by 34% compared to previous years. Analyses of the behavioural interactions between the two species around a food source and a baited trap were used to better understand the potential impacts of green crabs on lobsters in the natural environment. The presence of green crabs (1-25 animals) had no significant effect on the ability of lobsters to acquire food, but they did negatively impact lobster food consumption when present in high numbers (150 crabs). Agonistic interactions between the two species increased with green crab density. Green crabs also significantly affected lobster behaviour around a baited trap; when green crabs were present and could freely move around the trap, a lobster approached, attempted to enter and successfully entered less frequently compared to trials when no crabs were present. Analyses of predator-prey interactions between adult lobsters and green crabs were also used to determine if lobsters from Newfoundland would recognise green crabs as a potential prey item. Lobsters originating from Nova Scotia and Newfoundland actively consumed green crabs of all sizes and the size of the green crab determined the likelihood of being damaged and consumed by a lobster. The longer a green crab remained in the presence of a lobster, the more likely it would be captured and eaten. This research provides information on the potential impact of green crab on the lobster fishery in Newfoundland and Labrador and may be used by stakeholders in the management this fishery.

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Co-authorship Statement

The work described in the present thesis was conducted by Gemma Rayner with guidance from Dr. Iain McGaw. Gemma Rayner was responsible for all laboratory and field data collection. Statistical modelling for chapter 3 was performed by Gemma Rayner with assistance from Dr. Tomas Bird. All chapters were written by Gemma Rayner with intellectual and editorial input by Dr. Iain McGaw, Dr. Patrick Gagnon and Dr. Cynthia McKenzie. Any publication in the primary literature resulting from work in the present thesis and from complementary work not presented will be co-authored by Gemma Rayner and Dr. Iain McGaw.

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1. General Introduction

The fishing industry is a highly important business to the island of Newfoundland, both historically and economically (Schrank, 2005) and the American lobster (*Homarus americanus,* H. Milne Edwards, 1837) fishery is currently one of the most profitable (Boudreau & Worm, 2010). In recent years the overall value of the lobster fishery in Placentia Bay, Newfoundland, has, in part, been decreasing due to a decrease in total annual landings (DFO; Department of Fisheries and Oceans -raw data, pers. comm. Elizabeth Coughlan, 2016). Lobster harvesters (Roy Murphy; Hayward Eddy, lobster harvesters, pers. comm. 2016) and industry members are very concerned that the introduction and spread of the invasive green crab is having a negative impact on the lobster population and may be a factor in the decline in lobster landings. Additionally, the Fish, Food and Allied Workers' Union (FFAW), a labour union that represents 12,000 employees in the fishing industry in Newfoundland, has also expressed concern over the reduction in landings in Placentia Bay which has coincided with the presence of the green crab (FFAW, Jackie Baker, Dwan Street, pers. comm., 2015). Due to the concerns over the potential negative impacts that the green crabs may have on the local lobster populations, this study hopes to identify behavioural interactions between the two species and implications therein.

American lobster biology and life history

The American lobster is found along the east coast of North America ranging from Labrador to South Carolina and occurs from shallow intertidal zones down to depths of 700 m (Aiken & Waddy, 1986). *Homarus americanus* engages in temperature-dependent migrations, often moving offshore into warmer water in the winter months to enhance their rate of growth and reproduction (Aiken & Waddy, 1986; Factor, 2005). They can be found in temperatures ranging from 0-25^{0}C depending on the season and water depth (Camacho et al., 2006). At temperatures below 5^{0}C, metabolism slows down and can inhibit moulting, and temperatures above 25^{0}C are stressful or lethal (Waddy et al., 1995). American lobsters can live for more than 30 years (Lawton & Lavalli, 1995) and growth is achieved through moulting, or ecdysis, which is the loss and removal of an old shell to accommodate a new, larger shell. Moulting usually occurs from late July to early September, or when water temperatures are above 5°C. Lobsters can grow by 10-17% in carapace length and by 30-60% in weight at each subsequent moult (Ennis, 1972).

Importance to the fishing industry

Homarus americanus is very important to the fishing industry in North America; The fishery is one of the most economically viable fisheries due to the relatively low cost of fishing vs. the return of the product (Boudreau & Worm, 2010), with annual landings in Atlantic Canada reaching 74,686 tonnes in 2013 (CAN $680.5 million) (DFO, 2016). In Canada, the fishery has substantial socioeconomic value in rural communities and annual landings had increased in 2013 by more than 11, 000 tonnes since 2011 (DFO, 2013). Fishing zones in Canada are divided into lobster fishing areas (LFAs, Figure 1.1) that vary in opening times, but generally can be categorized into the following; Newfoundland: April-July, Quebec: June-August, Prince Edward Island: April-October, New Brunswick: April-December and Nova Scotia: April-December. In addition to fishing areas, there are also limitations on the number of licenses available, the capture of berried females (egg-carrying), the presence of a v-notch of the telson of a female (large females are v-notched to prevent them being landed by harvesters due to their importance in re-stocking the fishery with larvae), the minimum and maximum landing sizes, the fishing season length and the number of traps permitted (Ennis, 1982; Davis et al., 2006). The minimum landing size of lobsters in Newfoundland is a carapace length (CL) of 82.5 mm, which takes an individual approximately 8-10 years to reach (DFO, 2016). In the USA, the lobster fishery is open all year, but also has restrictions on minimum/ maximum landing size (82.5-171.5mm CL respectively), v-notch possession, the landing of ovigerous females and trap requirements depend on state law (National Oceanic and Atmospheric Administration - NOAA, 2016).

History of the lobster fishery in Newfoundland

In North America lobsters are caught using a baited trap which sits, unattended, for 12-48 hours (Miller, 1990), generally at depths less than 20 m (DFO, 2016). There is great diversity in the types of traps that can be used (Fig. 1.2) and the trap used in the Newfoundland fishery is typically of the “D- shape wooden slat” design. These traps have a twine entry funnel that leads to the colloquially named “kitchen” part of the trap and an additional entrance that leads to the “parlour”. The parlour is the area where bait is stored and where the animals are unable to escape once they have entered (Slack-Smith, 2001). In the 1970s and 1980s the lobster fishery was not heavily utilised in Newfoundland. Landings in 1975 in all LFAs were 1,381 metric tonnes, increasing to 2,921 in 1985 (Fig. 1.3). However, after the cod moratorium in 1992, the lobster fishery was heavily targeted by harvesters (Roy Murphy; Hayward Eddy, lobster harvesters, pers. comm.). Lobster landings in 1992 increased by 50% to total 3,232 tonnes, equal to CAD $21,356,634 landing value (DFO, 2016).

The lobster fishery is now Newfoundland's most profitable decapod fishery and was the landed value generating between $20-30 million per year throughout the 2000s. The fishery across Newfoundland started to show signs of a decline in 2004 as harvests across the island total were only 1,913 tonnes, but followed an increase to 2,613 tonnes in 2005 have generally remained stable over the past decade (DFO, 2016). Although lobster landings in LFA 10 (Placentia Bay) began to decrease in the late 1990's and early to mid 2000's when green crabs were first thought to have invaded Newfoundland (Blakeslee et al., 2010; McKenzie et al., 2010; Matheson et al., 2016), landings dramatically decreased by over 30% from 2006 to 2007, the same year as the first report of European green crab, *Carcinus maenas,* in Newfoundland waters (Klassen & Locke, 2007). Also, during this time scallop dredges became more widespread in the area after the cod moratorium, and the dredges may have destroyed juvenile lobster habitat (Hayward Eddy, lobster harvester, pers. comm.).

<u>Green crab biology and life history</u>

The European green crab (*Carcinus maenas*, Linnaeus, 1758) is a benthic intertidal species native to the Eastern Atlantic, ranging from Norway to Morocco (Williams, 1984). Green crabs are not confined to the intertidal zone and many individuals move up and down the shore, from shallow to deeper depths, with the flood and ebb of the tide. The species migrates annually to warmer, deeper waters (up to 40 m) during the autumn and winter months in their native range (Crothers, 1968).

Green crabs can reach a maximum carapace width of 90-100 mm in their home range, but are generally smaller in Newfoundland, and probably live for 4-7 years (Klassen & Locke, 2007). Body size, however, has been negatively correlated with water temperature, as body size decreases to around 60mm CW at 16^{0}C compared to 80mm+ CW at 9^{0}C in their native and Northwestern Pacific ranges (Kelley et al., 2015).

The green crab is classified as an “invasive species” in North America, and has since been named one of the “top 100 worst invasive alien species” (Lowe et al., 2000). An invasive species is an organism that is introduced into a non-native area through human activity and may alter the community structure through competition, predation, parasitism, habitat alteration and trophic cascades (Mack et al., 2000; Kurle et al., 2008). It was first recorded in the Northern Atlantic in Massachusetts, USA in 1817 (Grosholz & Ruiz, 1996) and in the Bay of Fundy, Canada in 1951 (Audet et al., 2003; Klassen & Locke, 2007). It has also been recorded on the west coast of North America in Oregon and Washington, USA, and in British Columbia, Canada where it has most recently been recorded in the Salish Sea (Behrens Yamada et al., 2017).

Green crabs have proven to be such competent invaders due to their ability to tolerate a range of different environmental conditions such as wide temperature ranges, low salinity and aerial exposure (Simonik & Henry, 2014). Adult green crabs can survive between temperatures of $<0^{0}$C to $>35^{0}$C, but prefer temperatures between 3-26^{0}C (Eriksson & Edlund, 1977; Hidalgo et al., 2005). The requirements for successful egg hatching and larval metamorphosis is limited to temperatures between 9-22.5^{0}C (Broekhuysen, 1936; Dawirs et al., 1986; DeRivera et al., 2006) but in Newfoundland females can begin brooding between 3-18^{0}C (Best et al., 2017).

History and effects of crab invasion to Newfoundland

Green crabs were first recorded in North Harbour, Placentia Bay in 2007, however, the first introduction likely occurred in 2001 or 2002 (Blakeslee et al., 2010; McKenzie et al., 2010; Matheson et al., 2016). Since 2007 the crabs have moved southwards throughout Placentia Bay and been found in Fortune Bay, and on the west coast of Newfoundland (Fig. 1.3). It is widely regarded that the initial mode of transport for green cab invasion to Newfoundland was through domestic ballast water (Grosholz & Ruiz, 2002; Blakeslee et al., 2010). Once introduced into an area, the speed of the invasion has been closely linked to larval dispersal, followed by recruitment rate and adult survival in Atlantic Canada (Gharouni et al., 2015).

Analysis of nuclear and mitochondrial DNA (mtDNA) show that green crab populations in Atlantic Canada (Gulf of St. Lawrence) show little genetic similarity to those in the USA (Gulf of Maine) and most likely represent a separate introduction event (Roman, 2006; Williams et al., 2009; Jeffery et al., 2017). Previous studies initially concluded that green crab populations in the north-eastern region of North America (Gulf of Maine, USA, Nova Scotia, Canada) resulted from range expansion from the south (Audet et al., 2003), however, it was since discovered that these populations originated from two separate invasions from Europe; the first from a very limited number of individuals from Southern Europe, and the second invasion consisted of individuals from a Norwegian population (Roman, 2006). Further, green crab populations in Placentia Bay, Newfoundland, appear intermediate between the northern and southern regions and may originate from two independent invasions (Roman, 2006; Blakeslee et al., 2010; McKenzie et al., 2010; Jeffery et al., 2017). These green crabs show different thermal tolerances between lineages (Tepolt & Somera, 2014) compared to those found in their native range which has likely contributed to their invasion and range expansion success in North America (Roman, 2006). These thermal tolerances may mean that the crabs will tolerate cold water temperatures as they can survive in winter conditions in Newfoundland (Audet et al., 2003).

Green crabs can prey on a large variety of marine organisms from at least 14 phyla (Cohen et al., 1995), including, but not limited to bivalves (*Mytilus edulis*), gastropods (*Littorina sp*.), crustaceans (*Cancer irroratus),* algae and several echinoderm and fish species (League-Pike & Shulman, 2009). Green crabs therefore potentially overlap in diet with that of other taxa and may pose a threat to commercial shellfish fisheries (Mach & Chan, 2013; McClenachan et al., 2015; Pickering et al., 2017). They may also be responsible for regional reductions of eelgrass beds (Matheson et al., 2016), with reports of loss of eelgrass up to 75% in Nova Scotia (Garbary et al., 2014) and up to 80% in Maine, USA in areas with abundant green crab (Neckles, 2015).

In the native range of the green crab there are many natural predators including; molluscs *(Octopus vularis, Eledone cirrhosa, Sepia officinalis)*, fish *(Labrus bergylta, Gadus callarias, Limanda limanda, Pleuronectes platessa* etc.), birds *(Actitis hypoleucos, Alle alle, Larus sp., Phalacrocorax sp.* etc), and mammals *(Halichoerus grybus, Lutra lutra, Phoca vitulina*) making them a very important species in the ecosystem (Crothers, 1968). In Newfoundland, there are potentially fewer predators that can recognise them as prey, or consume the green crabs, which may explain the dramatic increase in populations.

<u>Behavioral interactions between *Homarus sp.* and *Carcinus maenas*</u>

Previous experiments have shown agonistic behaviours between the American lobster and green crabs. Wahle and Steneck (1992) found that green crabs in Maine, USA, would prey on small juvenile lobsters (5-7 mm CL) when lobsters were tethered to the benthos in the field, but also stated that if the lobster was not tethered, there could be potential for them to escape and hide in cobble substrate. Adult green crabs will actively consume juvenile lobsters (28-57 mm CL) *in situ* when they are not in a shelter (Rossong et al., 2006). Interestingly, the larger juvenile lobsters in this study were more frequently consumed by green crabs than the smallest lobsters, which were attributed to the fact that the smaller individuals used the shelters more frequently. Green crabs (14-26 mm CW) will actively consume stage IV lobster larvae in the laboratory (Sigurdson & Rochette, 2013). Lobster larvae survival decreased to 0-20% within 18 hours when exposed to green crabs, compared to 80% survival in the control. After 18 hours, it was noted that no further mortality occurred; this change was attributed to the larvae finding suitable shelter after settling or due to green crab satiation (Sigurdson & Rochette, 2013).

In a follow-up study using small (28-57 mm CL), medium (55-70 mm CL) and large (72-80 mm CL) lobsters in the presence of individual adult male green crabs around a food source, the highest number of agonistic interactions (described here as one animal approaching the other that was in possession of the food, and initiating contact) occurred when initiated by small lobsters on adult green crabs (Williams et al., 2011). These initiations however, had a success rate of only 3% in taking over the bait, in contrast to a 50% chance in large lobsters. They concluded that the first species to possess the food gains a competitive advantage over the other, and green crabs reached the food first more frequently than lobster.

A study on the impact of crab-origin on the outcome of interactions between adult crabs and juvenile lobsters in Nova Scotia (NS) and New Brunswick (NB), Eastern Canada, found that green crabs (50-80 mm CW) were effective predators of lobsters (18-43 mm CL) in a tank environment and that crab origin did influence predation levels (Harr & Rochette, 2012). Crabs from Chedabucto Bay, NS and St. Georges Bay, NS killed more lobsters (67% and 65% survival rate, respectively) than crabs from Passamaquoddy Bay, NB (89% survival). Differences in crab predation on juvenile lobsters associated with geographic origin may reflect the crab's genotype and invasive history, because crabs from different areas may reflect different invasion events (Roman, 2006; Jeffery et al., 2017). For example, Chedabucto Bay and St. George's Bay crabs appear to be more closely related than crabs from Passamaquoddy Bay. This study also quantified agonistic interactions between adult crabs and juvenile lobsters including a) initiation b) threat displays c) physical contact without chelae d) physical contact with chelae e) physical contact with chelae, grasping and f) rapid pursuit of opponent. Agonistic interactions between the species was higher when a food source was present because the intensity of interactions was higher with crabs from Chedabucto Bay and St. George's Bay (physical contact with chelae and grasping) than in Passamaquoddy Bay where the intensity of interactions was lower (approaching, physical contact without chelae) which may reflect a different population response.

Studies conducted by Rossong et al. have also shown that there genetic differences in green crab foraging behaviour based on their origin, as green crabs from Newfoundland dominated a food source over crabs from New Brunswick and Nova

Scotia, whereas there was no difference in foraging between Newfoundland crabs and those from Prince Edward Island (Rossong et al., 2011b).

A study into the behavioural responses of the American lobster to invasive crabs, green crabs and Asian shore crabs *(Hemigrapsus sanguineus),* showed that both species may display aggressive behaviour towards lobsters but green crabs pose more of predation threat than Asian crab, because they consumed over 80% of juvenile lobsters within a 24-hr period (Lord & Dalvano, 2015).

Several experiments have investigated the possible effects of green crab food competition on other crab species, *Hemigrapsus sp*., (Jensen et al., 2002) and *Cancer sp.* (Elner, 1981; Matheson & Gagnon, 2012a; 2012b), and concluded that green crabs can out-compete other crabs for shelters and limited food sources. Experiments on juvenile and sub-adult (28-75 mm carapace length) *Homarus americanus* (Rossong et al., 2006; Williams et al., 2006) showed that green crabs out-competed lobsters to a food source, but were displaced if a sub-adult initiated feeding first.

<u>Lobster and crab interactions around baited traps</u>

Lobsters and crabs can accurately track an odour trail of bait, and catchability therefore generally increases with temperature as activity, appetite, and the rate at which bait molecules diffuse in water increases at warmer temperatures (Morrissy, 1975; Miller, 1990). In addition to the effect of temperature on catch rates, the presence and density of catch in the trap reduces the potential for additional catch in what is known as the "saturation effect" (Miller, 1990), and can be seen when traps have been pre-stocked (Watson & Jury, 2013). *In situ* video analysis on the saturation effect and the behaviour of American lobsters in and around traps showed that baited traps catch only 6% of the lobsters that entered the trap; allowing 94% to escape (Jury et al., 2001). Of the escapees, 72% of them left the trap via the entrance funnel and 28% via the escape gap. One explanation for the low catch rate is aggressive interactions between lobsters in and around the trap. Jury et al. (2001) noted additional competition outside the trap for the opportunity to be the next individual to enter, a pattern reported in other studies; Richards et al. (1983) found that stocking traps with lobsters reduced the catch of lobster by 43-65%, and Addison (1995) reported a 54% reduction. This behaviour has also been noted in crabs, where the presence of large green crabs reduced the catch of small green crabs as smaller conspecifics actively avoided large individuals (Miller & Addison, 1995).

Experiments conducted in the field using stocked baited lobster traps with either *Cancer irroratus*, *Cancer borealis*, or *Homarus americanus* showed significant reduction in the catch of both *Cancer* species when the trap was stocked with lobsters (Richards, 1983), but no significant effect on the catch of lobsters when stocked with crabs. Lobsters also influence green crab catch rates, as shown in a study on the trapping interactions between crabs and lobsters, which concluded that the presence of a lobster in the tank may deter crabs from entering (Miller & Addison, 1995). When lobsters were present, 33% of the total number of green crabs in the experiment entered the parlour-end of the trap, whereas 87% of crabs entered when lobsters were absent.

This study was one of the first to report decreased catchability of green crabs in the presence of lobsters. However, Newfoundland lobster harvesters report a decrease in the presence of lobsters in traps since the arrival of the green crab circa. 2002-2007

(DFO, 2016). The goal of my thesis was to investigate interactions between adult green crabs and adult lobsters.

Thesis objectives

This thesis provides new insight into how the presence of green crabs may affect the behaviour of American lobsters in Newfoundland waters. The objectives are to investigate specifically the effects of green crabs on: (1) behavioural interactions between lobsters and green crabs in laboratory conditions and how this interaction, in turn, affects food acquisition and the catchability of lobsters and (2) whether lobsters prey on green crabs, and whether interactions depend on size of both species.

I formulated the following hypotheses and predications:

> H1. The presence of green crabs affects the behaviour of lobsters in and around a food source and baited traps.

First, I predict that interactions between lobster and green crabs will increase with temperature and crab density, because the animals become more active at higher temperatures and competition for food increases at higher crab densities.

Second, I predict that the presence of freely moving green crabs actively deters lobsters from entering a trap more than when crabs are trapped inside, and that animals will exhibit higher activity at the higher water temperature. In order to test how the position of green crabs in or around a baited trap affects how a lobster behaves around the trap, I investigate the specific behaviours of approaching, attempting to enter, and escaping the trap in a tank environment at different water temperatures (4^{o}C, 12^{o}C). To this end, I positioned crabs: 1) in the trap and unable to escape, 2) outside the trap and able to move freely around the tank and in and out of the trap, or 3) with no crabs in the trial whatsoever.

H2. Green crab density and water temperature affects the amount of food a lobster can obtain.

I predict decreased food consumption as crab density increases as a result of increased interspecific competition around a food source, and increased food consumption at a higher temperature, assuming that animals will be more physically active and digest food faster at warmer temperatures. In order to test my hypotheses, I quantified the amount of food consumed (or, acquired) by an individual lobster in the presence of green crabs, using four different densities of green crabs (0, 1,5, 25) and two water temperatures (4^0C, 12^0C) in a tank environment.

H3. Lobster capture location and size of individual crabs and lobsters influence predation behaviour and impact predation rates on green crabs

I predict that lobsters from Newfoundland (NL) may not recognize or prey less on green crabs, compared with lobsters from Nova Scotia (NS), given the novelty of green crabs as a prey item in NL lobsters and longer exposure in lobster populations originating from NS. I predict reduced damage and consumption of lobster as the size of crabs increases. Through this work I will determine whether green lobsters eat crabs and whether there is a size refuge for green crabs to evade or reduce damage and predation.

H4. Lobster state and habitat complexity alter lobster predation on green crabs

In experiments with lobsters either fed prior to experimental trials or provided with an alternative food source in addition to a potential refuge for crabs to escape predation, I predict that lobsters consume more crabs when starved and when shelter is unavailable for the green crabs. If lobsters have been fed beforehand, or provided with a shelter or alternative food source, I predict low crab mortality.

Benefits to Newfoundland and Communications

The results from the thesis will offer insight on lobster and green crab interactions that may be of interest to the lobster fishing industry, and to federal and provincial governments managing the lobster fishery or undertaking future green crab mitigation projects.

Figures

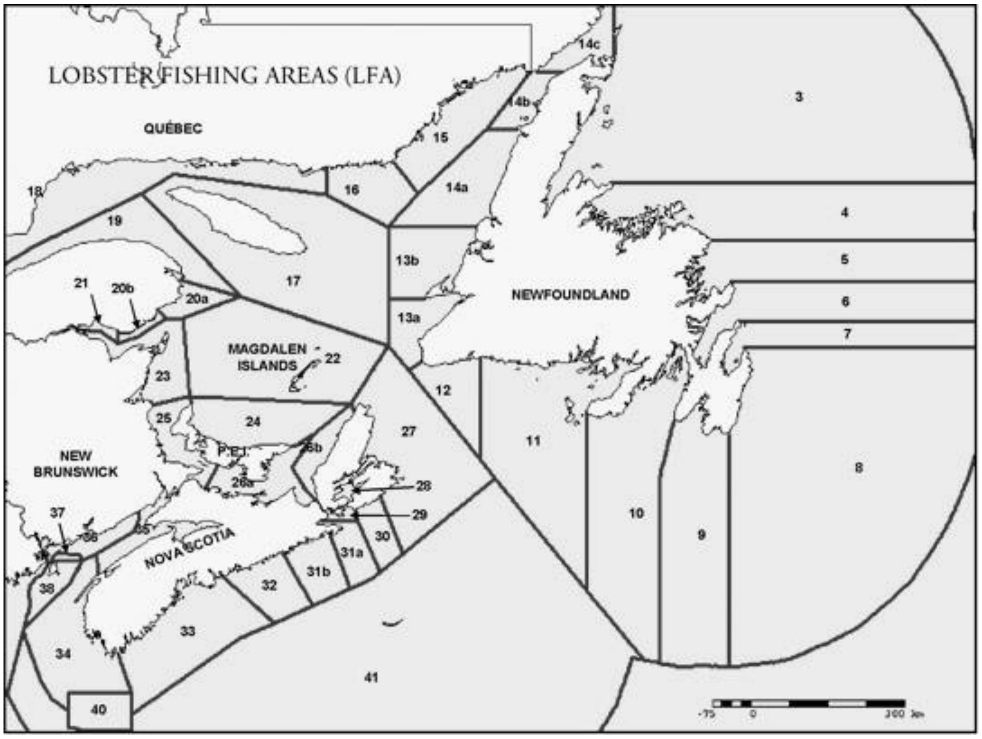

Figure 1.1. Lobster fishing areas in Canada (DFO, 2015).

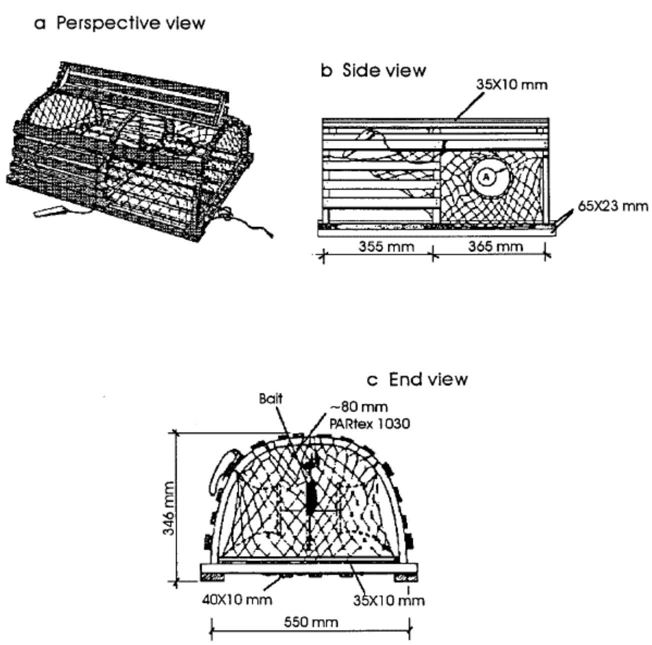

Figure 1.2. Lobster trap design used in the fishery in eastern Canada (reproduced from Slack-Smith, 2001).

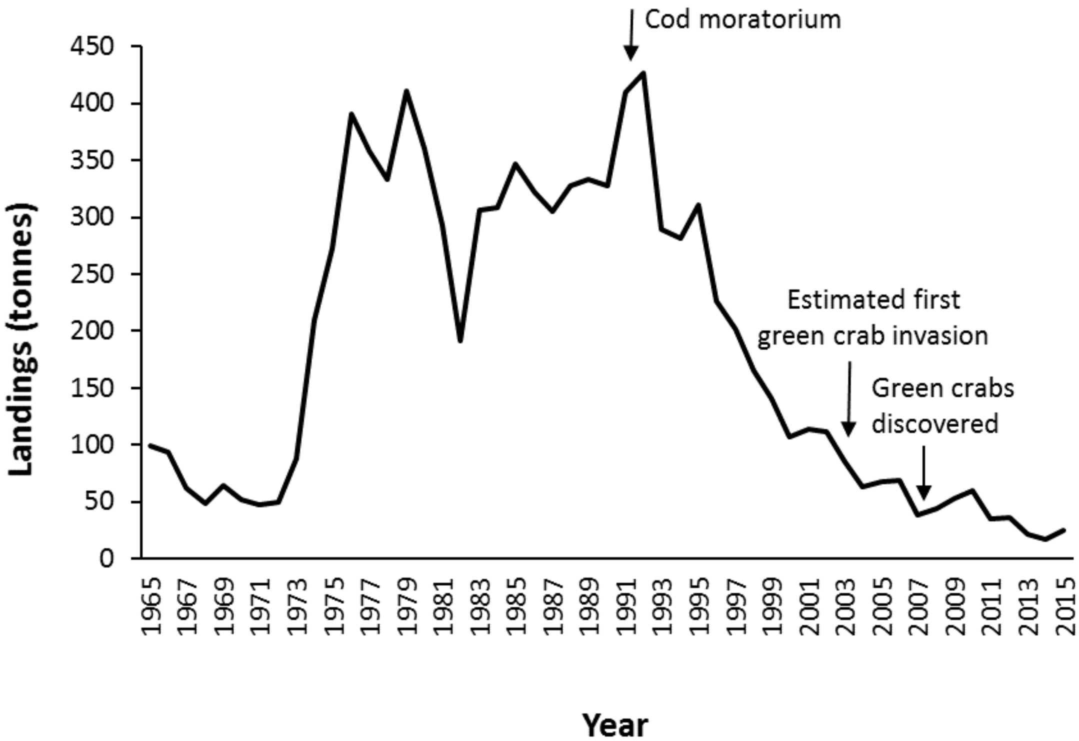

Figure 1.3. Lobster landings in LFA 10 (Placentia Bay) from 1965-2015 showing the general decrease in lobster landings after 1990 cod moratorium, the estimated first invasion of the green crab circa. 2002 and the first recorded sight in 2007 (DFO raw data, pers. comm. Elizabeth Coughlan, 2016).

2. Quantifying behavioural interactions between lobsters and green crabs around a food source and baited trap

2.1 Abstract

The American lobster (*Homarus americanus*) is the most commercially important crustacean species in Canada, however, fishery landings in Placentia Bay, Newfoundland, have decreased steadily since the 1990s, with another noticeable drop in 2002, when the first invasion of the European green crab (*Carcinus maenas*) was likely to have happened. The effect of green crabs on the food consumption and catchability of lobsters was quantified in relation to crab density (n= 0, 1, 5, 25) and water temperature (4^0C, 12^0C). Green crabs consumed more food at the higher temperature because they were more active and out-competed the lobsters for food. Behavioural interactions around the food source were also quantified: as crab density increased the number of agnostic interactions increased at both temperatures. I also investigated the effects of green crabs on the catchability of lobsters around a baited trap, with crabs freely mobile outside the trap or contained within the trap. Lobsters were more likely to approach and enter the trap at 12^0C than at 4^0C, however, they were also more likely to escape. Lobsters were less likely to enter or approach a trap if they interacted with crabs outside the trap. The present results suggest that interactions between green crabs and adult lobsters may influence lobster catch rates in Newfoundland.

2.2 Introduction

The American lobster, *Homarus americanus,* (H. Milne Edwards, 1837) is of high commercial importance (Boudreau & Worm, 2010), and is distributed along the Atlantic coast from Labrador to South Carolina (Aiken & Waddy, 1986). American lobsters can live up to 30 years (Lawton & Lavalli, 1995) and reach weights in excess of 10 kg. They grow through a process called ecdysis, or moulting, where the lobster sheds its old shell and a new, larger shell hardens over the next few weeks (Ennis, 1972). Lobsters are classified as opportunistic omnivores that primarily feed on bottom invertebrates such as crabs, polychaetes, bivalves, echinoderms, as well as seaweeds, but also scavenge on dead fishes (Ennis, 1972).

The lobster fishery represents a multi-billion dollar industry in New England and Canada. In 2013 the fishery landings in Canada exceeded 70,000 tonnes (DFO raw data, pers. comm. Elizabeth Coughlan, 2016). Canada divides the lobster fishery into zones (LFAs) that vary in opening and closure times, and further regulates the fishery through the number of fishing licences issued, the release of ovigerous females, minimum landing sizes, and numbers of traps permitted (Ennis, 1982; Davis et al., 2006).

In the province of Newfoundland and Labrador (NL), Canada, American lobsters are the most commercially important decapod species, generating 2,280 tonnes of lobster worth ~CAD $34 million in 2016 (DFO, 2016). On average, the fishery generates 2,000 tonnes of catch across the island each year, with catches remaining stable between 1,913-2,613 tonnes. However, local harvesters in Placentia Bay (the island of Newfoundland) report a gradual decrease in lobster landings since the cod moratorium in the early 1990s. During this time, lobster stocks in Newfoundland likely came under more pressure as harvesters began to devote more time to the fishery once cod was no longer fished (Davis et al., 2006). In addition, increased scallop trawling in the area may have had significant negative effects on lobsters and the macrofaunal benthic community (Hinz et al., 2009). Harvesters report potential damage or destruction of important nursery habitats for juvenile lobsters by the trawlers (Hayward Eddy, lobster harvester pers. comm.).

Lobster landings in Placentia Bay had been decreasing steadily since 1992, however there was another smaller drop in landings between 2001-2002, which coincide with the likely first invasion of the green crab ((Blakeslee et al., 2010; McKenzie et al., 2010; Matheson et al., 2016: Fig. 1.3). Also, in 2007, lobster landings in Placentia Bay dropped by 34.2% in just one year. This year (2007) notably coincided with the first record of the invasive European green crab *(Carcinus maenas* Linnaeus, 1758*)* in northern areas of Placentia Bay, Newfoundland (Blakeslee et al., 2010; McKenzie et al., 2010). Within a few years of this first sighting, harvesters in Placentia Bay reported high densities of green crab and that crabs were rapidly filling lobster traps and consuming the bait (Roy Murphy, lobster harvester, pers. comm.). The European green crab has been classified as one of the worlds "top 100 worst invasive species" because it can tolerate a wide range of environmental conditions (Lowe et al., 2000). In their natural range, green crabs occur in the shallow subtidal and intertidal zones, migrating shallower and deeper with the tide (Crothers, 1968). Green crabs are opportunistic omnivores and consume a large variety of marine organisms including bivalves, gastropods, echinoderms, other crustaceans, and dead fishes (League-Pike & Shulman, 2009). Green crabs can affect many ecosystems directly and indirectly through increased competition, predation, and through habitat modification (Grozholz & Ruiz, 1996; Matheson et al., 2016) and have been described as ecosystem engineers because of this ability (Crooks, 2002). Green crabs can potentially decimate entire bivalve communities through their predation, and the potential economic loss on bivalve (McClenachan et al., 2015) and crustacean fisheries has been estimated at between $42-109 million in the Gulf of St. Lawrence (Colautti et al., 2006).

Since the first reported sightings in North Harbour, Placentia Bay, green crabs have spread throughout Placentia Bay, and into the neighboring south coast Fortune Bay. They were also reported on the west coast in St. George's Bay (2008) and Bonne Bay by 2010 (DFO, 2016). Although the first record of green crabs in Newfoundland was in 2007, their actual arrival in Newfoundland may have been as early as 2002, (Blakeslee et al., 2010; McKenzie et al., 2010).

Green crabs may pose a threat to native American lobsters because of increased competition for food, noting overlap in diet between the species (Ennis, 1973; Bélair & Miron, 2009). Adult green crabs typically range in size from 50-90 mm carapace width (Grosholz & Ruiz, 1996) and 28-112g ($\bar{x}$ = 61.31g, Gemma Rayner, personal data) and are thus much smaller than adult lobsters, which typically range from 80-90mm carapace length and 445-682g ($\bar{x}$ = 578.25g, Gemma Rayner, personal data). However, despite the size disparity, green crabs (55-75mm CW) dominated the food source 38% of the time in the presence of an adult lobster (72-80mm CL) and consumed the food an equal number of times as the lobsters (Williams et al., 2009). This success suggests that a significant capacity for green crabs to compete with lobsters for a food source. In addition, green crabs enter physical conflicts with conspecifics and other crustacean species (Williams et al., 2006; Rossong et al., 2011a), potentially resulting in aggressive fighting (Sneddon et al., 1997a,b).

Previous studies have also noted the importance of quantifying interspecific crustacean behaviour in and around a trap (Bennett, 1974; Miller, 1990; Addison, 1995; Jury et al., 2001; Watson & Jury, 2013) because behaviour significantly influences catch rates. For example, the presence of adult *H. americanus* inside of a trap reduces the number of *Cancer borealis* individuals entering the kitchen area, and the proportion of individual *Cancer irroratus* that moved from the kitchen to the parlour of a trap was also significantly lower in traps stocked with a lobster (Richards et al., 1983). The presence of large green crabs reduces the catch of smaller green crabs, and traps pre-stocked with *H. americanus* result in markedly reduced green and rock crab catches (Miller & Addison, 1995).

Green crabs in Newfoundland can change fish community structure through foraging effects on eelgrass *(Zostera)* beds. Green crabs can decimate eelgrass beds by damaging rhizomes and plant shoots when burrowing for prey and shelter (Matheson et al., 2016). Eelgrass is an important of nursery and foraging habitat for commercial species such as juvenile Atlantic cod *(Gadus morhua)* (Robichaud & Rose, 2006) and adolescent American lobsters (Short et al., 2001). Other studies attribute the decline in lobster landings to predation on juvenile lobsters (25-51mm CL) by adult green crabs (Rossong et al., 2011a). Nevertheless, to date, links between the appearance of the green crab and the decline of the lobsters remain anecdotal. Most studies pit a single crab against a lobster (Rossong et al., 2006; 2011; Williams et al., 2006; 2009), which is not reflective of their density in the wild. Other studies document interactions between green crabs and juvenile lobsters only (Haarr & Rochette, 2012; Lord & Dalvano, 2015). In addition, temperature strongly influences crustacean behaviour and feeding (Morrissy, 1975; Thomas et al., 2000; Lagerspetz & Vainio, 2006) and previous studies have not addressed this important factor (Rossong et al., 2006; 2011; Willams et al., 2006; 2009). Therefore, the present study aimed to quantify the effects of green crab density and temperature on adult American lobster behaviour around a food source and baited trap (Hypothesis 1) and to determine any potential effects of green crabs on lobster food acquisition (Hypothesis 2) and catchability.

2.3 Materials and methods

Animal collection and housing

Adult male green crabs ranging in size from 50–78mm (carapace width (CW) were collected using baited net traps in Long Harbour, Placentia Bay, Newfoundland (45^0 25’46”N 53^{0}51’30”W). Crabs were transported to the Ocean Sciences Centre, Logy Bay, St. John’s, Newfoundland via road in secure fish boxes and covered with wet towels to prevent desiccation and escape. Only male crabs were kept and females were either destroyed or returned to the same site. Adult lobsters (82-97mm) carapace length (CL) were purchased from Clearwater Ltd (Nova Scotia). The animals were maintained in seawater tanks (31-32ppt) at the Department of Ocean Sciences at Memorial University of Newfoundland. The green crabs were held in a flow-through seawater system and acclimated to temperatures of either 4^{0}C ± 2^{0}C or 12^{0}C ± 2^{0}C. No female crabs were housed, thus preventing reproduction and potential further spread of gametes via the flow-through system. Perforated PVC pipes placed in the tanks acted as shelters and reduced aggressive interactions between conspecifics

Because of space limitations, the lobsters were held in a recirculating seawater system and also acclimated to temperatures of either 4^0C ± 2^0C or 12^0C ± 2^0C. Perforated PVC pipes were also placed in lobster tanks as shelters to reduce aggressive interactions between conspecifics. The lobster tanks were covered with black plastic to reduce horizontal gradients in light levels (Miller & Addison, 1995) and to minimize disturbance to the animals. Both species were acclimated to experimental temperatures for at least three weeks (Camacho et al., 2006) and fed *ad libitum* once per week with mackerel (*Scomber scombrus*). Fasting for 4-8 days prior to experiments allowed the evacuation of all food from the digestive system without inducing a physiological starvation response (Wallace, 1973; McGaw & Whiteley, 2012; Wang et al., 2016a). Individual lobsters were re-used for different treatments and were acclimated for two weeks at the experimental temperature before use.

Experimental protocol

The first series of experiments examined the behavioural interactions between an individual lobster and crabs around a food source as a function of crab density (n= 0, 1, 5, 25) and temperature (4^0C, 12^0C). A total of 15 replicates were conducted at each density-temperature combination. Green crab densities were chosen to reflect densities observed in the field (pers. obs.) and given the experimental tank size. An additional experiment used a density of 150 green crabs at 12^0C (n=10 replicates), a density similar to the average number of green crabs caught in Fukui traps in Placentia Bay over a typical soak time of 12-24 hours (pers. comm. Jonathan Bergshoeff, Memorial University). The temperatures used reflected typical spring (or fall) and summer mean temperatures in shallow coastal areas in southern Newfoundland (Methven & Piatt, 1991; Matheson & Gagnon, 2012b; Colbourne et al., 2016). Each experimental trial was conducted in 3,000 L tanks (1.8m diameter, 40cm water depth) with a seawater flow rate of 6 L/min (Figure 2.1a,b). A video-camera (AXIS, 221 Day and Night Network Camera) mounted above the tank recorded interactions between crabs and a lobster around a food source. All trials were conducted under red light because these wavelengths do not significantly affect crustacean behaviour (Cronin, 1986; Weissburg & Zimmer-Faust, 1994). A black tarpaulin surrounded the entire tank, excluding any other light and minimizing disturbance to the animals (Lawton, 1987).

The animals were offered a prepared meal during each trial: mackerel (*Scomber scombrus.*) fillets were added to seawater and reduced to a puree in a commercial blender. The resultant liquid (75g) was combined with 5g of liquid gelatin and 0.45g of lead glass ballotini beads (125-180µm diameter) (Wang et al., 2016a) and stirred until thoroughly mixed. These radio-opaque inert beads allowed us to X-ray the animals at the end of the experiment to determine whether they fed and to estimate food consumption rate of each animal. A low-intensity fluoroscope (LIXI, WS50 Huntley, IL, USA) provided images of the radio-opaque glass beads in the food. Technical specifications for the LIXI scope were: 22-50kV tube voltage, 10Watt with a 25mm FOV. Five 1g subsamples were taken from the mixture to determine the average number of beads per gram of food. Mean number of beads per 1g sample were calculated from images taken of each subsample. Counts of ballotini beads in the foregut and midgut of each animal were then used to determine the total mass of food consumed in grams (Figure 2.1c,d)

Before initiation of each experiment the lobster and crabs were placed in separate bottomless weighted, perforated buckets (30cm diameter x 37.5cm deep) in the experimental tank for a 15-minute period. The food dish was then added to the opposite side of the tank. The animals remained in the holding buckets for an additional 15 minutes, during which time the scent of the food percolated around the tank. The two buckets were then lifted simultaneously, releasing the lobster and crabs. The behavioural interactions were video-recorded for a total time of three hours. We used a three-hour time period because preliminary trials showed that lobsters stopped feeding and moved away from the food source after this time. At the end of each three hour trial, animals were removed from the tank and X-ray images were taken of the foregut of each individual in order to quantify the amount of food consumed. Experimental tanks were drained and rinsed to ensure any remaining odour plumes were removed through the flow-through system.

Due to limitations in the experimental design, lobsters were used more than once in the study. However, after use, lobsters were starved and left to acclimate to the experimental condition that they were used in. This acclimation period is used to “erase” seasonality as much as possible. Other studies on the agonistic interactions between green crabs and American lobsters have also re-used experimental lobsters (Williams et al., 2009), and waited two weeks before using them again as “this period is sufficient for lobsters to lose the ability to chemically recognise an individual”. Other studies have also re-used animals in the same experiment such as Rossong et al. (2011) who re-used green crabs in behaviour experiments.

The video recordings were analysed to determine a) the time for the lobster and first crab to approach food source (touch the food dish), b) the time for the lobster and the first crab to first handle food (initiate feeding) and c) the total time a lobster spent feeding. Feeding time for lobsters was only counted if each event lasted ≥10 seconds to omit events where the lobster walked over the food source. For the trials using a density of 150 crabs, we also quantified the time taken for crabs to consume the whole food source. The behavioural interactions between lobsters and crabs were quantified by adapting a protocol from Huber & Kravitz (1995): a) number of interspecific retreats (the animal actively moves or turns away from the opponent) b) number of interspecific body raises (the body of the animal is raised high above the substratum, to fully extend the walking legs) c) number of interspecific claw raises (one or both claws above the horizontal and are extended laterally) d) number of claw grasps (animal uses one or both claws to grasp onto the appendage of the opponent). We selected these specific behaviours because they have been quantified in other studies, and document an obvious pattern of increasing intensity during confrontations, starting with an energetically inexpensive response (a retreat) and intensifying to displays at first contact, ritualised aggression and restrained claw use (body and claw raises), following by and ending with, a brief period of unrestrained combat (claw grasps) (Huber & Kravitz, 1995). Further, lobsters and other decapod crustaceans exhibit these behaviours (Scrivener, 1971), noting that decapods can “assess” an opponent via a meral spread (Huber & Kravtiz, 1995), i.e. the first individual will elevate its body and claws when in the presence of another as it recognises the second individual as a threat.

Statistical analysis

We used two-way ANOVAs to determine the effects of crab density (n=0,1,5,25) and water temperature (4 & 12^{0}C) on the amount of food consumed, the first approach time to the food source by lobsters and green crabs, and the total food handling time (sum of all food handling periods) in lobsters. Significance was based on a $p<0.01$ level; a Bonferroni-corrected significance level (Rossong et al., 2011). Post hoc Tukey (HSD) tests compared between groups where we found significant differences between factors. We used model residuals to test for normality (chi-square goodness of fit) and homoscedasticity (Levene) of all parametric tests that were conducted. In the majority of cases the assumptions were upheld ($p>0.05$) however where they were violated (tests on the number of retreats, body raises, claw raises, and claw grasps in lobsters and green crabs), caution is noted when interpreting the results based on the p-value <0.01 (Haarr & Rochette, 2012). Analyses were conducted in SPSS v. 23.

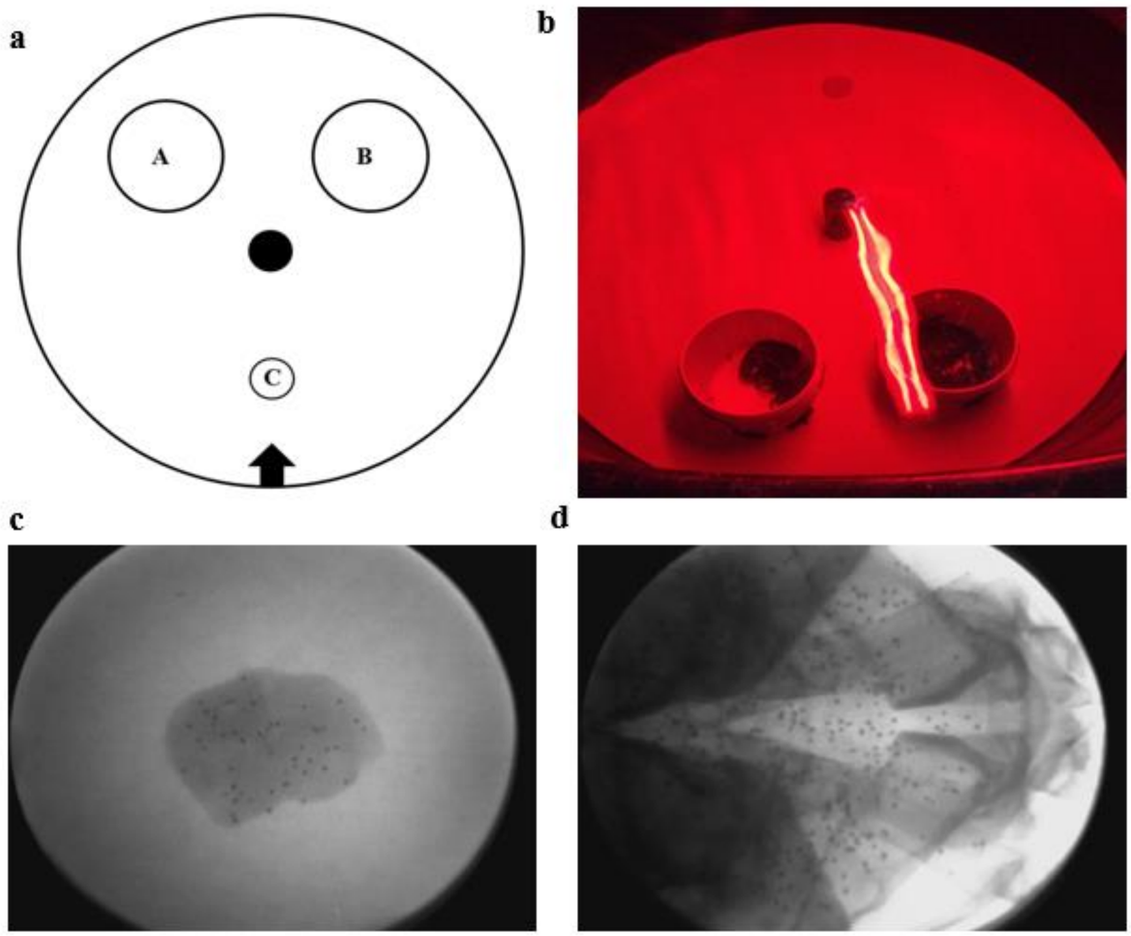

Figure 2.1. Food acquisition experimental set-up. a) Diagram of top-down view of tank A, B = perforated buckets that housed a lobster and the crabs, C = food dish, black arrow = tank inflow, black circle = tank outflow, b) Photograph of tank set-up, c) X-Ray photograph of 1 g subsample of food source containing ballotini glass beads, d) X-Ray photograph of lobster maxilla and stomach containing ballotini glass beads.

<u>Catchability experiments</u>

The catchability experiment examined how the presence of green crabs affected individual lobster behaviour around a baited trap. All trials were conducted in a 45,000L, 6.8m diameter fibreglass tank in 90cm of water with a seawater flow rate of 25L/min (Figure 2.2a,b). A time-lapse video camera (Panasonic, WV-BP120 - Laguna, Philippines) mounted above the middle of the tank recorded interactions around the trap. The trap was baited with a whole mackerel, as is common in the fishery. These experiments were also conducted under red light to minimize light effects on crustacean behaviour (Weissburg & Zimmer Faust, 1994) and we again covered the entire tank set-up with black tarpaulin to reduce visual disturbance (Lawton, 1987). The experiments were conducted at the same temperatures used for the behavioural assays (4^0C, 12^0C). A wooden slat, D-shape trap (100cm x 50cm x 35cm height, $4cm^2$ mesh size) with an escape gap of 4cm was placed on one side of the tank. This trap was a modified version used in the Newfoundland fishery to include two, rather than one, entry funnels so the "parlour" section of the trap could be sealed with $1cm^2$ mesh to prevent crab escape (Figure 2.2c,d).

The control experiment was run with an individual lobster only, and then repeated with 25 crabs contained within the parlour portion of the trap (and unable to escape), or with 25 crabs outside the trap that could move freely around the tank and trap and interact with the lobster (n=20 trials per experiment). We selected a density of 25 crabs because this was the maximum number of crabs that could be contained within the modified trap and the feeding experiment showed no highly significant differences in lobsters foraging response when exposed to 1, 5 and 25 crabs. As with the previous experiment, we introduced the lobsters and crabs into the experimental tank in bottomless, perforated, weighted buckets for a 30-minute period prior to beginning the experiment. Both species were then released simultaneously by lifting the bottomless buckets, this methodology ensured that the animals were not exposed to air after the initial adjustment period. Each trial was recorded for 12 hours (average trap soaking time in fishery). In trials where crabs were inside the trap, we placed them in the “parlour” area, at the same time as the lobster was introduced into the tank. The experiments began at the same time each day (9am) and water temperature was maintained at either 4^0C or 12^0C ($\pm 1^0$C) throughout the experimental period. After each trial, both species were returned to their respective holding tanks, and the experimental tank was left for a further 12 hours to ensure any remaining odour plumes were rinsed through the flow-through system.

We analyzed the videos from each trial to quantify: a) time for the lobster and the first crab to approach the baited trap (an “approach” was quantified when the animal touched the trap), b) the number of unsuccessful attempts a lobster made towards a baited trap (an “unsuccessful attempt” was quantified when the animal attempted to go in the funnel entrance but was unsuccessful in entering the trap), c) the time taken for each species to enter the baited trap d) number of times a lobster successfully attempted to enter the trap e) number of times a lobster escaped from the trap (Jury et al., 2001).

Field data (CPUE of lobsters, green crabs, and native rock crabs *(Cancer irroratus)*, size of lobsters and green crabs, sex of lobsters) was also collected during a five day period with lobster harvesters in Garden Cove, Placentia Bay and is covered in detail in the appendix section of this thesis

<u>Statistical analysis</u>

We conducted two-way MANOVAs (Scheiner & Gurevitch, 2001) to determine the effect of crab (absent from the tank, inside the trap, outside of the trap) and water temperature (4 & 12^0C) on the frequency of lobster behaviours towards the baited trap (number of approaches, number of attempts to enter the baited trap, number of catches). Interaction terms were incorporated into the models. Significance was based on a $p<0.01$

level; a Bonferroni-corrected significance level (Rossong et al., 2011). All analyses were conducted in SPSS v. 23.

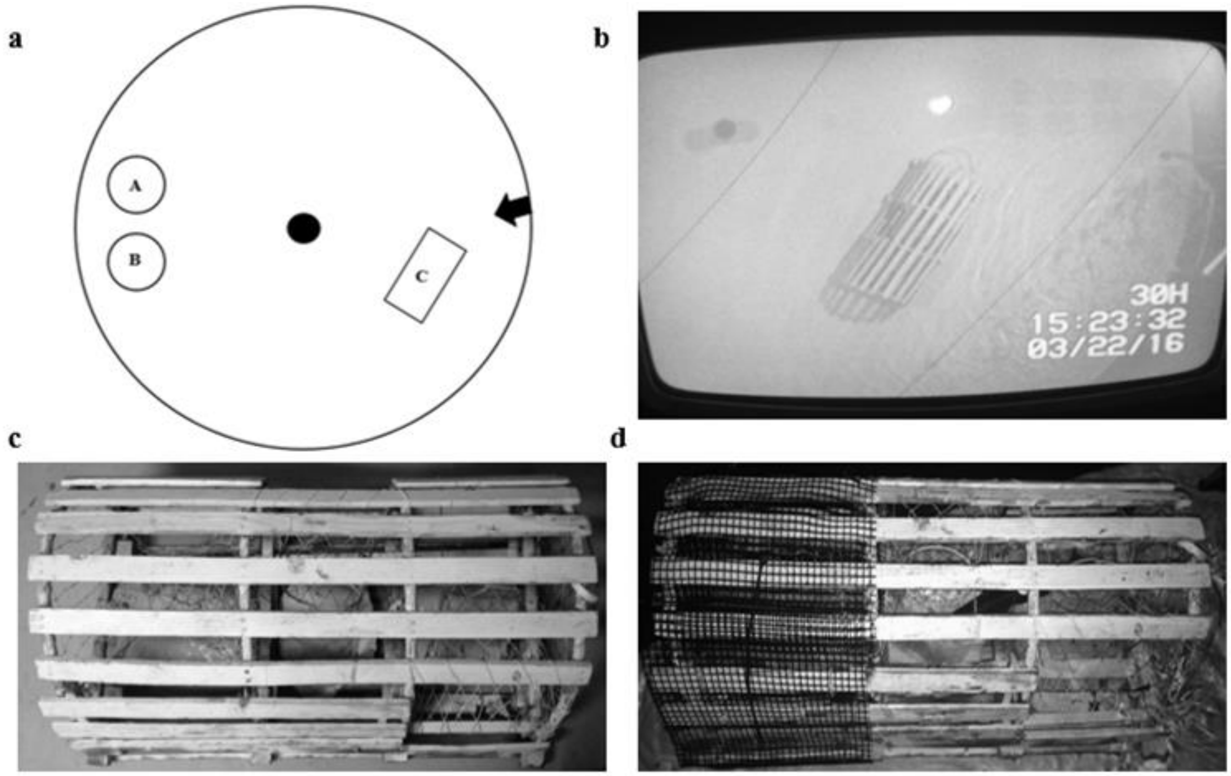

Figure 2.2. Catchability experimental set-up. a) Diagram of top-down view of tank A, B = perforated buckets that housed a lobster and the crabs, C = baited trap, black arrow = tank inflow, black circle = tank outflow, b) Photograph of tank set-up, c) Photograph of "D-slat" trap used in experiments pre-modification, d) Photograph of "D-slat" trap used in experiments post-modification.

2.4 Results

<u>Behavioural interactions around a food source</u>

There were no statistically significant effects of temperature (two-way ANOVA; $F_{(1,67)}$=2.92, p=0.093, Table 2.1) or crab density ($F_{(3,67)}$=0.296, p=0.828) on the amount of time it took the lobster to first approach the food source, but lobsters generally approached the food source in less time at 12^0C (32 minutes) compared to 4^0C (49 minutes, Figure 2.3a). Crab density (two-way ANOVA; $F_{(1,59)}$=2.393, p=0.079) and water temperature ($F_{(3,59)}$=1.475, p=0.232, Table A.1 - appendix, Fig. 2.3b) did not significantly affect the amount of time a lobster spent feeding (physically handling the food source) . In contrast, temperature (two-way ANOVA; $F_{(1,72)}$=31.141, p<0.01) and crab density ($F_{(2,72)}$=14.404, p<0.01) significantly affected the amount of time it took the first crab to approach the food source (Table A.2, Fig. 2.3c), and crabs approached the food source in significantly less time at 12^0C than at 4^0C. At both temperatures at a density of 25 crabs, an individual crab approached the food source at a significantly faster rate compared to densities of 5 crabs (p<0.01) or an individual crab (Tukey test, p<0.01).

Crab density significantly affected the number of times a lobster retreated away from a crab (two-way ANOVA; $F_{(2, 89)}$=21.516, p<0.01) because lobsters increased in frequency of retreats as crab density increased (Table A.3, Fig. 2.4a), but temperature had no effect on this behaviour ($F_{(1, 89)}$=0.769, p=0.383). The number of lobster body raises was not significantly affected by temperature (two-way ANOVA; $F_{(1,89)}$=2.525, p=0.116, Table A.4, Fig. 2.4b), or crab density ($F_{(2,89)}$=0.681, p=0.509). However, the number of crabs in the trial significantly affected the number of lobster claw raises and claw grasps, with more lobster claw raises (two-way ANOVA; $F_{(2,89)}$=10.830, p<0.01) at a density of 25 crabs (p=0.01) compared to densities of 1 and 5 crabs (Table A.5, Fig. 2.4c). Similarly, lobsters displayed more claw grasps ($F_{(2,89)}$=11.365, p<0.01, Table A.6) when in the presence of more crabs. However, water temperature had no statistically significant effect on the number of lobster claw raises ($F_{(1,89)}$=0.099, p=0.754), nor did it affect the number of claw grasps (two-way ANOVA; $F_{(1,89)}$=3.812, p=0.054, Table A.6, Fig. 2.4d). To further investigate the noticeable variation in the pattern of interactions as a function of water temperature and crab density, we pooled the “approach” behaviours displayed by lobsters to test for any “general” patterns of behaviour (Table A.7, Fig. 2.5). Water temperature (two-way ANOVA; $F_{(1,90)}$=4.836, p=0.031) and crab density ($F_{(2,90)}$=4.143, p=0.019) significantly affected the frequency of occurrence of pooled approach behaviours, because significantly more lobster interactions occurred when comparing densities of one and 25 crabs to the treatment with no crab (p=0.019) and more interactions were observed at 12^0C compared to 4^0C.

We also detected several significant behavioural responses in green crabs to lobster. Crab density significantly affected the number of times a crab retreated away from, and displayed a body raise towards a lobster because crabs retreated from the lobster more frequently (two-way ANOVA; $F(_{2,89})$=122.450, p=<0.01, Table A.8, Fig. 2.6a) and displayed more body raises ($F_{(2,89)}$=42.891, p<0.01, Table A.9, Fig. 2.6b) at a density 25 crabs compared to that at the lower crab densities. Water temperature also significantly affected the number of crab retreats ($F_{(1,89)}$=7.730, p<0.01), but not the number of crab body raises ($F_{(1,89)}$=0.006, p=0.938). Crab density significantly affected the number of crab claw raises (two-way ANOVA; $F_{(2,89)}$=45.778, p<0.01, Table A.10, Fig. 2.6c) and claw grasps ($F_{(2,89)}$=18.429, p<0.01, Table A.11, Fig. 2.6d) initiated towards a lobster, with significantly more claw raises at the highest crab density and more claw grasps with increased crab density. In addition, water temperature affected the number of claw raises (two-way ANOVA; $F_{(1,89)}$=34.442, p<0.01) with more raises at 12^0C compared to 4^0C. Temperature had no significant effect on the number of claw grasps ($F_{(1,89)}$=0.343, p=0.560). The total number of approach interactions displayed by crabs towards a lobster significantly increased with increasing water temperature (two-way ANOVA; $F_{(1,90)}$=21.97, p<0.01) and increasing crab density ($F_{(2,90)}$=87.588, p<0.01) because more interactions were observed at higher crab densities, and at 12^{0}C compared to 4^{0}C (Table A.12, Fig. 2.7).

X-ray analysis of the lobsters showed that they fed in 44% of the cold-water trials and 54% in the warm water trials (Fig. 2.8a), whereas green crabs fed in 33% of the trials at 4^{0}C and 77% of trials at 12^{0}C (Fig 2.8c). Food consumption rates were routinely low with no significant differences in the amount of food a lobster consumed as a function of crab density (two-way ANOVA; $F_{(3,131)}$=0.07, p=0.178) or water temperature ($F_{(3,131)}$=0.011, p=0.915, Table A.13, Fig. 2.8b). However, at densities of 150 crabs (n=10), the lobsters did not consume any food in any of the trials and the crabs consumed the entire food source in 7.42 ± 0.71 minutes. The amount of food a crab consumed depended on water temperature (two-way ANOVA; $F_{(2,928)}$=84.410, p<0.01) in that crabs consumed more food at the warmer water temperature. The number of crabs in the tank the amount of food an individual crab consumed ($F_{(2, 928)}$=1.039, p=0.354, Table A.14, Fig. 2.8d).

Catchability

Crab position significantly influenced some lobster behavioural responses in and around the trap. Lobsters approached the trap less often when crabs were positioned outside of the trap (MANOVA; $F_{(2,58)}$=4.283, p=0.01, Table 2.2, Fig. 2.9a, ANOVA, Table 2.3), compared to when crabs were positioned inside of the trap (Tukey test; p=0.031) or when no crabs were present (Tukey test; p=0.045). Although crab position significantly affected the approach behaviour of lobsters, temperature had no effect (MANOVA; $F_{(1,59)}$=0.066, p=0.799) on how many times a lobster approached the trap.

Similarly, crab position significantly affected the number of lobster attempts to enter the trap (MANOVA; $F_{(2,58)}$=5.591, p<0.01, Table A.15, ANOVA, Table A.16 - appendix, Fig. 2.9b). Fewer attempts were made when crabs were positioned outside of the trap compared to when crabs were absent from the trial (p=0.005), but this behaviour was unaffected by water temperature (MANOVA; $F_{(1,58)}$=1.273, p=0.264). Neither temperature (two-way ANOVA; $F_{(2, 27)}$=0.047, p=0.955, Table 2.3, Fig. 2.10a) nor treatment ($F_{(2,27)}$=0.572, p=0.073) significantly affected on the time to first entry by a lobster . In contrast, water temperature affected the time of first green crab entry (one-way ANOVA; $F_{(1, 19)}$=5.445, p=0.031, Table 2.4), in that green crabs entered the trap faster in warmer water.

Lobsters successfully entered the trap significantly more times at 12^{0}C than at 4^{0}C (MANOVA; $F_{(1, 58)}$=8.354, p<0.01, Table A.17, ANOVA, Table A.18, Fig. 2.9c). The same pattern was observed regarding number of lobster escapes from a trap, in that lobsters escaped significantly more at the warmer temperature ($F_{(1,58)}$=9.221, p<0.01, Fig. 2.9d) but were not significantly affected by the position of green crabs (p>0.01). At 4^{0}C lobsters were never successfully entered when crabs were positioned outside. The first entry time of green crabs was significantly earlier at 12^{0}C than at 4^{0}C ($F_{(1, 18)}$=5.445, p=0.031, Fig. 2.10b).

2.5 Discussion

The results from this study show that the presence of green crabs in the tank environment could affect negatively influence lobster feeding and trapping behaviour as the presence of crabs decreased the lobster food consumption and prevented a lobster from entering a baited trap, however as some of the data did violate the assumptions of ANOVAs to deliver unbiased parameter estimates in all cases. Crustacean behaviour is important (e.g. Bell et al., 2001; Chiasson et al., 2015; Haarr et al., 2012; Hanson 2010; Jury et al., 2001; League-Pike et al., 2009; Mehrtens et al., 2005; Rossong et al., 2006; 2011; Ryan et al., 2014; Watson et al., 2009; 2013; Williams et al., 2006; 2009) and previous literature highlight the importance of this branch of research, our findings build on previous studies and presents new findings on how lobsters and green crabs interact with each other when in the presence of food and baited traps.

Behavioural interactions

Crab density had no significant effect on the time it took lobsters to approach the food source and the subsequent handling of food, perhaps reflecting the larger adult lobsters and smaller green crabs in our study. Adult green crabs can outcompete smaller juvenile lobsters for food items smaller than the crabs themselves (Rossong et al., 2006; Williams et al., 2006). However, lobster behaviour in our study was unaffected by green crabs at any of the densities tested, likely reflecting the size disparity between the smaller adult green crabs and the much larger lobster.

Although the presence of between 1 and 25 green crabs did not affect food acquisition of lobsters, at a density of 150 crabs, the lobsters were unable to acquire any food because the crabs consumed it all before the lobster reached it. Typically, green crabs are more active in the presence of food than lobsters, consistent with their rapid detection and feeding on food (Haarr & Rochette, 2012). The 150 crabs consumed the entire food source (75g) in approximately eight minutes. In the wild, the lobster diet typically consists of molluscs, echinoderms, other crustaceans and, occasionally, fish carcasses (Ennis, 1973). Given the comparatively small size of most of these items and the capacity of green crabs to detect food quickly, 150 crabs could congregate over and consume many prey items before a lobster could feed on those items.

The behaviour of lobsters was also unaffected by the water temperature, with similar approach times at both 4 and 12^{0}C. In contrast, the approach time of the green crabs was faster when more conspecifics were present and also at the higher temperature. This difference between the two species as a function of temperature may reflect optimal functionality, where biological processes can be carried out most efficiently, in crustaceans at temperatures typical of their natural habitat (Wieser, 1972). The optimum temperature range for the American lobster is between 8-18^{0}C (Ennis, 1984; Aiken & Waddy, 1986; Ugarte, 1994; Watson & Jury, 2013; Nielsen & McGaw, 2016). Green crabs have an optimal range of 10-18^{0}C, but feed most efficiently at 17-24^{0}C (Crothers, 1969; Wallace, 1973; Elner, 1980; Behrens-Yamada, 2001; Miron et al., 2002). Unlike lobsters, green crabs are less tolerant of colder temperatures in their natural range, and below $\leq 7^{0}$C they decrease activity and enter into a torpor-like state (Berrill, 1982; Behrens-Yamada, 2001). Adult green crab migrate to deeper waters when temperatures fall below 8^{0}C (Sanchez-Salazar et al., 1987) and at 6^{0}C, slow and intermittent feeding activity occurs. This response explains significantly longer crab approach time to the food source at 4^{0}C. In contrast, lobsters remain active at low temperatures of 2-5^{0}C (McLeese & Wilder, 1958), and we would expect a reduced temperature effect on approach and handling time in lobster. However, green crabs in Newfoundland actively feed even during winter, suggesting greater thermal adaptation than their native counterparts (Tepolt & Semero 2012; Jeffery et al., 2017); thus they continued to feed in our experiments, even at the lower temperature.

Agonistic behaviour

In general, any conflict between individuals can be resolved by agonistic behaviour, defined here as "the set of patterns that share a common function; to adjust to a situation of conflict" (Huber & Kravitz, 1995). Agonistic behaviour can be subdivided into approach behaviour: the act of an animal directly approaching the opponent, and avoidance behaviour: the animal moves away from the opponent (Huber & Kravitz, 1995). Agonistic behaviour in crustaceans includes displays such as raising the body high above the substratum and presenting the chelae to the opponent (Sneddon et al., 1997b). Our study quantified four types of agonistic behaviours between lobsters and green crabs, based upon categories defined by Huber & Kravitz (1995). These behaviours included retreating away from another animal (avoidance), and three agonistic interactions: body raises, claw raises, and claw grasps. As defined by (Huber & Kravitz (1995) these three different agonistic displays are clearly and reliably distinguishable through the separation of each behaviour into bouts. Here, we define bouts as "periods of no contact or of avoidance behaviour by one or the other of the combatants" (Scrivener, 1971; Atema & Cobb, 1980). Other studies also distinguish similar behavioural interactions between individuals through agonistic levels, where each interaction (level) increases with physical intensity (Karavanich & Atema, 1998; Haarr & Rochette, 2012). Division of behaviours here into similar categories enabled comparison of our results with previous work on this and other species. The frequency by which these behaviours were displayed varied considerably, especially when comparing lobster interactions with green crabs. The lobsters in our study displayed, on average, twice as many agonistic behaviours (body and claw raises) and seven times more agonistic interactions with physical contact (claw grasps) compared to those observed by Haarr & Rochette (2012). We used large adult lobsters interacting with numerous adult green crabs as opposed to a single juvenile lobster interacting with one similar sized green crab (Haarr & Rochette, 2012), which presumably contributed to the higher number of incidents observed. As categorised by Haarr and Rochette (2012), lobsters displayed the least threatening approaches (body raises) most frequently and were less likely to display highly threatening approaches (claw grasp) towards the crabs. In contrast, green crabs were more likely to display more aggressive behaviours to the lobsters (claw raises and grasps) and were 10-25 times more likely to retreat from a lobster in our study. Given the size discrepancy, the crabs would perceive a lobster as a greater threat rather than vice versa. In addition, within conspecifics, lobster relationships quickly dichotomise into dominant and subordinate roles, and conflicts can be resolved with threatening displays. Lobsters use chemical cues to remember familiar opponents when kept *in situ* (Karavanich & Atema, 1998). In contrast, green crabs go directly into physical fighting rather than using displays to avoid a fight (Sneddon et al., 1997a) which is consistent with the large number of aggressive agonistic interactions observed in our study.

Despite some underlying patterns, agonistic interactions varied considerably. It is also unclear whether the lobsters and crabs actually respond differently or could differentiate between a body raise and a claw raise, for example, or a claw raise and a claw grasp. To investigate some of the common patterns we observed further, we grouped interactions into retreating behaviour and approach behaviours. This approach clarified patterns somewhat; lobster retreat behaviour generally increased at the higher temperature and also at higher crab density. This underlying pattern was more variable but also evident for the approach behaviour between lobsters and green crabs. Both retreat and approach behavioural patterns were much clearer when investigating the interactions of green crabs towards the lobster, with more defined increases in behavioural interactions as a function of temperature and crab density. Presumably when temperature increases, crabs become more active and continue to act aggressively towards the lobster and to one another.

The increase in interactions with increasing crab density can be explained by the greater number of animals to interact with, and as such, these behaviours should increase. However, dividing the total amount of interactions by the number of individuals did not yield a stable number of interactions. In order to account for density in this experiment, the experiment would have to be redesigned specifically to address the number of interactions and types of interactions between the two species within a set time frame, however, the actual behavioural interactions were not the main focus of this study. Instead the number of individual interactions decreased as crab density increased, perhaps because green crabs tended to mass together in clumps and the effect of an individual was lowered as the lobster only potentially recognised and interacted with the mass as one individual. This has also been observed in other studies as they report increased agonistic interactions with increased number of encounters (Williams et al., 2006; Williams et al., 2009). Furthermore, animals are more likely to encounter one another at higher densities, potentially leading to adaptation whereby an individual no longer responds to another as a threat. This type of behaviour has been noted in several other taxa whereby potential threats, once encountered, are ignored more often as the individual becomes habituated to the threatening display with repeated exposure (e.g., male threat displays in Siamese fighting fish (Meliska & Meliska, 1976) and in the claw display response of fiddler crabs to repeatedly approaching dummy predators (Hemmi & Merkle, 2009)).

Food acquisition

Even though all the lobsters were observed around the food source at some time during the experiment and appeared to handle the food, a subsequent X-ray of the gut showed that on average only 45-55% of lobsters actually ingested the food. This pattern is interesting because they were starved for 8-10d prior to experimentation, an ample time for them to empty their gut system (McGaw & Curtis, 2013a; Wang et al., 2016a). In contrast to the low number of lobsters that fed, temperature produced a more pronounced effect on green crabs: 33% crabs fed at 4^{0}C, whereas 77% ingested food at 12^{0}C. Once released from the buckets the crabs tended to head straight for the food and started feeding, whereas the lobsters circled the tank and remained active. This exploration of a novel environment has been reported before for lobsters; the acquisition of shelter is highly important for lobster (Cobb, 1971; Nielsen & McGaw, 2016) and they will often spend time seeking out shelter; this behaviour could explain why not all the lobsters fed.

We observed no significant change in the amount of food a lobster consumed as a function of crab density, or water temperature, however many previous studies on lobsters and other crustaceans report increased consumption rates with increasing temperature (Jury & Watson, 2013; Watson & Jury 2013; Nielsen & McGaw, 2016; Wang et al.

2016a). Bait diffusion rates increase at warmer temperatures and activity and appetite also increases in decapods (Morrissy, 1975; Worden et al. 2006), because increased metabolic rates presumably increase hunger (Lagerspetz & Vainio, 2006). However, lobsters ate a similar amount of food at both temperatures in our study. A general increase in activity observed for the lobsters at 12^{0}C associated with exploring the novel environment may have negated any potential differences in foraging associated with temperature. Crabs exhibited the expected increase in food ingestion at warmer temperatures, again reflecting a sharp decrease in activity and feeding at approximately 7^{0}C (Berrill, 1982; Behrens-Yamada, 2001).

For lobsters that fed, the actual amount of food ingested was routinely low, at 0.2-0.5% of their body mass. Lobsters and other crustaceans typically ingest between 2-4% of their body mass at any one time (McGaw & Curtis, 2013a; Wang et al., 2016a), so it is unusual that intake was so low, especially considering that they had been starved for 8-10d beforehand. Food intake levels were also low in the green crabs at both temperatures. When offered whole mackerel, both species apparently consumed a significant amount of the flesh. The low amount of prepared food ingested by both species could be because the gelatin and radio-opaque markers contained in the food reduced its palatability and lobsters have even been seen to prefer fresh bait as opposed to frozen bait both in the fishery (Roy Murphy; Hayward Eddy, lobster harvesters, pers. comm. 2016) and in this study during preliminary trials. In the aquaculture industry, few promising artificial diets have been developed for culturing *H. americanus* (Conklin et al., 1975). Some studies report that spiny lobsters *(Jasus edwardsii)* reared in cages are less likely to consume artificial foods (Sheppard et al., 2002) and virtually no feeding behavior has been detected in freshwater prawn (*Macrobrachium rosenbergii)* offered an artificial food source (Harpaz, 1997). Thus, the novel approach used here to try to quantify the amount of food ingested may have impacted overall ingestion rates. However, this method did show a discrepancy between the appearance of food handling (video analysis) and actual food ingestion (X-Ray analysis). This difference suggests a need for caution when interpreting behavioural assays, because food handling might not necessarily equate to food ingestion. Indeed, previous studies noted the difficultly in accurately assessing whether a crab is feeding when it is on the food source (Ramsay et al., 1997; Steen & Ski, 2014; Hold et al., 2015).

Catchability

Attracting a lobster to a trap typically required bait. The area of bait influence (ABI) is the area within which the target can detect the bait and where the bait measurably influences the orientation and movement of the target species; investigations on the catchability of crustaceans must consider this key component (Bell et al., 2001). The ABI for *H. americanus* in the field is between 9-17m (Smith & Tremblay, 2003) with an area of 382cm^2 (Watson et al., 2009). The release of attractants from the bait during feeding activity of other crustaceans may also contribute to a higher frequency of trap entry, and hence, catchability (McLeese & Wilder, 1958; Watson & Jury, 2013). In general, only 2-6% of approaches lead to capture within a traditional wood-lath parlour trap (Richards et al., 1983; Karnofsky & Price, 1989; Watson & Jury, 2013). In our study, lobsters also often approached the trap without attempting to enter.

Water temperature significantly affected lobster behaviour and catchability in and around the baited trap. In the wild, crustacean catchability generally increases with temperature as a result of increased activity, appetite, and the rate at which bait molecules diffuse in water (Morrissy, 1975; Watson & Jury, 2013). Lobsters and crabs were both more active at the warmer temperature (12^{0}C) and were thus successfully entered more rapidly and more often, but also escaped from the trap more often at 12^{0}C compared to 4^{0}C.

Behaviour around a trap

Crab position significantly affected lobster behaviour and they also significantly reduced lobsters attempts to enter the trap when crabs could move freely around the tank. We observed this lobster response at an experimental crab density of 25 individuals. In the field, small Fukui traps often catch up to 150 crabs in Placentia Bay, NL (Bergshoeff, MSc Thesis, in prep), suggesting crab abundances near traps may often exceed 25 individuals. The presence of such high numbers of green crabs could reduce the frequency at which target species enter traps. Miller (1990) linked the frequency of crabs entering a trap with the presence of crabs already in a trap, and suggested that the presence of crabs in a trap may intimidate other crabs from entering, either via odour, sound, or threatening posture. The presence of lobsters already in a trap also inhibits the entry of other lobsters because of a saturation effect (Addison, 1995; Watson & Jury 2013) and the same may apply to green crabs, however no study has examined how many green crabs would be needed to induce this effect.

In addition to a possible intimidation factor, green crabs may physically block the entry funnel in the trap, especially at high crab densities (Bennett, 1974). Crabs appear to aggressively compete for the opportunity to enter the trap next (Jury et al., 2001). We observed crabs entering the trap and wrapping their legs and claws around the twine of the kitchen and parlour sections, potentially reducing the ability of lobsters to enter the trap. Previous studies showed that the presence of lobsters inside a trap reduces catches of green and rock crabs (Richards et al., 1983; Miller & Addison, 1995) and other lobsters (Watson & Jury, 2013), and green crabs attempt to hide or seek shelter in the presence of lobsters (League-Pike and Shulman, 2009). In our study, green crabs instead entered the trap in every trial, with many individuals remaining in the trap at the end of the experiment. The green crabs and lobsters were both starved for 8-10 d before experiments to ensure they would feed. Classic predator-prey experiments show that prey take more risks and enter areas with predators with increasing hunger because they behave so as to maximise their net rate of energy intake (Abrahams & Dill, 1989; Brown & Kotler, 2004).

The saturation effect of green crabs reduced the frequency at which lobsters approached and attempted to enter a trap. Trap saturation may also be considered as a form of competition given that crabs always approached and entered the trap first. However, we found no difference in the amount of times a lobster successfully entered the trap based on crab position, given that lobsters were presumably attracted to the trap, the same number of times. The presence of crabs may enhance lobster movement towards a trap in the field as bait odor is released and crabs tear apart and feed on the bait (Karnofsky & Price, 1989). In our trials, the crabs were contained within the parlour section of the trap to prevent their escape, so crab feeding did not enhance the attraction of the traps.

Our preliminary field sampling rarely caught green crabs and lobsters together (Fig. A.3 appendix), which is in contrast to our laboratory results. The lobster harvesters left the baited traps to soak for 1-2 days. Video data from the lab study showed that crabs frequently moved in and out of the trap, eating the bait, leaving and returning, which suggests they may behave similarly in the field. The laboratory studies showed that crabs may enter a trap within a few minutes; we have found while collecting green crabs in the field, traps fill with 50-100 individuals in under an hour. In contrast, lobsters did not enter the traps for over 100 minutes. Given even a conservative estimate of a trap attracting 150 crabs in the field (Bergshoeff, MSc thesis, in prep.), these animals could consume typical lobster bait (two mackerel/pot) within 45 mins. Thus, green crabs in Placentia Bay likely deplete the bait source within the trap rapidly and exit before lobsters even approach a trap. This pattern could potentially reduce capture rates because lobsters virtually ignore un-baited traps (Karnofsky & Price, 1989). In addition, Placentia Bay lobster harvesters use whole bait in the trap secured with bait ties. Our results suggest that using a bait cup/pot that limit green crab consumption will increase trap effectiveness over longer time periods; bait pots are already in use in the field to prevent this depletion (Zargarpour, MSc thesis, In prep).

Green crabs have likely been in Newfoundland for a maximum of 15 years (Blakeslee et al., 2010; McKenzie et al., 2010; Matheson et al., 2016), and we may not yet see their full effect on the lobster fishery. In addition, nearly all previous studies on interactions between lobsters and green crabs were carried out in New England and the Canadian Maritimes where green crabs and lobsters have interacted for 60-160 years. With any new invasion into an area, several changes occur with both the native and invading populations (Edgell & Neufeld, 2008; McGaw et al., 2011). Because predator-prey interactions may not be fully developed, predators may not recognize potential prey and vice versa (Agrawal 2001; Edgell & Neufeld, 2008; McGaw et al., 2011; Kuehne & Olden, 2012). This possibility leads into the next chapter which investigates whether Newfoundland lobsters attack and eat green crabs, and if so, whether they so do to feed or to defend a territory, and whether size and feeding status modulates such interactions.

Conclusion

Water temperature was the primary factor in crab foraging behaviour in that crabs consumed less food at the colder temperature but water temperature had no effect on lobster food consumption or behaviour whilst foraging. This temperature-dependent crab behaviour will likely affect the Placentia Bay fishery because water temperature during the fishing season typically varies between 7-14^{0}C (see Appendix), which exceeds the critical temperature where green crab feeding and metabolism is depressed; green crabs will therefore enter traps more often and consume more food during the fishing season than at other times of the year. Green crabs rapidly consume the bait within traps before a lobster can enter, thereby reducing lobster catch rate.

Although the presence of green crabs did increase agonistic behaviour by lobsters around a food source, this may only reflect that interactions are increased only due to the fact that the organism was exposed to an increased number of additional organisms. This could suggest that in an environment where there are more organisms overall, a lobster may spend more time interacting with another individual. In addition, for a lobster to be prevented from feeding completely, crab density in the tank environment must be high enough.

Tables

Table 2.1 Summary of the two-way ANOVA examining the effects of temperature (4 & 12^{0}C) and green crab *(C. maenas)* density (n=0/1/5/25) on the amount of time taken for an adult lobster *(H. americanus)* to approach the food source in the food acquisition trials.

Source of variation	Df	F	MS	p
Temperature	1	2.92	4650.987	0.093
Crab Density	3	0.296	471.028	0.828
Temperature *Crab Density	3	0.805	1282.79	0.496
Error	60		1592.764	
Corrected Total	67			

Table 2.2 Summary of the MANOVA examining the effects of temperature (4 & 12^{0}C) and green crab *(C. maenas)* position (absent/in/out) on the number of times an adult lobster *(H. americanus)* would approach the baited trap in the catchability trials.

Source of variation	df	F	MS	p
Temperature	1	0.066	50.102	0.799
Treatment	2	4.283	3267.474	0.01
Temperature *Treatment	2	0.194	148.063	0.824
Error	53			
Corrected Total	58			

Table 2.3 Summary of the subsequent one-way ANOVA to confirm the above MANOVA examining the effects of temperature (4 & 12^{0}C) and green crab *(C. maenas)* position (absent/in/out) on the number of times an adult lobster *(H. americanus)* would approach the baited trap.

Source of variation	df	F	MS	p
Temperature	1	0.07	57.836	0.793
Treatment	2	4.524	3294.428	0.015

Table 2.4 Summary of the two-way ANOVA examining the effects of temperature (4 & 12^{0}C) and treatment of green crab *(C. maenas)* position (absent/in/out) on the amount of time taken for an adult lobster *(H. americanus)* to first enter the baited trap in the catchability trials.

Source of variation	Df	F	MS	p
Temperature	1	0.047	0.007	0.955
Treatment	2	3.559	0.572	0.073
Temperature *Treatment	2	0.842	0.135	0.444
Error	22		0.161	
Corrected Total	27			

Table 2.5 Summary of the one-way ANOVA examining the effects of temperature (4 & 12^{0}C) on the amount of time taken for a green crab *(C.maenas)*to first enter the baited trap in the catchability trials.

Source of variation	Df	F	MS	p
Between Groups	1	5.445	3.362	0.031
Within Groups	18		11.115	
Total	19		14.477	

Figures

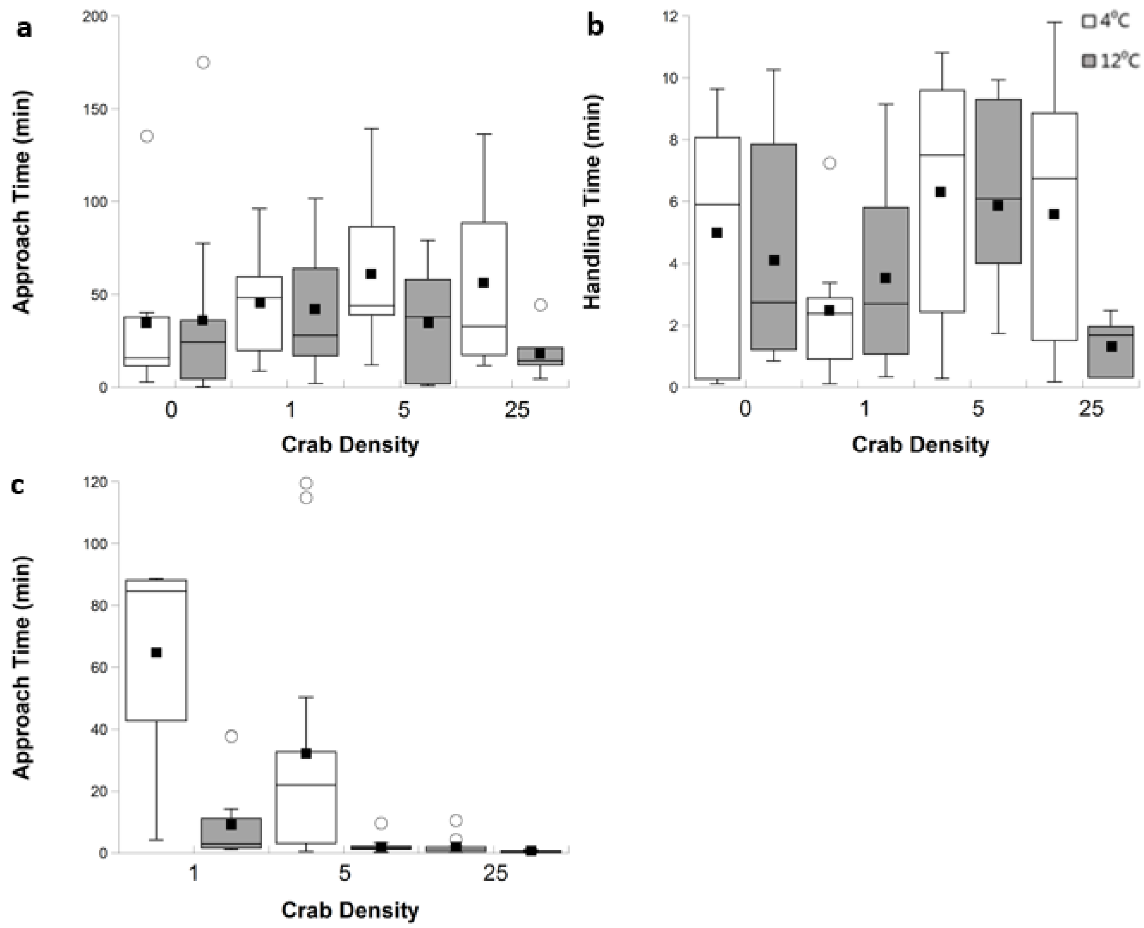

Figure 2.3. a) Amount of time (min) for an adult lobster, *H. americanus*, to approach the food source at different densities of adult green crabs, *C. maenas* and water temperatures, b) amount of time an adult lobster handled the food at different densities of adult green crabs and water temperatures, c) amount of time for adult green crabs to approach the food source at different crab densities and water temperatures. Black squares represent the mean.

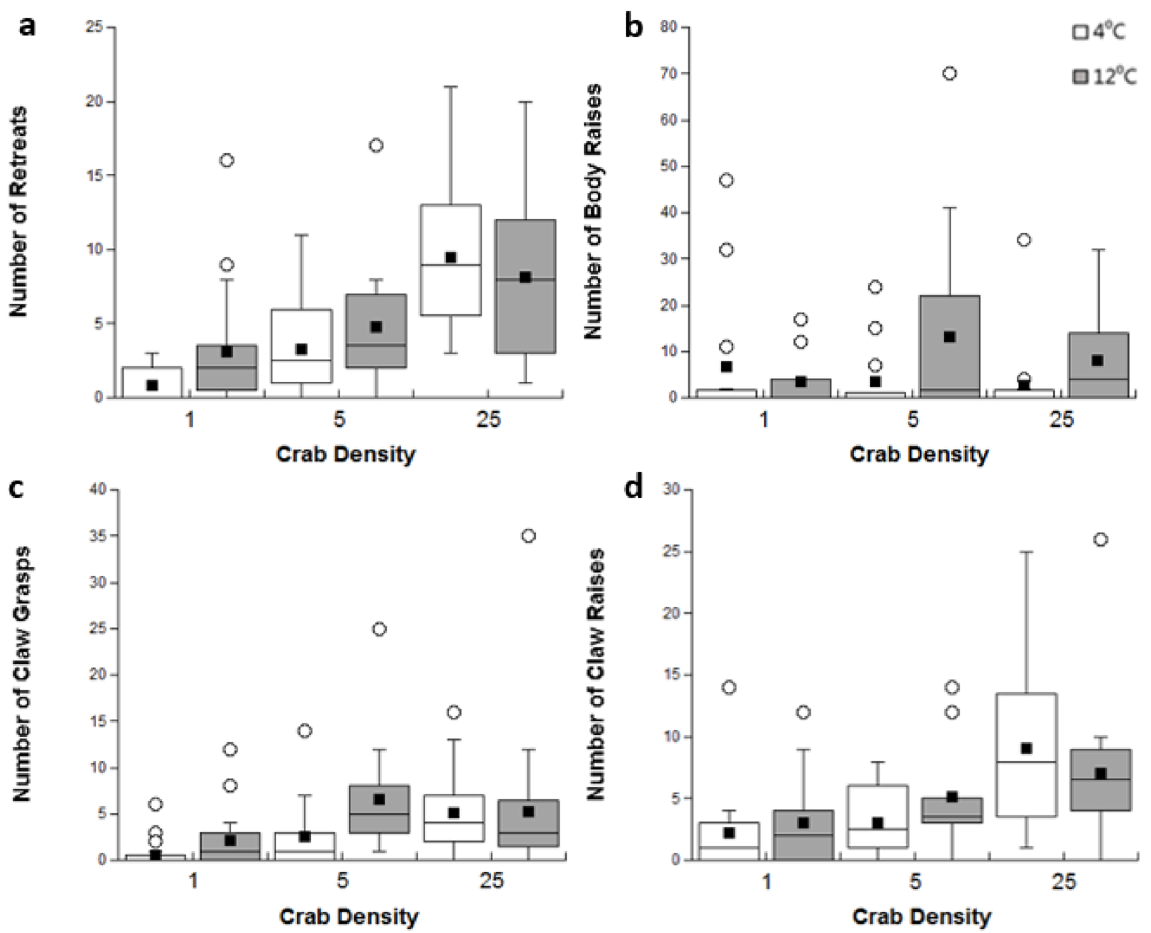

Figure 2.4. a) Amount of times an adult lobster, *H. americanus,* retreated from an adult green crab, *C. maenas* at different crab densities, b) number of times an adult lobster displayed body raises around adult green crabs, at different crab densities, c) number of times an adult lobster displayed claw raises around adult green crabs, at different crab densities, d) number of times an adult lobster displayed claw grasps around adult green crabs, at different crab densities. Black squares represent the mean.

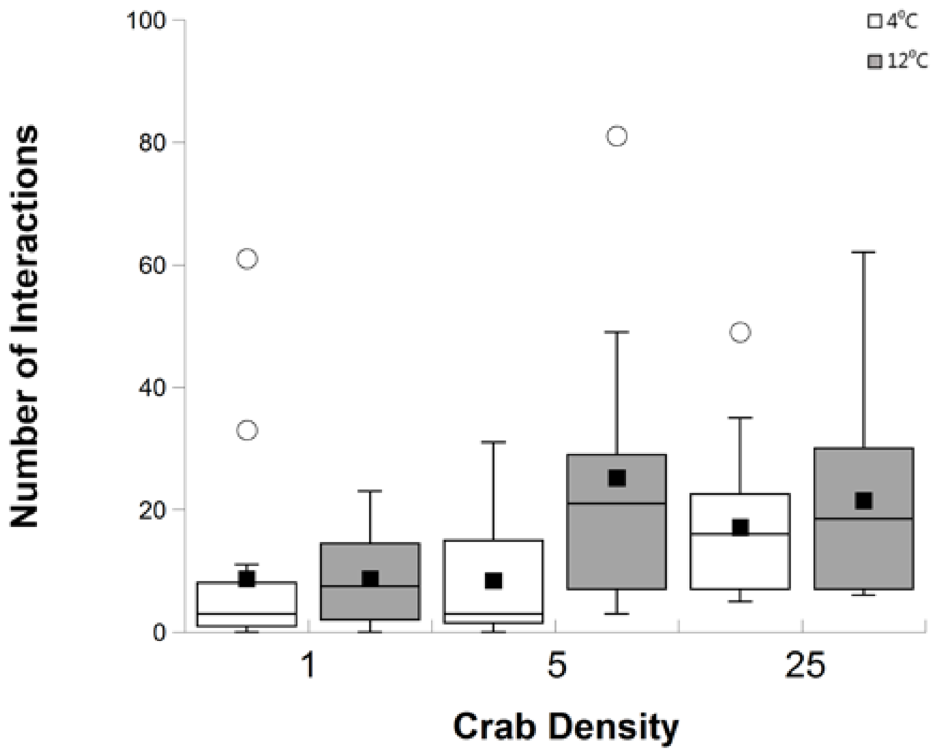

Figure 2.5. The total number of behavioural interactions displayed by an adult lobster, *H. americanus*, towards adult green crabs, *C. maenas*, at different crab densities. Black squares represent the mean.

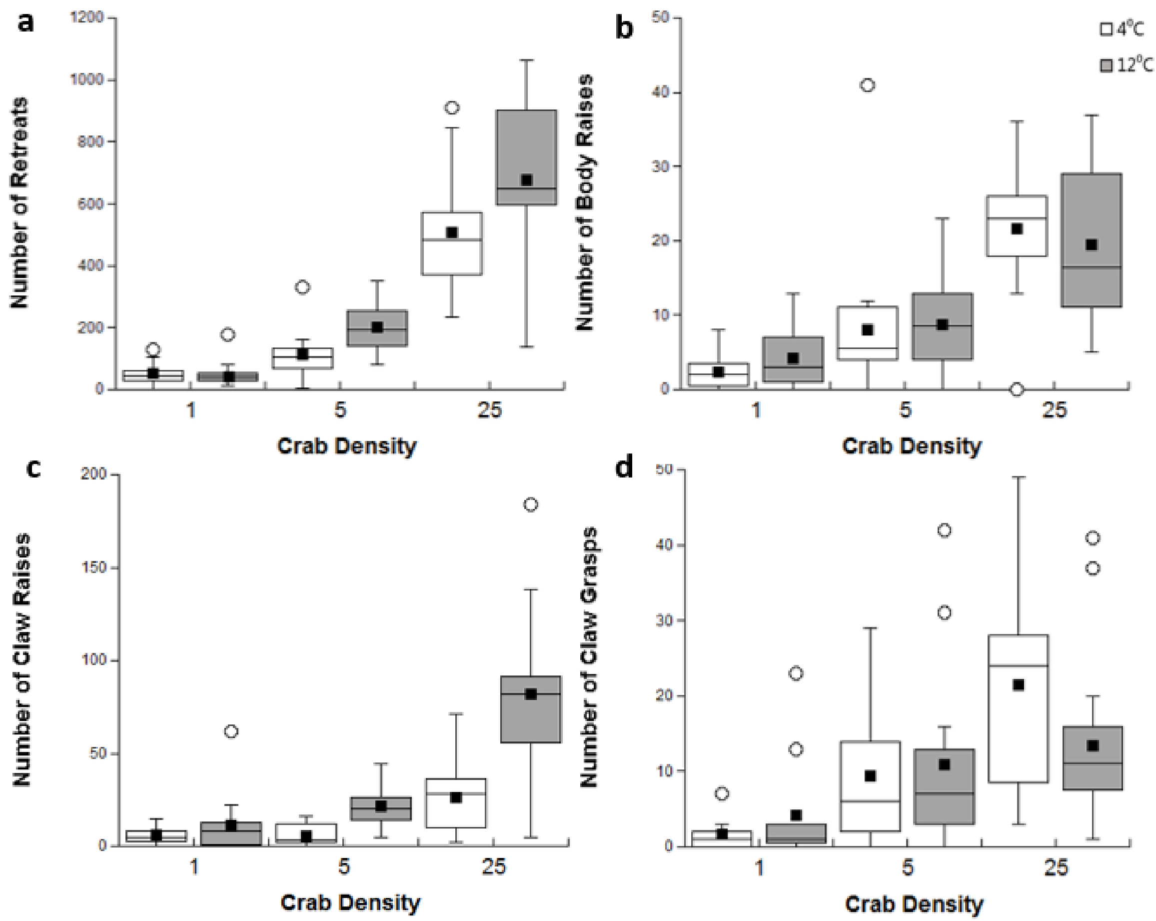

Figure 2.6. a) Amount of times adult green crabs, *C. maenas,* retreated away from an adult lobster *H. americanus*, at different crab densities, b) amount of times adult green crabs displayed body raises around an adult lobster at different crab densities, c) amount of times adult green crabs displayed claw raises around an adult lobster, at different crab densities, d) amount of times adult green crabs displayed claw grasps around an adult lobster, at different crab densities. Black squares represent the mean.

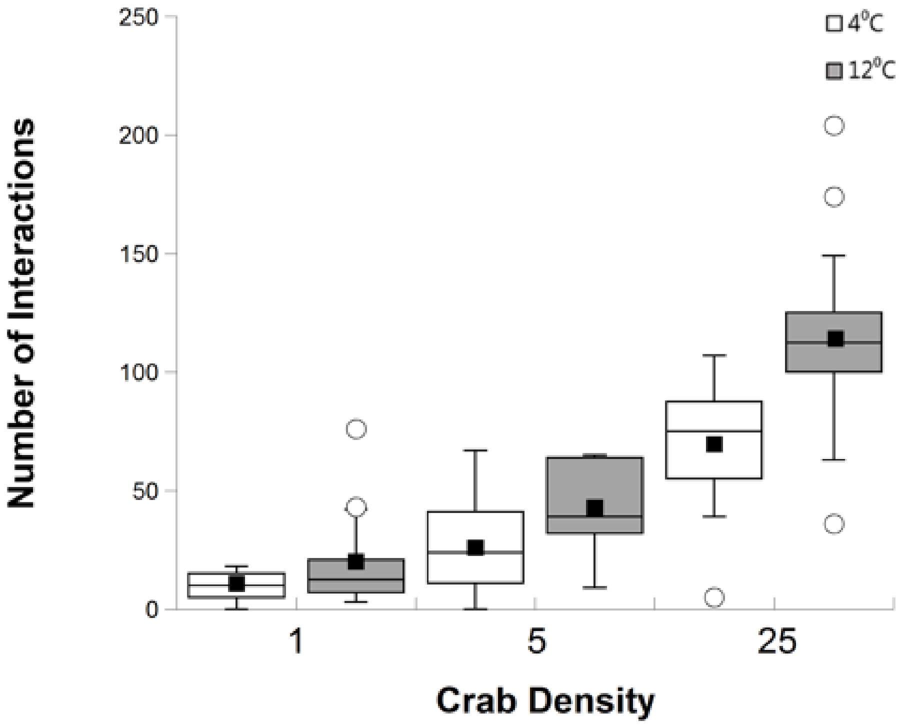

Figure 2.7. The total number of behavioural interactions displayed by green crabs, *C. maenas,* towards an adult lobster, *Homarus americanus,* at different crab densities. Black squares represent the mean.

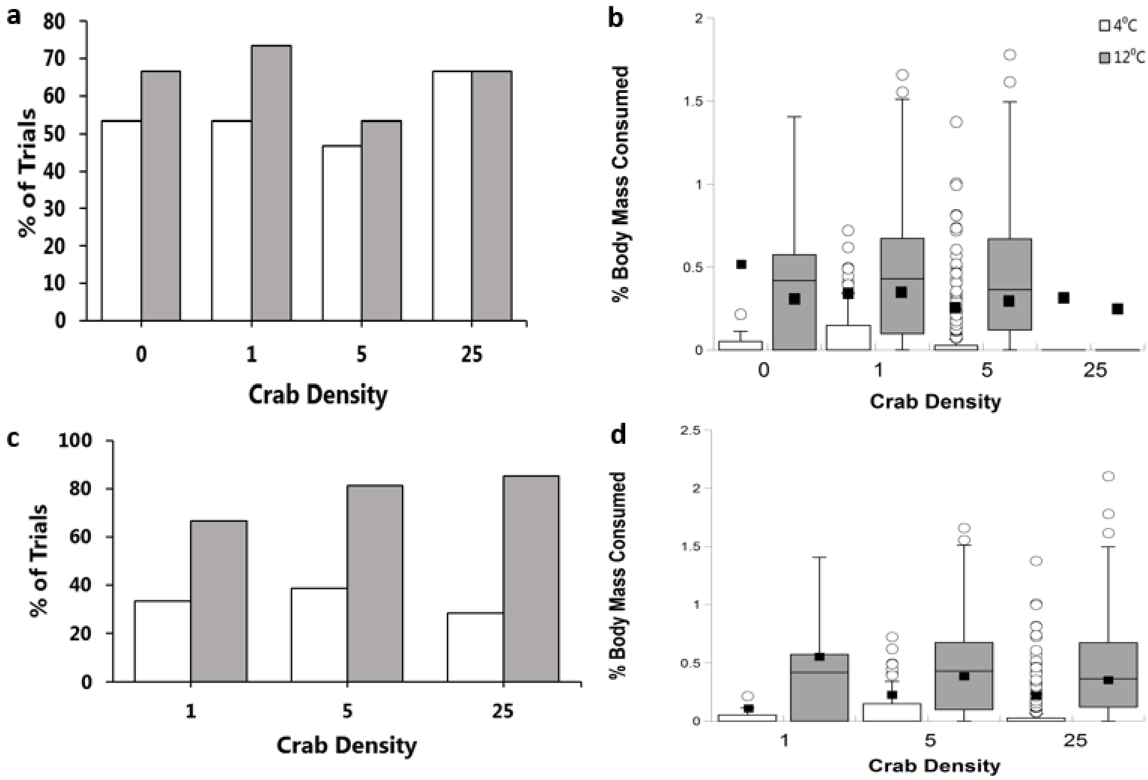

Figure 2.8. a) Percentage of trials in which adult *Homarus americanus* consumed the food source, at different densities of *Carcinus maenas* and water temperatures, b) amount of food consumed by an adult lobster in relation to body mass at different densities of adult green crabs and water temperatures, c) percentage of trials in which adult green crabs consumed the food source, at different densities of green crabs and water temperatures, d) amount of food consumed by adult green crabs in relation to body mass at different crab densities and water temperatures. Black squares represent the mean.

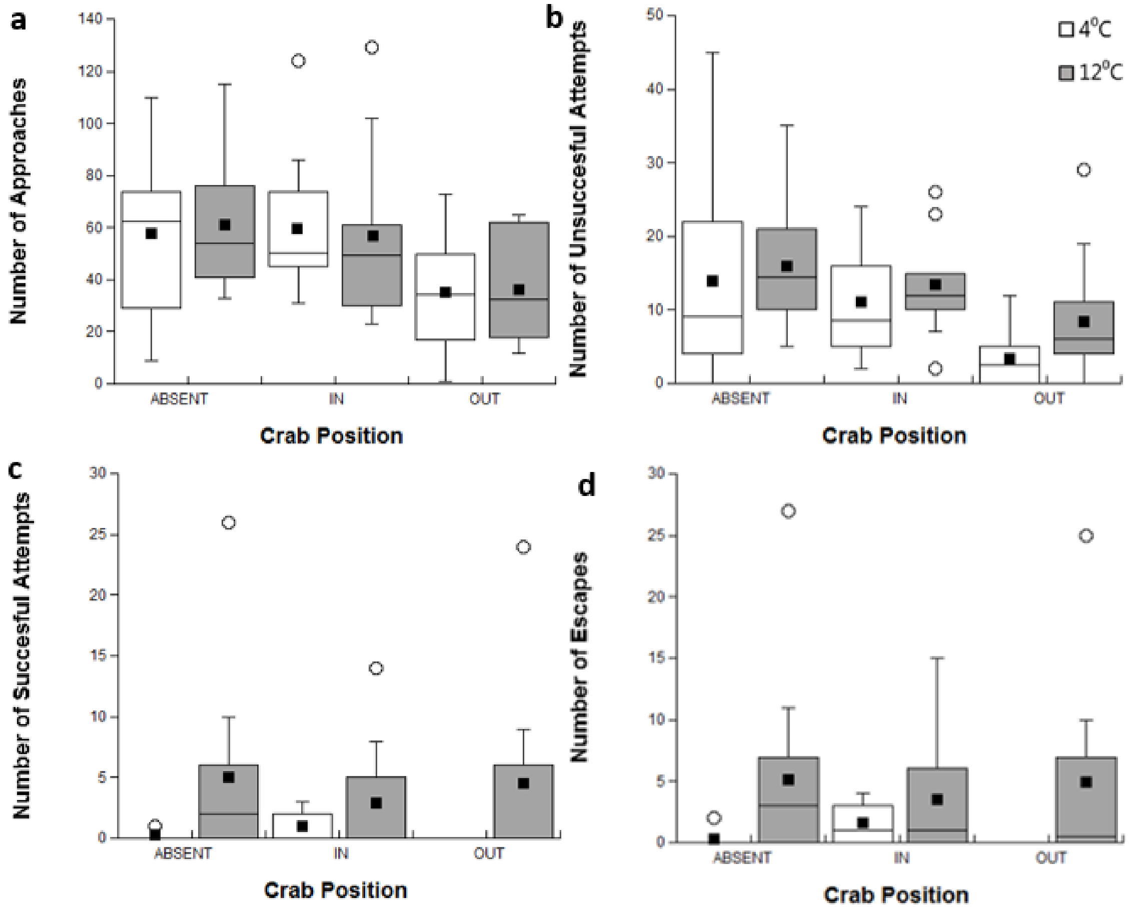

Figure 2.9. a) Number of approaches *Homarus americanus* made to a baited trap at 4^{0}C and 12^{0}C dependent on crab position, b) number of unsuccessful attempts a lobster made to enter a baited trap at 4^{0}C and 12^{0}C dependent on crab position, c) number of times an adult lobster successfully entered a baited trap at 4^{0}C and 12^{0}C dependent on crab position, d) number of times a lobster escaped from a trap at 4^{0}C and 12^{0}C dependent on crab position. Black squares represent the mean.

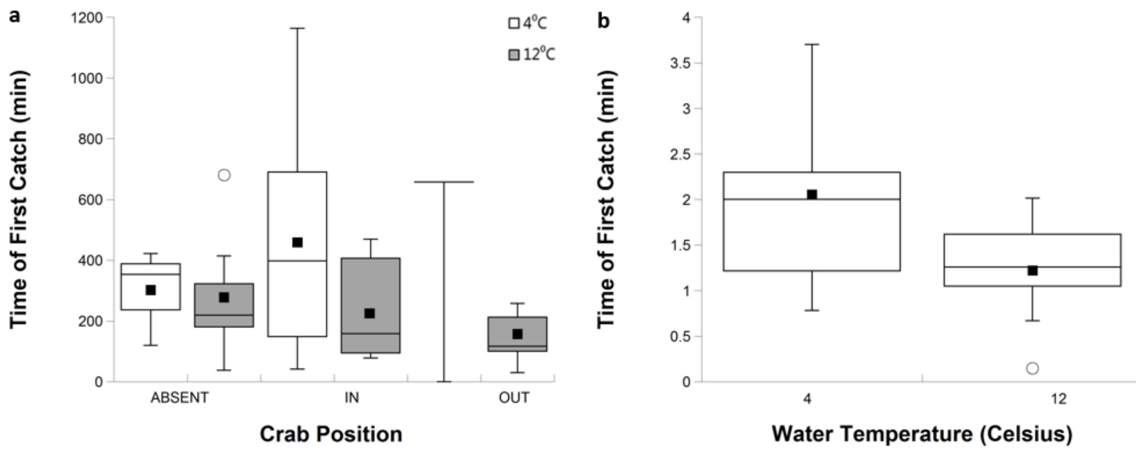

Figure 2.10. a) Time (min) for *Homarus americanus* to first enter the baited trap at 4^0C and 12^0C dependent on crab position, b) Time (min) for the first *Carcinus maenas* to enter the baited trap at 4^0C and 12^0C dependent on crab position. Black squares represent the mean.

3. Quantifying lobster predation on green crabs

3.1 Abstract

The European green crab (*Carcinus maenas*) first invaded the east coast of North America in the 1800s and comprises part of the diet of American lobster (*Homarus americanus*) in some locations. Green crabs are used as bait in lobster fisheries in Nova Scotia, Canada but predation has not yet been quantified in Newfoundland, where crabs were first reported 10-15 years ago. This study aims to determine whether lobsters from Newfoundland recognise and prey upon this new species and, if so, do green crabs reach a size refuge where they became too big for lobster to handle. Lobsters from Newfoundland were compared with lobsters from Nova Scotia that have coexisted with green crabs for over 60 years. Individual juvenile (≤40 mm), sub-adult (40-65 mm) or adult (≥65 mm) carapace width (CW) green crabs were introduced into a tank with single lobsters. Lobster origin had no significant effect on crab predation. Although the lobsters consumed some adult crabs, larger crabs (>72 mm CW) were less likely to be injured and eaten. The experiments were repeated with lobsters fed prior to experimentation, adding a shelter as a potential refuge for green crabs, and adding an alternative food source (fish flesh). Predation on green crab did significantly among the treatments, as crabs were less likely to be attacked or eaten when an alternative bait and a shelter were provided in the tank and larger crabs were less likely to be attacked or eaten than smaller crabs. Our results suggest that green crabs may be an important prey item for lobsters and could potentially be used as bait in the Newfoundland lobster fishery.

3.2 Introduction

The European green crab (*Carcinus maenas*, Linnaeus, 1758) is a benthic intertidal species native to the Eastern Atlantic, ranging from Norway to Morocco (Williams, 1984). It primarily inhabits sheltered bays and estuaries and grows to about 10 cm carapace width (Crothers, 1967). *C. maenas* has been described as one of the "100 worst invasive alien species" (Lowe et al., 2000) because adults are aggressive competitors and consume a variety of marine organisms (Ameyaw-Akumfi & Hughes, 1987; Klassen & Locke 2007) including annelids, molluscs, fish, and other crustaceans (Baeta et al., 2007). They were first recorded in North America in Massachusetts in the 1800s, gradually spreading northward to Nova Scotia, Canada in the 1950s (Klassen & Locke, 2007). Adult green crabs were first recorded in North Harbour, Newfoundland in 2007 but were likely first introduced in 2002 (Blakeslee et al., 2010; McKenzie et al., 2010) and have since spread to the south in Placentia Bay and westward into Fortune Bay and the west coast of Newfoundland. Unlike the European lobster (*Homarus gammurus*), whose distribution range does not overlap with that of the green crab in their native environments, the natural range of American lobster overlaps with that of green crab in the low intertidal and shallow subtidal zones (Carlson et al., 2006; Goldstein et al., 2017). In Newfoundland, the presence of green crab is a major concern, specifically in terms of their deleterious effects on eelgrass beds (Matheson et al., 2016), increased predation on shellfish (Grosholz & Ruiz, 1996; McClenachan et al., 2015), and their ability to predate upon, and negatively affect the behaviour of juvenile lobsters (Rossong et al., 2006; 2011; Williams et al., 2006; 2009).

Studies report varying outcomes following invasion of an exotic species. In some cases exotic prey may be beneficial to a native predator, because predators may become more effective at feeding on the invasive prey, via existing phenotypic plasticity or natural selection (Carlsson et al., 2009). For example, the invasive round goby (*Neogobius melanostomus*) in the Great Lakes has become an important food source to the threatened Lake Erie water snake *(Nerodia sipedon insularum)* (King et al., 2006). turtles (*Graptemys geographica*) (Bulte & Blouin-Demers, 2008) and numerous bird (Petrie & Knapton, 1999) and fish species (Magoulick & Lewis, 2002) now prey on invasive zebra mussels *(Dreissena polymorpha)* in the Great Lakes, and in the Hudson river zebra mussels now form an important part of the diet of blue crab, *Callinectes sapidus* (Molloy et al., 1994). Although new invaders may sometimes become prey, other studies show that the predator may fail to recognize the new invader as a food item, and allow populations of invaders to flourish and individuals to attain larger sizes than in their native range (McMahon et al., 2014). Predators may not approach or consume unfamiliar food because of "neophobia" or "dietary conservatism" (McMahon et al., 2014). Neophobia has been reported in birds (zebra finch, *Taeniopygia guttata*) (Kelly & Marples, 2004) where the hesitant approach from the predator to the prey species is brief, sometimes lasting only a few minutes. Dietary conservatism refers to situations where the predator refuses the novel food altogether, as reported in numerous bird (Marples et al., 2005) and fish species (Thomas et al., 2010; Richards et al., 2011; Richards et al., 2014).

American lobster predation behaviour

The American lobster (*Homarus americanus,* H. Milne Edwards, 1837) is native to the east coast of North America, ranging from Labrador to South Carolina. This species generally occurs from shallow subtidal areas up to depths of 50m (Pringle & Burke, 1993). This commercially valuable species supports a multi-billion dollar industry in the northeastern USA and Canada. Total annual landings in eastern Canada often exceed 70,000 tonnes (DFO, 2016) and it is the most important decapod crustacean to the fishing industry in Newfoundland, especially in rural outports, where 2016 landings of 2,280t were worth CAD$34,550,783 (DFO raw data, pers. comm. Elizabeth Coughlan, 2016).

H. americanus is a predator and scavenger with a broad omnivorous diet that includes molluscs, echinoderms, fish, algae and other crustaceans such as rock crab *(Cancer irroratus)* (League-Pike & Shulman, 2009). Crabs, in particular form an important part of lobster diets (Fogarty 1976; Scarratt, 1980; Gendron et al., 2001). Lobsters prefer size-specific prey (Elner & Jamieson, 1979) and strongly select rock crabs both in lab and field studies (McLeese, 1970; Reddin, 1973; Wilder, 1973; Gendron et al., 2001); they also prefer crabs when given the choice between crabs or sea urchins (Evans & Mann, 1977). Catching and consuming crabs offers a clear bioenergetic advantage given lobster requirements for high protein intake (Castell & Budson, 1974). Lobsters that lack crustaceans in their diet do not develop normal colouration (Hughes & Matthiessen, 1962) and they require calcium for successful moulting in order to strengthen the new shell. Lobsters fed a diet without rock crab (a reference diet containing similar protein levels) had lower glycogen and lipid levels and higher water content in their digestive gland, as well as reduced chela growth compared to a diet containing crabs (Gendron et al., 2001).

The natural range of the American lobster overlaps that of green crab in the low intertidal and shallow subtidal zones (Carlson et al., 2006; Goldstein et al 2017). In areas where lobsters and green crabs have co-existed for long periods, lab-based studies show that adult American lobsters inflict high mortality rates on *Carcinus.* In a lab study in Maine, large lobsters (72-79mm CL) killed and consumed 27% of medium sized (40-43mm CW) green crabs within a 24-hour period (League-Pike & Shulman, 2009). Similarly, Goldstein et al. (2017) reported that large lobsters (>80mm CL) kill and consume a variety of different sized green crabs when held together in a small enclosure. Although there was no significant difference in the average size of green crabs eaten by lobsters, the lobsters that actually consumed crabs were generally larger (>470g) than lobsters that did not feed on green crabs (<347g).

In Newfoundland (NL) green crabs have likely been present no longer than 13-15 years (Blakeslee et al., 2010; McKenzie et al., 2010; Matheson et al., 2012). Therefore, the first aim of the present study was to determine whether Newfoundland lobsters can recognize this newly invasive species when compared to lobster populations from Nova Scotia (NS) that have been exposed to green crabs many decades (Hypothesis 3). Further experiments determined whether lobsters attack and kill crabs for food or dispute over territory. Finally interactions dependent on the size of both the lobster and green crab were investigated to determine whether green crabs gain refuge from predation by growing above a certain size threshold (Hypothesis 4).

3.3 Materials and methods

Animal collection and housing

Adult male green crabs, *Carcinus maenas*, ranging in size from 30–76 mm (carapace width (CW) were collected using baited Fukui traps in Long Harbour, Placentia Bay, Newfoundland (45^{0} 25’46”N 53^{0}51’30”W). Crabs were transported to the Ocean Sciences Centre, Logy Bay, St. John’s, Newfoundland via road in secure fish boxes and covered with wet towels to prevent desiccation and escape. Only male crabs were kept and females were either destroyed or returned to the same site. The animals were maintained in seawater tanks (31-32ppt) at the Department of Ocean Sciences at Memorial University of Newfoundland. The green crabs were held in a flow-through seawater system and acclimated to temperatures of either 4^{0}C ± 2^{0}C or 12^{0}C ± 2^{0}C. No female crabs were housed, thus preventing reproduction and potential further spread of gametes via the flow-through system.

Adult lobsters (460-660g, 82.97mm carapace) were either purchased from Clearwater Ltd (Nova Scotia) or from a local harvester in Garden Cove, Newfoundland (47^{0}51’11”N 54^{0}9’29”W). Because of space restrictions, lobsters were held in a re-circulating seawater system at 12^{0}C ± 2^{0}C and a salinity of 30-32ppt prior to use. Perforated PVC pipe shelters were placed in all tanks to act as shelters. Both species were acclimated to experimental temperatures for three weeks prior to experiments (Camacho et al., 2006). Lobsters and green crabs were fed *ad libitum* once per week with mackerel (*Scomber scombrus)* but were starved for 8 days prior to experiments; this time period ensured all food was cleared from the gut and that animals would feed during experiments (Wang et al, 2016a).

<u>Experimental protocol</u>

Experiments were conducted in 38L (52cm x 34cm x 22cm deep) opaque plastic tanks containing seawater (32ppt) and an airstone maintained oxygen levels at 90-100% saturation (Figure 3.1a,b). The tanks were maintained at a water temperature of 12^{0}C ± 1^{0}C, which reflects summer averages in the shallow coastal areas of Newfoundland (Methven & Piatt, 1991; Matheson & Gagnon, 2012a; Colbourne et al., 2016). Because lobsters are primarily nocturnal foragers (Lipcius & Herrnkind, 1982) all experiments were conducted in darkness. Individual lobsters were weighed, measured, and placed in the tank and left for 15 minutes after handling; a single green crab was then added to the tank. Green crabs were categorised into three size classes; small (≤40mm CW), medium (40-65mm CW) and large (≥65mm CW) and each size class was replicated 10 times per treatment. Once a green crab was added to the tank, the trial began. The tank was examined after 1, 6 and 24 hours to quantify any damage inflicted on the green crab on a scale of 1 to 3, where a damage rating of 1 signified an unharmed green crab with and no damage incurred, a rating of 2 signified a crab injured by the lobster (leg/claw missing, carapace damage) and a rating of 3 denoted the lobster had killed and partially or wholly consumed the crab. Given the costs and logistics of holding large numbers of lobsters, we used the same lobster up to three times in different experiments (detailed below), but they were returned to the holding tanks and allowed to recover for at least 8 days before re-use.

We carried out four separate sets of experiments. In the first experiment, 30 lobsters from Nova Scotia (exposed to green crabs since the 1950s) and 30 lobsters from Newfoundland (exposed to green crab since 2002- 2007) were compared to determine whether green crab predation depended upon lobster origin. This experiment allowed us to determine whether lobsters from NL could recognize this newly invasive crab as a prey item. Results from this first set of experiments suggested no obvious differences in predation rates between lobsters from NS and NL. Therefore, we pooled lobsters in further experiments using an equal number (n=15) from both locations, starving all lobsters for 8 days prior to experimentation. In the second set of trials, lobsters were offered mackerel and allowed to feed for 12 hours prior to introduction into the tank. This experiment was designed to determine whether lobsters that are not hungry would still attack or consume a green crab which might indicate that the interaction resulted from something other than predation. In the third series of experiments, we introduced a piece of mackerel (approximately 20g) to the tank at the same time as the crab to determine whether an alternative food source would alter interactions between the lobster and crab, and whether the lobster would prefer fish over the crab. In the final set of experiments, we starved lobsters for 8 days and added a PVC pipe (13 cm x 9 cm diameter, one side covered in 1mm^2 mesh panel) to the tank as a potential refuge for the green crab. This experiment was designed to determine whether lobsters would actively seek out and hunt down a crab, rather than simply attacking them or consuming them because they were easy to interact with or catch.

An additional series of experiments was conducted to determine whether the green crabs could use size to gain refuge from predation. The previous series of experiments (above) used a restricted size range of lobsters of (460-660g); we therefore added a wider size range encompassing both smaller and larger lobsters (308-1272g). Lobsters were starved for 8 d and large green crabs were measured and introduced into the tank and the experiment was checked at 1, 6 and 24h. The size of lobster used was plotted against the maximum size green crab that they consumed. This approach enabled us to determine whether size of a lobster was related to the maximum size of green crab that they would injure and consume.

Statistical analysis

Given three possible outcomes for each observation (crabs with no damage, crabs being attacked and damaged, crabs being attacked and eaten), we performed an ordinal logistic regression in R (R Core Team, 2012: package “ordinal”; Christensen, 2015) to test for significant differences between the probability of occurrence for each of these three outcomes given different factors. In an ordinal regression, the assumption is that the three possible outcomes can only occur sequentially; a crab can only been attacked and eaten after it has been attacked and damaged. The ordinal regression is used to estimate the probability of one outcome transitioning to another (with the assumption that all individuals start at the initial state) and how a set of covariates influence the probability of the transition.

In the experimental set-up, we checked for the influence of the continuous covariates; crab width and lobster mass, and the influence of the lobsters’ origin (either being from NL or NS). Additionally, due to the fact that crabs were checked for damage in multiple replicates (after 1 hr, 6 hrs, and 24hrs), the sequential replicates were non-independent; thus, the random effect for the replicate was included in the model. To account for the fact that individuals were used multiple times in separate replicates, the models were tested to include an individual level random effect.

To check for model fit, we estimated the amount of residual deviance explained by the model by comparing the deviance of the fully-saturated model against that of a null model –or a model containing only an intercept term.

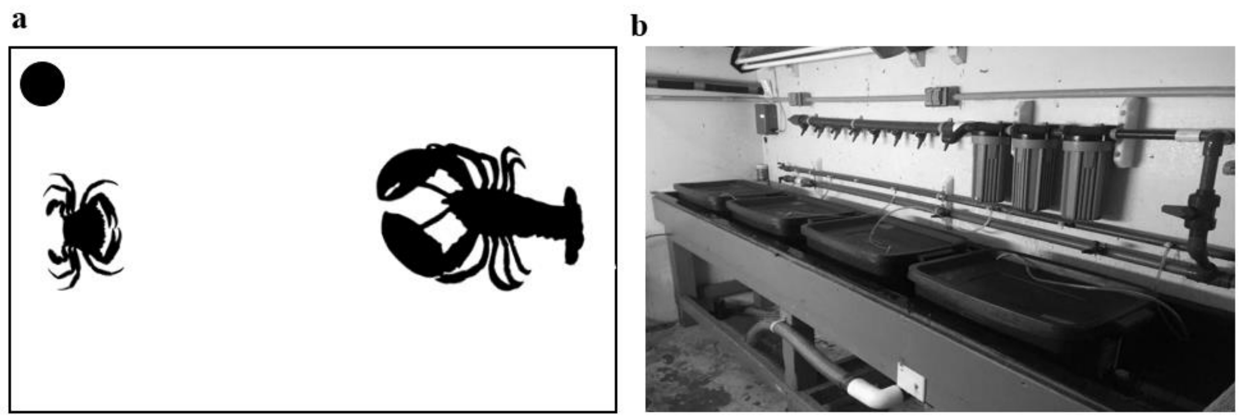

Figure 3.1. Predation experimental set-up. a) Diagram of top-down view of tank, black circle = airstone, b) Photograph of experimental set-up showing four individual tanks.

3.4 Results

The ordinal regression model revealed several significant results from the experiments. First, there was overall a greater likelihood of crabs being unharmed by a lobster than being eaten or damaged, however, crabs were more likely to be eaten once they had been damaged first (Table 3.1). It was also found that larger crabs were less likely to be attacked and injured, or eaten, than the smaller crabs, as seen in Fig 3.2.; as crab size increased, the probability of outcome 1 (the crab being left alone) occurring increased, and the probability of outcome 3 (the crab being eaten) decreased. There were no significant influences of lobster mass (Fig. 3.3) or lobster origin (NS vs NL, Figs. 3.4, 3.5) on the likelihood of a crab being attacked or eaten as lobsters from Nova Scotia and

Newfoundland, and of all sizes, were equally likely, or unlikely, to damage and consume a crab. Feeding the lobster shortly before the trial began, or offering an alternative bait source to the lobster, decreased the likelihood of the lobster attacking and consuming all sizes of green crabs, as there was high probabilities of crabs being left alone (outcome 1) and low probabilities of crabs being attacked and eaten (outcomes 2 and 3, respectively) (Figs. 3.6, 3.7, “Fed”, “Bait”). There was no significant difference between the presence of a shelter to the likelihood of a crab being damaged or eaten by a lobster, compared to when there was no shelter offered, as the probabilities of outcomes 1, 2, and 3 occurring where the same (Figs. 3.6, 3.7, “Shelter”). The regression analysis showed no significant effect on crab predation as a function of lobster size, and only lobsters sized between 308g - 1140g injured and consumed large green crabs, (Fig. 3.8, injured: $p = 0.967$, consumed: $p = 0.931$).

3.5 Discussion

Our experiments demonstrate that small and medium-sized green crabs represent a potential prey item for Newfoundland lobsters, suggesting that lobster predation could play a mitigating role on the impacts of green crab invasion in Newfoundland. This predatory behaviour has reported elsewhere; adult American lobsters prey upon green crabs in Maine, USA and in Nova Scotia, Canada (Jones & Shulman, 2008; League-Pike & Shulman 2009; Haarr & Rochette, 2012; Goldstein et al., 2017). As no difference in the predatory behaviour between Nova Scotian and Newfoundland lobsters was observed, lobsters presumably recognise crabs as potential prey without necessarily requiring exposure to the prey species for long periods of time. Haarr & Rochette (2012) also noted that green crabs from different regions of Atlantic Canada (St. George's Bay, Nova Scotia (NS) and Passamaquoddy Bay, New Brunswick (NB)) recognised juvenile lobsters as prey items and suggested underlying biologically significant differences between crab populations, but noting negative impacts of predation by green crabs on juvenile lobsters in all areas.

Lobster predation behaviour

Lobsters naturally consume crabs because they are an important food source that provide necessary energy and chemical compounds (Fogarty 1976; Scarratt, 1980; Gendron et al., 2001). Lobsters from both NS and NL prey on native rock crabs (*Cancer irroratus*), therefore they may also naturally recognise other crabs as potential food items because of a heritable component of feeding behaviour (Pyke, 1984). Indeed, crabs may comprise up to 80% of lobster energy intake (Evans & Man, 1977) in the wild and green crabs offer an efficient energy source for lobsters because they contain protein amounts (average 17.1g /100g protein; Skonberg & Perkins, 2002), similar to that that of their primary prey *Cancer sp.* (17.8g/100g; King et al., 1990).

In this study, lobsters injured and consumed green crabs of all sizes across all experimental treatments, however, as crab size increased, predation decreased. Optimum foraging theory (Pyke, 1984) suggests that animals prey on items within their functional constraint, i.e. a predator can kill and consume prey species small enough to effectively injure to result in death but large enough to supply sufficient energy to the predator. Lobsters in our study preferred small and medium sized crabs, perhaps as a direct result of their size, given that larger crabs may be harder to handle or kill, or alternatively because killing and eating smaller crabs has a higher energetic pay-off (Pyke, 1984).

Prey selection reflects a series of decisions by the predator that balance the costs of handling the food and the benefits of consuming the food, therefore, a predator must feed in a way that maximises their rate of net energy intake (Emlen 1966; MacArthur & Pinaka, 1966). For example, the amount of energy used by the lobster to catch and kill a large crab may yield a net deficit in caloric intake because it takes more energy to kill a larger animal. In addition, large green crabs may be fast enough to avoid attacks from a lobster or large enough to fight off a lobster. Studies of other crustaceans report an associated risk for the predator when choosing prey because the interaction may place the predator at risk to physical damage (Elner & Hughes, 1978).

Although the lobsters preferred crabs <65mm CW, even the smallest lobsters occasionally killed and consumed the largest green crabs. This observation suggests that even when lobsters and green crabs are closely matched in size, lobsters may win in combat. Smaller lobsters (<300g) also benefit by consuming large green crabs given their high energetic value (King et al., 1990). In the wild, lobsters also encounter large green crabs when the lobsters leave their burrows (Cobb, 1971; Dybern, 1973). Large green crabs occur in high numbers in the subtidal and intertidal zones, and medium- and small-sized green crabs largely restrict their distributions to the intertidal zone in order to avoid predation from fish and other crustaceans (Berril, 1982; Hunter & Naylor, 1993; Warman et al., 1993; Baeta et al., 2007). Although American lobsters primarily occupy the subtidal zone they will make excursions into the intertidal zone over nocturnal high tides to feed, and they readily prey on native rock crab *Cancer irroratus* and invasive green crab *C. maenas* (Jones & Shulman, 2008).

We found significant differences in predation on green crabs when lobsters had been fed mackerel shortly before the start of the trial; fed lobsters were less likely to damage and eat the crab, but this occurrence did still happen. Lobsters tend to feed approximately every 8h and 5h when maintained at temperatures of 10^{0}C and 15^{0}C, respectively (Wang et al., 2016a). As we did observe some lobsters eating crabs even when fed, the lobsters may well have become hungry again and fed upon the green crab due to the 24hr period of which the experiment was underway. After a lobster feeds, the time to digest and partially expel the food can be less than 24h at temperatures of 15^{0}C (Wang et al., 2016a). Additionally, lobsters begin to feed again when approximately 20% of the food in their foregut has cleared (Wang et al., 2016a). Therefore, although the lobster was fully satiated at the start of the experiment, it could start to process this meal and be ready to feed again within the 24h experimental period.

The results showed that there was less damage and predation upon a crab when alternative bait was added to the tank, an effect that was statistically significant. We added approximately 20g of mackerel to the tank, which represented roughly 3-4% of the lobster body mass, or a single meal (Wang et al., 2016). The lobster (and the green crab) may have consumed this entire food parcel and begun to pursue the green crab when it became hungry again. We chose not to add larger pieces of fish because the green crab tended to use it as a shelter and hide from the lobster. Therefore, at this stage, we cannot infer whether lobster with access to an unlimited food supply would prey upon green crab.

<u>Habitat complexity</u>

The addition of the shelter did appear to slightly reduce the likelihood of a crab being consumed by a lobster, however perhaps because of the nature of the shelter itself, this was not statistically significant (portion of PVC tube with one side covered in mesh). In nature, green crabs occupy structurally complex habitats and hide in rock crevices in order to evade predators (McDonald et al., 2001; Jensen et al., 2002). Previous laboratory studies have shown that juvenile green crabs structurally simple habitat (e.g. sand) increases predation risk (Gehrels et al., 2017) compared to structurally complex habitat (e.g. mussel/ oyster beds). In this study, the lobster could still access the one shelter available to the green crab as a refuge using their chelae. Additional smaller shelters in the tank, such as cobbles or rocks with crevices, may have yielded greater results given that spatial heterogeneity can affect predation rates (Gilinsky, 1984; Holt, 1984; Fortis et al., 2015). Other studies also report changes in green crab behaviour in the presence of a lobster. For example, medium sized crabs (30-43 mm CW) climb and hide significantly more, and walk around the tank significantly less in the presence of a lobster (League-Pike & Shulman, 2009). We did not observe such behaviour in our study perhaps because we did not monitor the experimental tanks or alternatively because the shelter we provided offered an adequate refuge.

We chose tanks in our study small enough to confine the green crab and allow an interaction with the lobster, and primarily to determine whether lobsters from Newfoundland would attack and prey upon a crab. However, this small tank size may have skewed our results somewhat because it left the green crab very limited escape options. Other experiments on lobster and green crab interactions have utilized widely ranging tank sizes from 90cm round fibreglass tanks (Rossong et al., 2006) to larger rectangular 60cm x 215cm tanks (Williams et al., 2006), some with increased spatial heterogeneity (Haarr & Rochette, 2012). When using larger tanks where crabs could escape (Chapter 1), we rarely observed lobsters consuming green crabs. Moreover, preliminary experiments (Rayner & McGaw, unpublished observations) with increased habitat complexity and space and a larger supply of food showed considerably reduced crab predation. In the wild in Newfoundland, lobster traps represent the only instance where these two species would be direct contact in such a small area (Carter & Steele, 1982). Lobsters in traps sometimes attack and kill green crabs, but this behaviour appears to be indiscriminate and driven by disputes over access to food, noting that lobsters also attack and kill rock crabs and other lobsters (Zargarpour, MSc thesis, in prep.). Whether green crabs form part of the natural diet of lobsters in Newfoundland remains unknown, however, studies in New England report frequent occurrence of green crabs in lobster guts (Jones & Shulman, 2008; Donahue et al., 2009; League-Pike & Shulman, 2009).

Use of green crab in lobster fishery

As laboratory studies show that lobsters feed on green crabs and the importance of other crab species in their diet (Evans & Man, 1977; Carter & Steele, 1982; Jones & Shulman, 2008; Donahue et al., 2009; League-Pike & Shulman, 2009), invasive green crab could be an effective and "free" bait source and a means of mitigating the population. Nova Scotia lobsters in the laboratory showed no significant differences in bait preference between traditional finfish bait and the green crab bait (Ryan et al., 2014). In addition Hancock (1974) observed that dead decapods effectively repel live conspecifics, which suggests that dead green crabs as bait might deter other green crabs from entering the trap. This strategy may prove effective if the main management objective is to deter green crabs from entering a baited lobster trap, while still attracting lobster.

At present there no field studies in Newfoundland have assessed green crab as lobster bait, this is due to licencing constraints because of a potential risk of disease transfer between green crabs and lobsters. The parasite *Polymorphus botulus* (Acanthocephala: Palacacanthocephala) reported in green crabs in Nova Scotia has the potential to infect lobsters (Clark et al., unpub. data). However, this parasite also infects eider ducks, scoters, and rock crabs across Atlantic Canada (Brattey & Campbell, 1985), and rock crabs comprise an important component of lobster diets. It is likely that *P. botolus* already occurs widely in local lobster populations. Nevertheless until the ban is lifted the potential for green crab as effective bait in Newfoundland cannot be tested. However the risk of distributing green crab to uninvaded regions must also be considered in evaluating green crab as bait. However recent studies have used parasite transfer in their favor by purposefully releasing the castrating barnacle parasite *(Sacculina carcini)* to control the spread and abundance of the green crab invasion (Marculis & Lui, 2015; Bateman et al., 2017) and resulted in the castrating parasite infecting commercial crab species with associated economic consequences.

Conclusion

It is important to assess the potential damage green crab is having on the lobster fishery and other marine habitats in Newfoundland, and to find innovative mitigation strategies. In addition to competing for food with adult lobsters (Chapter 2), green crabs may actively prey on juvenile lobsters. Previous laboratory studies showed that green crabs kill and consume juvenile lobsters (28-57mm CL) not within a shelter (Rossong et al., 2006) and green crabs ranging from 50-80mm CW actively predate upon juvenile lobsters ranging from 18-43mm CL (Harr & Rochette, 2012). Even smaller green crabs of 14-26mm carapace width actively consume newly settling stage IV lobster larvae (Sigurdson & Rochette, 2013).

As previously discussed, the natural diets of American lobster include crab, but they may not be the favoured prey item (Carter & Steele, 1982). The fishery typically uses mackerel and other finfish as bait; lobsters can detect their oil hundreds of metres away (Miller, 1990). However, the results presented here and elsewhere (Ryan et al., 2014) suggest the green crab could be an effective bait for lobster fishery while concurrently mitigating this invasive crab populations. Nonetheless, further research is required.

Tables

Table 3.1. Parameter estimates from the ordinal regression on whether crabs were left alone (outcome =1), attacked (outcome=2) or eaten (outcome=3). All coefficients are on the logit scale. The notation '1|2' indicates the likelihood of outcome 2 occurring given a non-attacked crab. All values in bold indicate significant effects at alpha = 0.001

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
1|2	**-2.42**	**0.6**	**-4.01**	**0**
2|3	**-1.78**	**0.6**	**-2.98**	**0**
CrabLength	**-0.05**	**0.01**	**-6.02**	**0**
LobsterOrigin	-0.41	0.22	-1.87	0.06
LobsterMass	**-6.1**	**2.08**	**-2.93**	**0**
TreatBait	**-1.26**	**0.3**	**-4.17**	**0**
TreatFed	**-0.93**	**0.29**	**-3.17**	**0**
TreatShelter	-0.12	0.28	-0.43	0.67

Figures

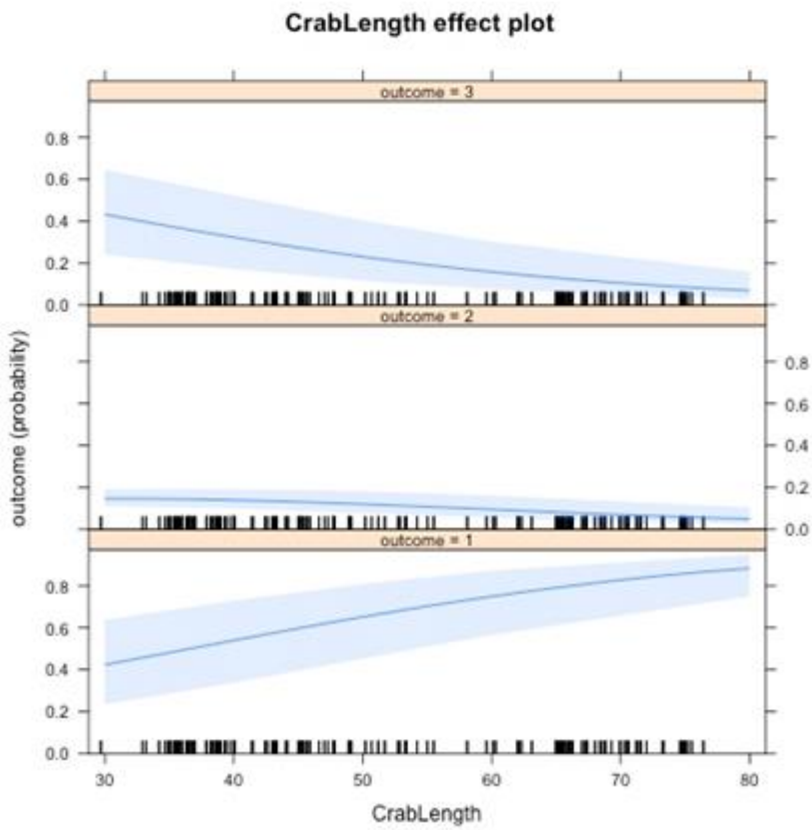

Figure 3.2. Marginal effects for the influence of Crab Length on the probability of its being left alone (outcome=1), attacked (outcome =2) or eaten (outcome=3). Blue lines indicate the linear fit on a logit scale, while blue shading indicates 95% confidence intervals.

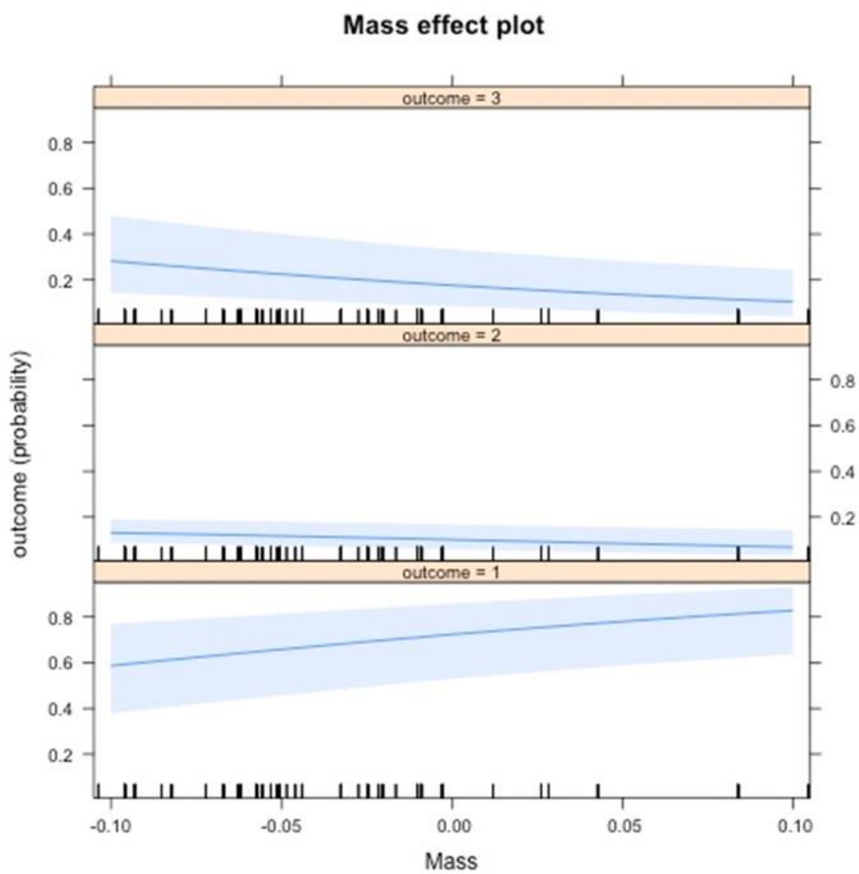

Figure 3.3. Marginal effects for the influence of Lobster Mass on the probability of its leaving a crab alone (outcome=1), attacking a crab (outcome =2) or eating a crab (outcome=3). Blue lines indicate the linear fit on a logit scale, while blue shading indicates 95% confidence intervals.

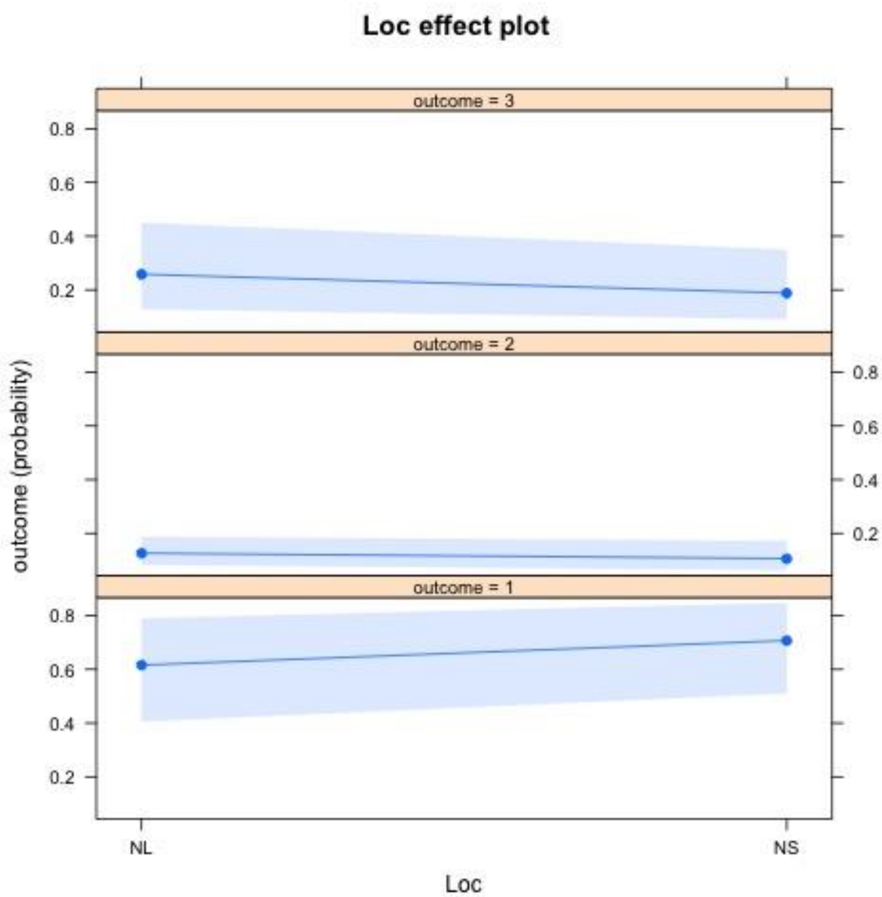

Figure 3.4. Marginal effects for the influence of Lobster Origin on the probability of its being left alone (outcome=1), attacked (outcome =2) or eaten (outcome=3). Blue lines indicate the linear fit on a logit scale, while blue shading indicates 95% confidence intervals.

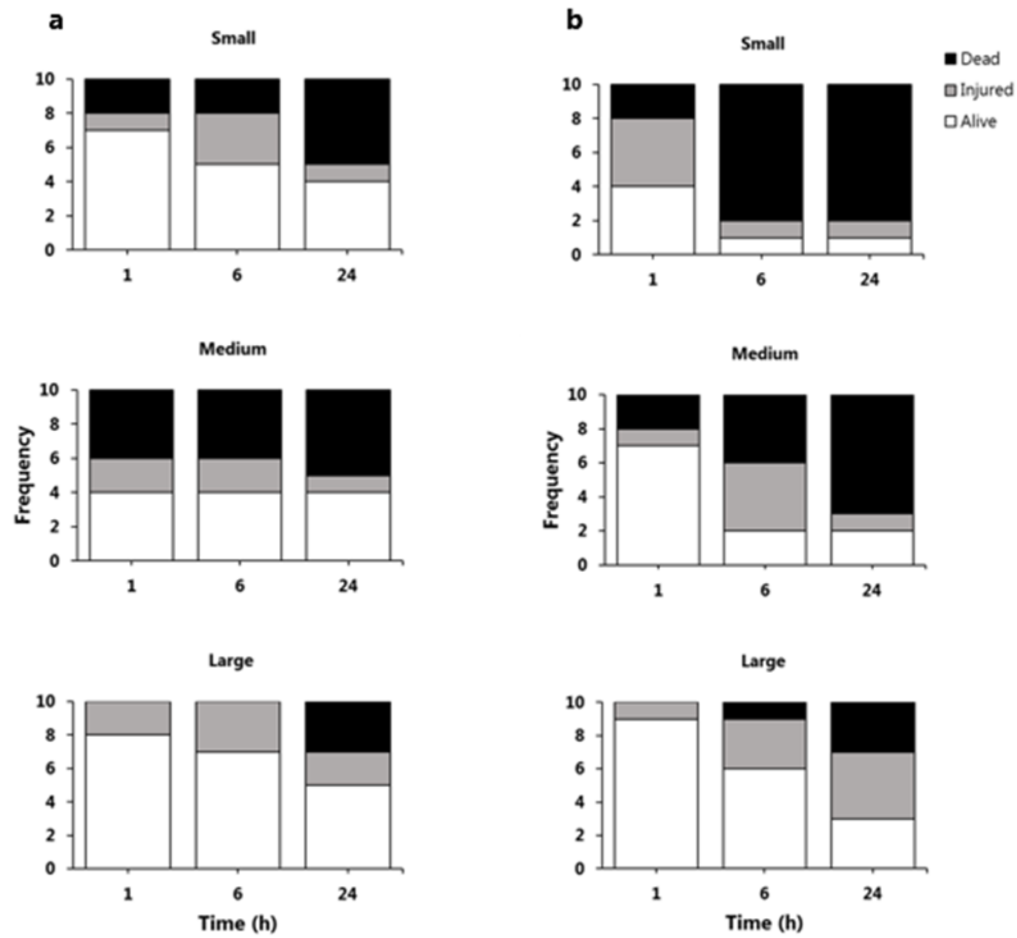

Figure 3.5. Frequency of damage inflicted on small, medium and large green crabs *(Carcinus maenas)* by an adult American lobster, *Homarus americanus,* originating from a) Newfoundland (NL) and b) Nova Scotia (NS).

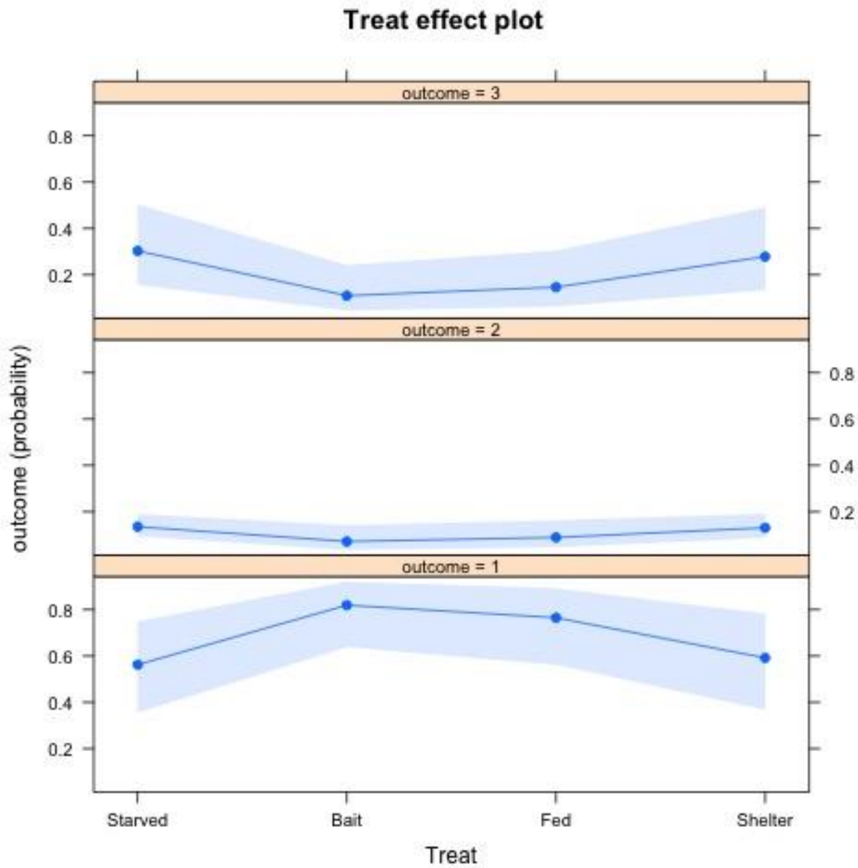

Figure 3.6. Marginal effects for the influence of Treatment (Starved, Bait, Fed, Shelter) on the probability of a lobster leaving a crab alone (outcome=1), attacking a crab (outcome =2) or eating a crab (outcome=3). Blue lines indicate the linear fit on a logit scale, while blue shading indicates 95% confidence intervals.

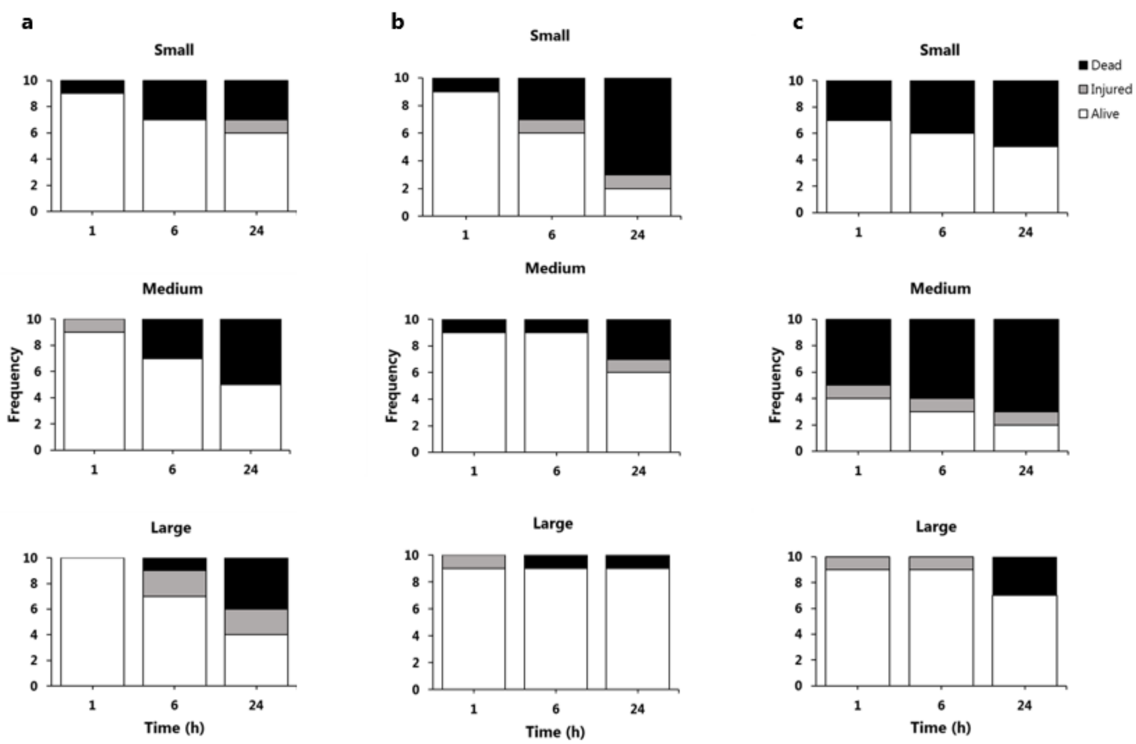

Figure 3.7. Frequency of damage inflicted on small, medium and large green crabs *(Carcinus maenas)* by an adult American lobster, *Homarus americanus,* when lobsters were a) fed with mackerel prior to the introduction of a green crab (group 2), when b) an alternative food source (mackerel) was added into the tank at the same time as the crab (group 3) and c) when a shelter was added as a refuge for the green crab (group 4).

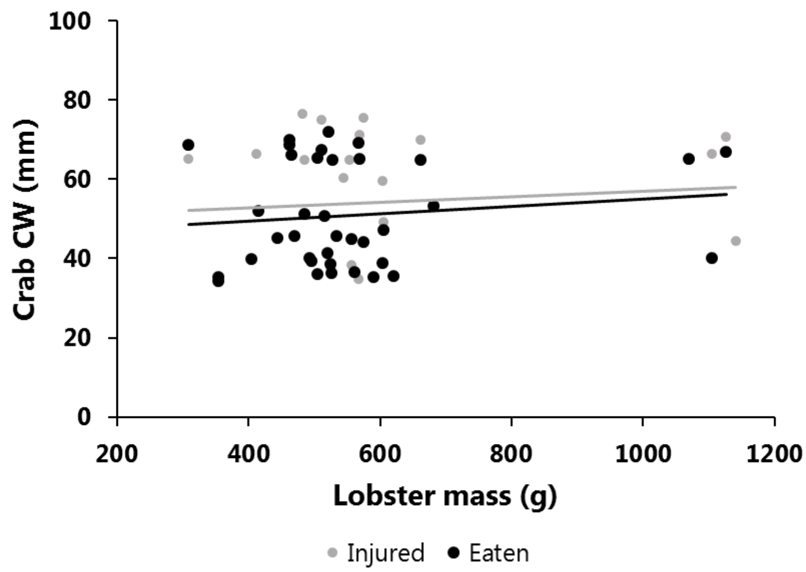

Figure 3.8. The largest sized green crab, *Carcinus maenas*, injured or consumed by an adult American lobster, *Homarus americanus*, using data from all trials. Injured: y=0.007x + 49.979, R^2=0.0104, p=0.967, Eaten: y=0.0092x + 45.791, R^2=0.0159, p =0.931.

4. General Discussion

Summary

The objective of this thesis was to determine how invasive green crab affects food acquisition and catchability of American lobster, and to investigate if lobsters will predate upon green crabs in the laboratory environment. In addition, I set out to evaluate effects of crab density and water temperature on lobster and green crab behaviour, and how these effects might influence a lobster's actions towards a food source or a baited trap. This is the first study on behavioural interactions between adults of the two species, and it addresses food acquisition and competition, and quantifies green crab effects on lobster catchability in the laboratory. My study showed a negative effect of green crabs at high densities on lobster behaviour around a food source, in that crabs readily consumed all of the food before a lobster could approach it. Further, I found that the number of agonistic behaviours emitted between the species increases, via retreating and approaching behaviours, increased with crab density. I also observed moderate densities of green crab deter lobsters from approaching and entering a baited trap within the laboratory, and that water temperature affects physical activity in both lobsters and green crabs. I also confirmed that American lobsters consume green crabs in the laboratory, and that lobster origin had no effect on crab predation, but crab size and time of exposure influenced predation rates.

Interactions

My study shows that the invasion of green crab in Newfoundland could have potentially affected the food acquisition of lobsters and the behavioral interactions around traps, which may have influenced local lobster populations or numbers of lobster caught in the commercial fishery. The effect of green crabs on lobster behaviour around a food source suggests localised high green crab densities in Placentia Bay will likely have detrimental effects on the local lobster population and these effects could be more prominent in the future as green crabs invade adjacent bays on the south coast. Water temperature significantly affected lobster and green crab behaviour. However, because the lobster fishery season begins when sea temperature starts to increase in the spring, increased emergence and activity of green crabs at that time could impact lobsters. Finally, Newfoundland lobsters will recognize the newly invasive green crab as potential prey. Despite a lack of evidence of predation in the wild, crabs could provide a food source for lobsters and, in turn, the lobsters may help reduce crab numbers.

Importance to Canada and the lobster fishery

This study can inform the provincial and federal governments on how to address the problems associated with green crab invasions in Newfoundland in terms of mitigation projects and on potential use of green crabs as a bait in the fishery. Suggestions for the Placentia Bay fishery include:

1. Shorter trap soak times to prevent the traps from filling with green crabs. Hauling traps more frequently will reduce the number of green crabs in the traps that may deter lobster from entering.
2. The use of bait within pots to prevent green crabs from eating it before a lobster can reach the trap. When bait is placed unprotected in the trap or in a mesh bag/ bait cage, green crabs can still reach the bait and fully consume it before the bait odour attracts a lobster.

3. Fishing in deeper areas away from green crabs because green crabs occur more commonly in the intertidal zones in contrast to subtidal areas favoured by lobsters.
4. Using green crab as bait in the lobster fishery to attract lobsters and to deter green crabs from entering, because traps baited with conspecifics may deter green crab entry.

<u>Future work</u>

Because this study was conducted fully in the laboratory, some caution should be taken when extrapolating results to the natural environment. However, this study provides data on agonistic interactions between lobsters and green crabs. Future studies that include field experiments would provide more comprehensive understanding of how the two species interact with each other in the wild. My initial data suggest a need for further studies on the catchability of lobsters and green crabs and the behavioural interactions between them. I also recommend more diving surveys to estimate lobster abundance in the field in Newfoundland in order to clarify the effects of green crabs on adult lobsters (Rossong et al., 2006; Zargarpour, MSc thesis, In prep.). Such *in situ* data on how these two species interact could help in stock assessment of green crab in Newfoundland waters. It would also be beneficial to compare the behavioural interactions seen here between lobsters and green crabs to those with native rock crab to evaluate retreat/approach behaviours around food and a trap. It would also be beneficial to conduct additional experiments using the native rock crab *(Cancer irroratus)* to assess the interactions between lobsters and a crab that it is naturally exposed to determine the effects they may have on lobster food acquisition and catchability.

Noting the essential role of laboratory studies in ecological research, studies in larger tanks could offer a more complex environment and control experimental parameters, reducing the number of necessary field studies. The use of newer camera equipment to document behavioural interactions more precisely e.g. the use of automatic computer vison tools to analyse lobster posture (Yan & Alfredsen, 2017) would also enhance these studies by quantifying a greater range of interactions between species. Additionally, studies on exploitable uses for green crab in Newfoundland are essential in order to mitigate rising green crab population, prevent further spread, and reduce the negative impacts of this species on native fauna.

Application to aquaculture industry

My study confirms that their may be negative effects of green crabs on lobsters in Newfoundland, however, I could not determine whether they have contributed to decreased lobster fishery landings. In recent years, a pilot study conducted in conjunction with the Marine Institute (Memorial University, St. John's, Newfoundland) and FFAW (Fish, Food and Allied Workers' Union) examined restocking Placentia Bay lobster with juvenile larvae. However, this pilot study only operated for one year. I believe that restocking Placentia Bay lobsters with juveniles or sub-adults reared in a hatchery could prove effective. Numerous lobster hatcheries in Europe, New England (USA) and New Brunswick (Canada) have helped to restock wild lobster populations for the commercial fishery. The Placentia Bay fishery could benefit from such a program both economically and socially, through direct benefits to lobster harvesters and local builders constructing the hatchery and potential indirect benefits though increased education and tourism for the local communities through the construction of a hatchery.

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Appendix

Additional tables for Chapter 1 lobster and crab behaviour experiments

Tables

Table A.1 Summary of the two-way ANOVA examining the effects of temperature (4 & 12^{0}C) and green crab *(C. maenas)* density (n=0/1/5/25) on the amount of time taken for an adult lobster *(H. americanus)* to handle the food source.

Source of variation	df	F	MS	p
Temperature	1	1.684	19.115	0.2
Crab Density	3	2.393	27.168	0.079
Temperature *Crab Density	3	1.475	16.742	0.232
Error	52		11.353	
Corrected Total	59			

Table A.2 Summary of the two-way ANOVA examining the effects of temperature (4 & 12^{0}C) and green crab *(C. maenas)* density (n=0/1/5/25) on the amount of time taken for a green crab to approach the food source.

Source of variation	df	F	MS	p
Temperature	1	31.141	12396.417	<0.01
Crab Density	2	14.404	5733.897	<0.01
Temperature *Crab Density	2	8.432	3356.422	<0.01
Error	67		398.075	
Corrected Total	72			

Table A.3 Summary of the two-way ANOVA examining the effects of temperature (4 & 12^{0}C) and green crab *(C. maenas)* density (n=0/1/5/25) on the number of retreats an adult lobster *(H. americanus)* would display.

Source of variation	df	F	MS	p

Temperature	1	0.769	13.828	0.383
Crab Density	2	21.516	386.938	<0.01
Temperature *Crab Density	2	1.883	33.871	0.158
Error	84		17.984	
Corrected Total	89			

Table A.4 Summary of the two-way ANOVA examining the effects of temperature (4 & 12^{0}C) and green crab *(C. maenas)* density (n=0/1/5/25) on the number of body raises an adult lobster *(H. americanus)* would display.

Source of variation	df	F	MS	p
Temperature	1	2.525	376.337	0.116
Crab Density	2	0.681	101.530	0.509
Temperature *Crab Density	2	2.088	311.249	0.130
Error	84		149.053	
Corrected Total	89			

Table A.5 Summary of the two-way ANOVA examining the effects of temperature (4 & 12^{0}C) and green crab *(C. maenas)* density (n=0/1/5/25) on the number of claw raises an adult lobster *(H. americanus)* would display.

Source of variation	df	F	MS	p
Temperature	1	0.099	2.174	0.754
Crab Density	2	10.830	237.230	<0.01
Temperature *Crab Density	2	1.491	32.660	0.231
Error	84		21.905	
Corrected Total	89			

Table A.6 Summary of the two-way ANOVA examining the effects of temperature (4 & 12^{0}C) and green crab *(C. maenas)* density (n=0/1/5/25) on the number of claw grasps an adult lobster *(H. americanus)* would display.

Source of variation	df	F	MS	p
Temperature	1	3.812	104.426	0.054
Crab Density	2	4.753	130.190	0.011
Temperature *Crab Density	2	0.879	24.079	0.419
Error	84		27.393	
Corrected Total	89			

Table A.7 Summary of the two-way ANOVA examining the effects of temperature (4 & 12^{0}C) and green crab *(C. maenas)* density (n=0/1/5/25) on the pooled number of interactions an adult lobster *(H. americanus)* would display towards a green crab.

Source of variation	df	F	MS	p
Temperature	1	4.836	1019.004	0.031
Crab Density	2	4.143	872.964	0.019
Temperature *Crab Density	2	2.801	590.118	0.066
Error	84		210.697	
Corrected Total	89			

Table A.8 Summary of the two-way ANOVA examining the effects of temperature (4 & 12^{0}C) and green crab *(C. maenas)* density (n=0/1/5/25) on the number of retreats green crabs would display.

Source of variation	df	F	MS	p
Temperature	1	7.730	160651.648	<0.01
Crab Density	2	122.450	2544728.035	<0.01
Temperature *Crab Density	2	2.710	56325.288	0.072
Error	84		20781.768	
Corrected Total	89			

Table A.9 Summary of the two-way ANOVA examining the effects of temperature (4 & 12^{0}C) and green crab *(C. maenas)* density (n=0/1/5/25) on the number of body raises green crabs would display.

Source of variation	df	F	MS	p
Temperature	1	0.006	0.334	0.938
Crab Density	2	42.981	2370.629	<0.01
Temperature *Crab Density	2	0.704	38.831	0.497
Error	84		55.155	
Corrected Total	89			

Table A.10 Summary of the two-way ANOVA examining the effects of temperature (4 & 12^{0}C) and green crab *(C. maenas)* density (n=0/1/5/25) on the number of claw raises green crabs would display.

Source of variation	df	F	MS	p
Temperature	1	34.442	14338.126	<0.01
Crab Density	2	45.778	19057.144	<0.01
Temperature *Crab Density	2	13.359	5561.249	<0.01
Error	84		416.292	
Corrected Total	89			

Table A.11 Summary of the two-way ANOVA examining the effects of temperature (4 & 12^{0}C) and green crab *(C. maenas)* density (n=0/1/5/25) on the number of claw grasps green crabs would display.

Source of variation	df	F	MS	p
Temperature	1	0.343	31.719	0.560
Crab Density	2	18.429	1704.931	<0.01
Temperature *Crab Density	2	2.517	232.812	0.087
Error	84		92.514	
Corrected Total	89			

Table A.12 Summary of the two-way ANOVA examining the effects of temperature (4 & 12^{0}C) and green crab *(C. maenas)* density (n=0/1/5/25) on the pooled number of interactions green crabs will display towards an adult lobster *(H. americanus)*

Source of variation	df	F	MS	p
Temperature	1	21.97	12661.512	<0.01
Crab Density	2	87.588	50476.995	<0.01
Temperature *Crab Density	2	5.08	576.299	<0.01
Error	84			
Corrected Total	89			

Table A.13 Summary of the two-way ANOVA examining the effects of temperature (4 & 12^{0}C) and green crab *(C. maenas)* density (n=0/1/5/25) on adult lobster *(H. americanus)* food consumption.

Source of variation	df	F	MS	p
Temperature	1	0.011	0.001	0.915
Crab Density	3	0.072	1.603	0.178
Temperature *Crab Density	3	0.016	0.363	0.780
Error	122		0.045	
Corrected Total	131			

Table A.14 Summary of the two-way ANOVA examining the effects of temperature (4 & 12^{0}C) and green crab *(C. maenas)* density (n=0/1/5/25) on green crab*)* food consumption.

Source of variation	df	F	MS	p
Temperature	1	84.410	7.327	<0.01
Crab Density	3	1.039	0.090	0.354
Temperature *Crab Density	3	0.050	0.004	0.951
Error	922		0.087	
Corrected Total	928			

Additional tables of tests for catchability experiments

Table A.15 Summary of the MANOVA examining the effects of temperature (4 & 12^{0}C) and green crab *(C. maenas)* position (absent/in/out) on the number of times an adult lobster *(H. americanus)* unsuccessfully attempted to enter the baited trap.

Source of variation	df	F	MS	p
Temperature	1	1.273	101.265	0.264
Treatment	2	5.591	444.688	<0.01
Temperature *Treatment	2	0.394	31.314	0.677
Error	53			
Corrected Total	58			

Table A.16 Summary of the one-way ANOVA examining the effects of temperature (4 & 12^{0}C) and green crab *(C. maenas)* position (absent/in/out) on the number of times an adult lobster *(H. americanus)* would attempt to enter the baited trap.

Source of variation	df	F	MS	p
Temperature	1	1287	116.463	0.261
Treatment	2	5.696	445.766	0.006

Table A.17 Summary of the MANOVA the effects of temperature (4 & 12^{0}C) and green crab *(C. maenas)* position (absent/in/out) on the number of times an adult lobster *(H. americanus)* successfully entered the baited trap.

Source of variation	df	F	MS	p
Temperature	1	8.354	208.537	<0.01
Treatment	2	0.085	2.122	0.919
Temperature *Treatment	2	0.531	12.247	0.591
Error	53			
Corrected Total	58			

Table A.18 Summary of the one-way ANOVA examining the effects of temperature (4 & 12^{0}C) and green crab *(C. maenas)* position (absent/in/out) on the number of times an adult lobster *(H. americanus)* was caught in the baited trap.

Source of variation	df	F	MS	p
Temperature	1	8.746	207.807	0.005
Treatment	2	0.112	3.134	0.894

Table A.19 Frequency of undersize (<82.5 mm CL) and oversize (>82.5 mm CL) of lobsters (*Homarus americanus*), green crabs *(Carcinus maenas)* and rock crabs *(Cancer irrotatus)* being caught in Placentia Bay.

Species	Number Caught
Lobster <82.5 mm CL	34
Lobster >82.5 mm CL	81
Green Crab <40 mm CW	129
Green Crab 40-65 mm CW	231
Green Crab >65 mm CW	79
Rock Crab	360

Table A.20 Frequency of American lobsters *(Homarus americanus)*, green crabs *(Carcinus maenas)* and rock crabs *(Cancer irroratus)* being caught in the same trap together in Placentia Bay.

	Lobster	Green	Rock
Lobster	23	1	5
Green	1	96	61
Rock	5	61	94

Field experiments

The distribution of crabs and lobsters in the field was conducted on a local lobster fishing vessel in Garden Cove, Placentia Bay (47^{0}51’11”N 54^{0}9’29”W, Figure 1). The catch per unit effort, species overlap and size ranges of lobsters and green crabs were recorded. Catch per unit effort is here defined as the number of individuals caught as a function of soak time (Bennett, 1974). Data was collected in June 2016 when the fishing zone is open in the study area. In total, data collection spanned over 5 days, hauling on average 100 traps per day (n=612) after a soak time of 12-48 hours. Each trap was of the traditional D-shape wooden slat design (Slack-Smith, 2001) and was baited with either herring (*Clupea sp*.), cod (*Gadus sp*.) or flatfish (*Hippoglossoides sp*.). Weather, water depth and temperature and coordinates of each hauled trap was recorded and any bycatch species was noted, along with lobster size, sex, if the lobster was berried and crab size and number per trap. The catchability of lobsters in the presence of the native rock crab *(Cancer irroratus)* was also quantified.

Out of 615 traps hauled in the field, only on one occasion was a lobster found in the same trap as a green crab, but overlap between rock crabs and lobster occurred five times throughout the sampling period. As previously stated, the presence of lobsters in a trap can actively deter crabs from entering a trap (Richards et al., 1983; Addison, 1995), so it is important to address this question in future studies as to whether low crab presence in the trap is due to a saturation effect of lobsters or vice versa. It can also be suggested that the reason for low species overlap or catch rates in general observed in Placentia Bay may be due to a number of factors. This data is presented here as preliminary data because;

1. Bait type and soak time were not controlled for and these may have influenced catch rates
2. The CPUE was determined at just one time point when the traps were hauled. There was no data on entry and exit of species over time. As green crabs rapidly detect and feed on bait it is likely they moved into the trap and then escaped once they had fed.
3. The nature of the traps allowed green crabs and small lobsters to easily escape, but tended to select for capture of larger lobsters, but we had no way to assess this.
4. The traps were positioned in different water depths and the overlap area of green crabs and lobsters may be limited in some deeper locales
5. The trapping time was limited to one season and 5 days in one bay. More comparative studies are needed to draw firmer conclusions.

Figures

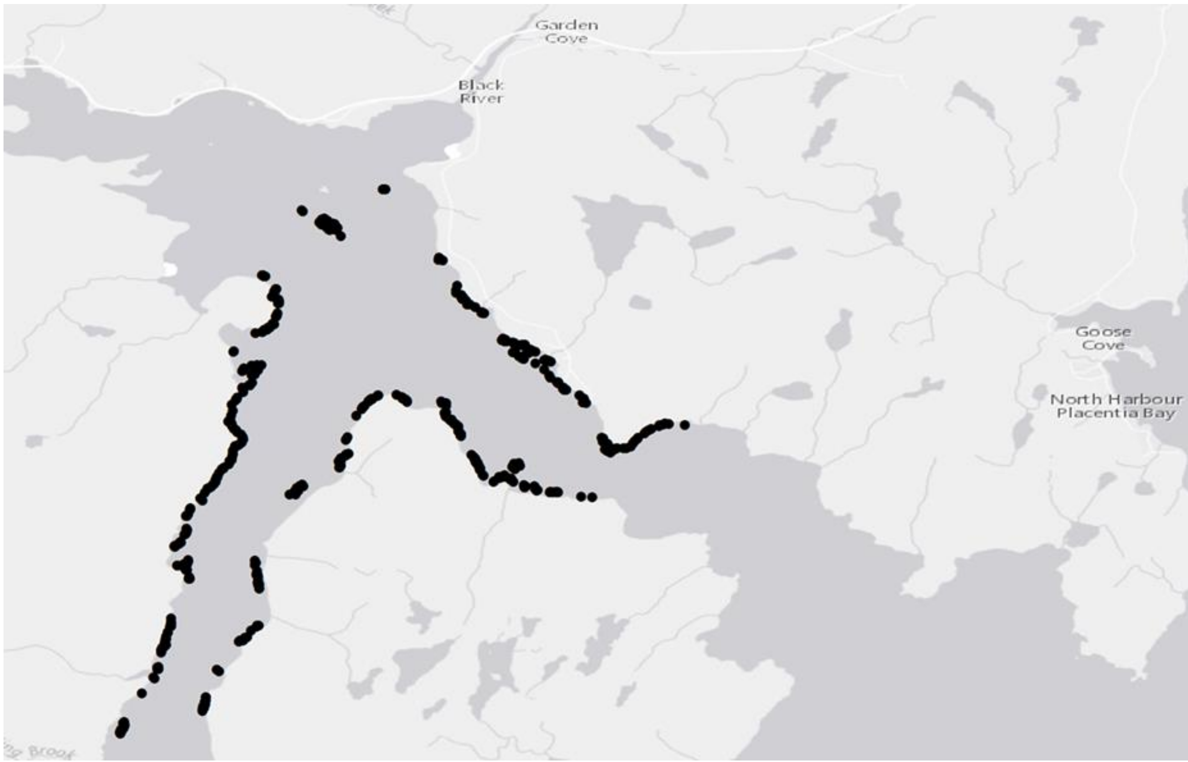

Fig A.1 Map of Garden Cove, Placentia Bay, Newfoundland. Markers represent the position of 612 traps hauled in June 2016. Map of the sampled field area were produced using ESRI Arcmap version 10.0, ArcGIS.

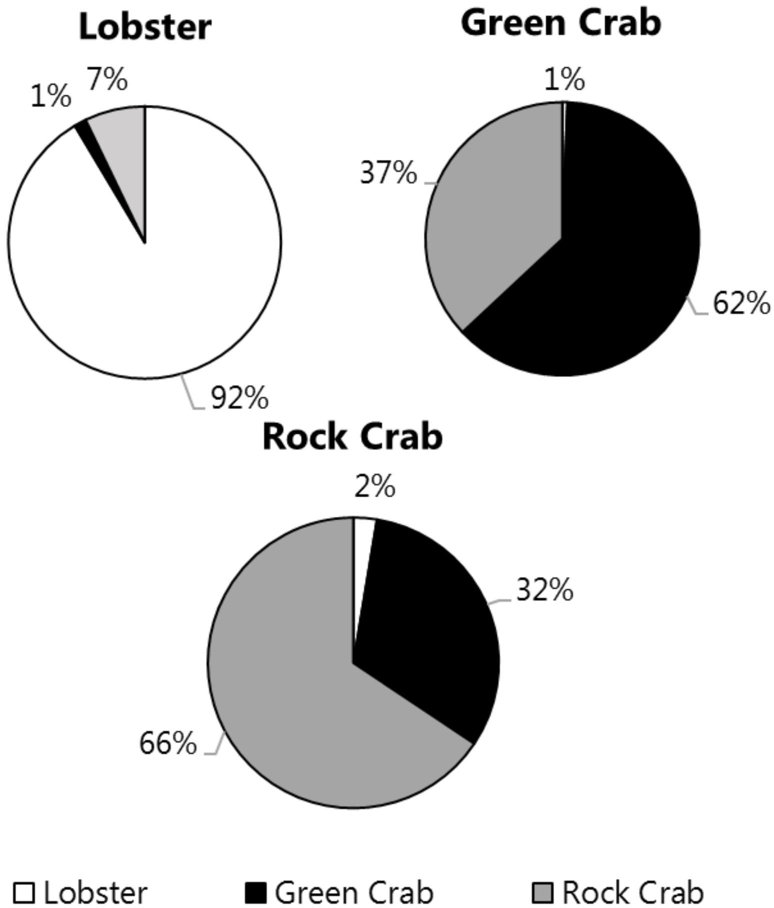

Fig A.2 Percentage of species overlap of lobsters *(Homarus americanus)*, green crabs *(Carcius maenas)* and rock crabs *(Cancer irrotus)* in traps in Garden Cove, Placentia Bay.

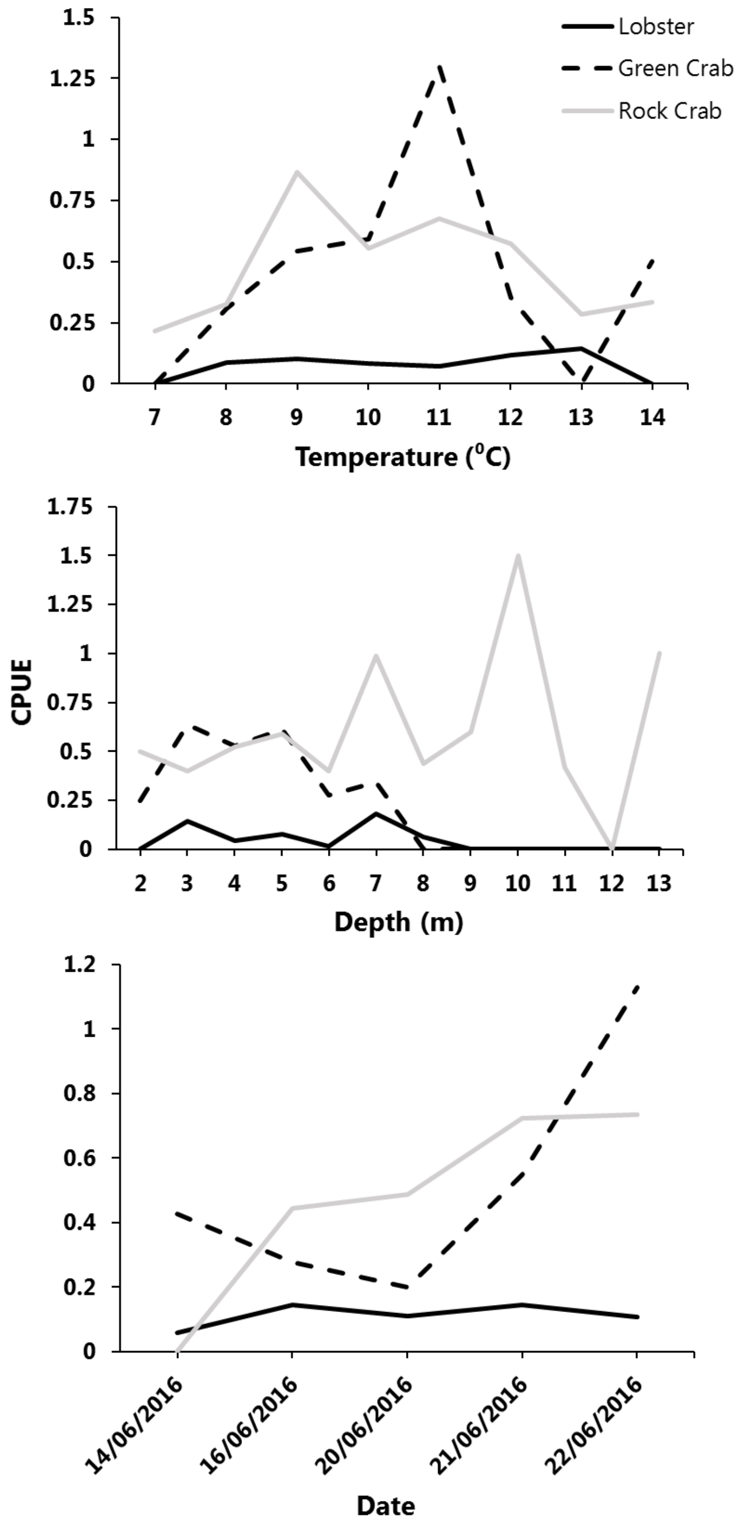

Fig A.3 Catch per unit effort (CPUE) of lobsters, *Homarus americanus,* green crabs, *Carcinus maenas,* and rock crabs, *Cancer irrroratus*, in Garden Cove, Placentia Bay, dependent on water temperature, depth and time.