EFFECTS OF TEMPERATURE AND COMPETITION ON FORAGING IN INDIGENOUS ROCK (Cancer irroratus) AND RECENTLY INTRODUCED GREEN (Carcinus maenas) CRABS FROM NEWFOUNDLAND AND LABRADOR, CANADA

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Effects of temperature and competition on foraging in indigenous rock (*Cancer irroratus*) and recently introduced green (*Carcinus maenas*) crabs from Newfoundland and Labrador, Canada

By

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ABSTRACT

This thesis determined experimentally how temperature (cold [4°C] versus warm [12°C] water) affects predation success in indigenous rock (*Cancer irroratus*) and recently introduced green (*Carcinus maenas*) crabs from Newfoundland and Labrador under non-competitive and competitive conditions. Prey (the blue mussel, *Mytilus edulis*) capture and size selection as well as associated foraging behaviors were measured in both crab species. Additional factors (crab size, prey size, chela loss, and chemical cues from conspecifics and heterospecifics) were included to gain further insights about how this green crab introduction may alter the structure of shallow benthic ecosystems in this region. Analysis of predation data under non-competitive conditions indicated that 1) mussel capture in rock and green crabs was higher in large than small individuals, 2) chela loss decreased mussel capture uniquely in rock crabs while causing only subtle changes in mussel size selection in both species, and 3) chemical cues from other crabs did not affect mussel capture in rock crabs, yet altered mussel size selection and the frequency of foraging behaviors in small rock crabs only. Increasing temperature from 4 to 12°C exacerbated these patterns by significantly increasing mussel capture in both species. Analysis of predation data under competitive conditions indicated that 1) green crabs primarily grasped the mussel before rock crabs regardless of temperature and body size and chela loss in rock crabs, 2) the number of contests between rock and green crabs was unaffected by temperature and body size and chela loss in rock crabs though the frequency of strong physical interactions was higher in contests with large than small rock crabs, and 3) large rock crabs initiated contests with green crabs more frequently than smaller conspecifics in warm water only while winning more contests than small rock crabs regardless of temperature. Therefore, the introduction of green crab to Newfoundland and Labrador (currently the northern distribution limit of the species) may negatively impact foraging in rock crabs, whether the latter are equal or larger in size than the largest green crabs. The observed marked preference by small green crabs for small mussels suggests that green crabs may alter mussel populations in this region, which could affect interactions with other species that rely on mussels as a food source.

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CHAPTER I

GENERAL INTRODUCTION

Biological invasion, broadly defined as the successful establishment of a species into a habitat with no historical record of occurrence, can substantially alter ecosystem structure and function. Biological invasions in aquatic ecosystems have increased markedly in the past few decades primarily through local, regional, and transoceanic transport of propagules, juveniles, and adults in ballast waters or on the surface of ships (Cohen and Carlton, 1998; Grosholz and Ruiz, 2002; Ruiz et al., 1997). One notorious example of global invasion by a marine species is that of the green crab, *Carcinus maenas* (Cohen et al., 1995; Elner, 1981; Gardner et al., 1994; Hidalgo et al., 2005; Le Roux et al., 1990; Yamada et al., 2005). Native to Europe, the green crab was documented for the first time in the northwest Atlantic in Massachusetts in 1817 (Say, 1817). Current geographic distribution ranges from southern Virginia (USA) (Williams, 1984) to Newfoundland and Labrador (Canada) where it was first discovered in 2007 (Blakeslee et al., 2010; McKenzie et al., 2010).

Field and laboratory studies partly attribute the successful establishment of the green crab throughout this oceanographically diverse region to its tolerance to broad changes in temperature and salinity (Beukema, 1991; Eriksson and Edlund, 1977; Hidalgo et al., 2005). However, food consumption, growth, and reproduction in larval and adult stages of the green crab typically decrease with decreasing temperature, and cold water temperature may therefore partly regulate the northern distribution limit of the species in the northwest Atlantic (Berrill, 1982; Glude, 1955; Wallace, 1973; Welch, 1968). This suggestion is supported by the slow, northward migration of the species throughout eastern Canada where it was first reported in the early 1950s in Nova Scotia (more than 50 years before it was recorded in Newfoundland and Labrador) and by the late 1990s in Prince Edward Island (Audet et al., 2003; Gillis et al., 2000). Moreover, genetic analyses suggest multiple green crab introductions occurred in the Canadian Maritime provinces (presumably from European populations), including that of a particularly cold-tolerant strain that spread to areas thought to be too cold for the species (Roman, 2006).

The green crab is a voracious predator with a broad diet that includes polychaetes, gastropods, crustaceans, and algae (Cohen et al., 1995; Ropes, 1968). Consequently, foraging (i.e. the course of actions leading to prey capture) in green crabs that invade new habitats with a new array of prey choices may be less affected than other invasive species that have narrower diets. Despite its generalist diet, the green crab exhibits a strong preference for bivalves (Dare et al., 1983; Mascaró and Seed, 2001; Miron et al., 2005; Ropes, 1968; Sanchez-Salazar et al., 1987), and has been responsible for declines in abundances of soft shell clam, *Mya arenaria,* in New England (Glude, 1955) and the clams *Nutricola tantilla* and *N. confuse* in the eastern Pacific (Grosholz et al., 2000). Green crabs are generally more abundant in embayments with low wave and current energy than along exposed coastlines (Grosholz and Ruiz, 1995), which increases the risk of mortality in potential prey in these habitats (Grosholz and Ruiz, 1996). Green crab can also affect populations of indigenous species through indirect effects across trophic levels (Trussell et al., 2002; Trussell et al., 2003; Trussell et al., 2004). For example, waterborne cues released by green crabs can reduce feeding in the dog whelk *Nucella lappillus*, which in turn decreases whelk consumption of barnacles and fucoid algae (Trussell et al., 2003). Green crabs can also induce phenotypic plasticity in prey as seen in the snail *Littorina obtusata* and the dog whelk, *N. lappillus*, which both develop thicker shells in the presence than absence of green crabs (Rochette et al., 2007; Trussell and Nicklin, 2002). These examples demonstrate that green crab introductions can affect recipient ecosystems significantly by altering feeding, behavior, and morphology of competitor and prey species.

In eastern Canada, rock crab, *Cancer irroratus*, is one of the most abundant, indigenous crustaceans in the shallow, rocky subtidal zone (Caddy and Chandler, 1976; Drummond-Davis et al., 1982; Scarratt and Lowe, 1972). Adapted to the cold water environments of this region, rock crab can maintain physical activity at sea temperature as low as 3ºC (Winget et al., 1974). Like green crab, rock crab exhibits a generalist diet and strong preference for the blue mussel, *Mytilus edulis* (Drummond-Davis et al., 1982; Scheibling, 1984), and both crab species can co-occur in sandy and rocky shallow subtidal habitats (Grosholz and Ruiz, 1995; Hudon and Lamarche, 1989; Jeffries, 1966). Such dietary and spatial overlaps between an indigenous and non-indigenous species can increase the frequency and intensity of competitive interactions, which can ultimately affect the structure of marine communities (Connell, 1961; Dayton, 1971; Grabowski and Kimbro, 2005). Green crabs can physiologically accommodate to changes in temperature within the range of 3 to 26 ºC (Eriksson and Edlund, 1977; Grosholz and Ruiz, 2002). However, predation success (i.e. the number of prey captured per unit of time) can decrease substantially in the lower part of this range and even cease below 7°C (Bélair and Miron, 2009b; Breen and Metaxas, 2008; Ropes, 1968). In Newfoundland and Labrador water temperature varies seasonally from approximately -2°C during winter to 16°C for only a few days during summer (Methven and Piatt, 1991). Effects of sustained low temperature on foraging in recently introduced green crabs from Newfoundland and Labrador are unknown. Understanding how the thermal environment affects predation and competition in green crabs in this province is an important step for predicting and mitigating their ecological and socioeconomic impacts in this fishery-oriented region.

In response to competition, decapod crustaceans can modify foraging strategies and their use of spatial refuges (Grabowski and Kimbro, 2005; Griffen et al., 2008). While processes that control the coexistence of competing species can differ across habitats, competition can be reduced and species can coexist if resources are partitioned spatially or temporally (MacArthur and Levins, 1964; Menge and Sutherland, 1976; Navarrete and Castilla, 1990). As shown by laboratory experiments, green crabs can physically displace Dungeness crabs, *Cancer magister*, of similar body size from shelters and win contests for prey in one-on-one competitive interactions (McDonald et al., 2001). Shelter loss can increase vulnerability to predation, and hence decrease survival rates (Hudon and Lamarche, 1989; Jeffries, 1966). Several studies show that in crustaceans large individuals can outcompete smaller individuals for space and food resources (Glass and Huntingford, 1988; Smallegange et al., 2007; Smith et al., 1994), which may ultimately affect patterns of distribution and prey selection. For example, large *Cancer productus* and *C. antennarius* can limit the distribution of green crabs in the eastern Pacific (Hunt and Yamada, 2003; Jensen et al., 2007), where five species of *Cancer* crabs grow larger in size than green crab, of which four grow more than twice the size of green crab (Jensen et al., 2007). In contrast, rock crab is the only *Cancer* species along the coast of Newfoundland and Labrador (Squires, 1990), where it too can grow twice as large (up to 140 mm in carapace width) as the largest green crabs (K. Matheson, personal observation). Nonetheless, a large body size does not necessarily provide a competitive advantage since aggressiveness, which can compensate for small body size, varies across crustacean species (Hazlett, 1971). Williams et al. (2006) found that large green crabs can outcompete larger and heavier sub-adult American lobsters, *Homarus americanus*, for a limited food source. Green crabs competing for food often initiate contests by establishing physical contact with their chelae rather than by displaying chelae as a warning signal (Sneddon et al., 1997a; Williams et al., 2006). In contrast, rock crabs facing other crustaceans often retreat without fighting and small individuals commonly hide in sediments, between rocks, or underneath seaweeds (Hudon and Lamarche, 1989; Scarratt and Lowe, 1972). These behavioral patterns therefore suggest that body size may not help achieve competitive dominance, if any, of rock crabs over green crabs.

The 2007 discovery of green crab in Placentia Bay, along the south shore of Newfoundland (Blakeslee et al., 2010; McKenzie et al., 2010), provided the opportunity to experimentally determine and compare predation success and competitive ability in this recently introduced crab species and a likely indigenous competitor (the rock crab) adapted to cold water environments under a suite of conditions reflecting natural environmental variability. In Chapter II two laboratory experiments are used to determine effects of changes in water temperature, body size, chela loss, and chemical cues on capture and size selection of blue mussels (*Mytilus edulis*) and associated behaviors in rock and green crabs from Newfoundland and Labrador held individually in microcosm tanks. Specifically, it tests the hypotheses that: 1) mussel capture in rock and green crabs increases with increasing body size, 2) large rock and green crabs select larger mussels than small crabs, 3) chela loss in both species decreases mussel capture while altering mussel size selection, and 4) chemical cues from conspecifics [rock crab] and heterospecifics [green crab] alter mussel capture and size selection in rock crabs. Each hypothesis is tested in cold (4°C) and warm (12°C) water to determine how temperature representative of the current northern limit of green crab distribution in the northwest Atlantic affects patterns. In Chapter III rock and green crabs from Newfoundland and Labrador are used to determine experimentally how changes in water temperature (4°C versus 12°C), body size, and the loss of one chela affects the ability of one rock crab to compete with one large green crab for prey (a single blue mussel). It tests the hypotheses that: 5) the ability of the rock crab to grasp the mussel before the green crab decreases with decreasing body size and chela loss, 6) the proportion of time the rock crab holds the mussel decreases with decreasing body size and chela loss, 7) the number of contests and associated degree of physical interactions between rock and green crabs decrease with decreasing body size and chela loss, 8) the likelihood that the rock crab initiates and wins contests with the green crab decreases with decreasing body size and chela loss, and 9) the proportion of time the rock crab is buried in sediments or within a cavity increases with decreasing body size and chela loss. Both Chapters II and III are written in a format compatible with the publication of research articles, which explains the repetition of information where appropriate, as well as the use of first-person plural pronoun ("we") and possessive determiner ("our") throughout. Chapter IV presents a summary of main findings and briefly explains their significance and contribution to our knowledge of the potential impacts of the introduction of the green crab to coastal habitats of Newfoundland and Labrador.

Co-authorship statement

The work described in this thesis was conducted by Kyle Matheson with guidance from Patrick Gagnon, Cynthia McKenzie, and Paul Snelgrove. Kyle Matheson was responsible for field and laboratory data collection and analysis (with assistance by Patrick Gagnon) and contributed to modifications brought to the original design by Patrick Gagnon. All chapters were written by Kyle Matheson with intellectual and editorial input by Patrick Gagnon. A shortened version of Chapter II is published in the journal *Journal of Experimental Marine Biology and Ecology* (full reference below). A shortened version of Chapter III is currently being reviewed by the same journal. Any additional publication in the primary literature resulting from this work will be co-authored by Kyle Matheson and Patrick Gagnon.

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CHAPTER II

Temperature mediates non-competitive foraging in indigenous rock (*Cancer irroratus* Say) and recently introduced green (*Carcinus maenas* L.) crabs from Newfoundland and Labrador

2.1 INTRODUCTION

The green crab, *Carcinus maenas*, is a voracious predator with a broad diet consisting primarily of bivalves, but also gastropods, polychaetes, and crustaceans (Cohen et al., 1995; Elner, 1981; Ropes, 1968). Predation by green crabs can directly or indirectly alter benthic communities, reduce fishery stocks, and cause economic losses in the aquaculture industry (Grosholz et al., 2000; Leber, 1985; Walton et al., 2002). In eastern Canada, the indigenous rock crab, *Cancer irroratus*, is a numerically dominant crustacean predator in shallow subtidal ecosystems (Caddy and Chandler, 1976; Drummond-Davis et al., 1982). Diets of green and rock crabs overlap and the two species exhibit strong preference for the blue mussel, *Mytilus edulis* (Cohen et al., 1995; Elner, 1981; Hudon and Lamarche, 1989; Mascaró and Seed, 2001; Miron et al., 2005; Ropes, 1968). Although rock crab can forage at temperatures as low as 3°C (Winget et al., 1974), foraging in the green crab generally decreases rapidly below 7°C (Bélair and Miron, 2009b; Eriksson and Edlund, 1977; Ropes, 1968) and death can occur in green crab during prolonged periods of exposure to subzero temperatures (Crisp, 1964; Welch, 1968).

Intra- and interspecific competition and predation are largely determined by the diet of organisms (Sih et al., 1985; Wilbur and Fauth, 1990). In eastern Canada, the overlapping diets and shared preference of rock and green crabs for the blue mussel suggest these crab species may compete for food. For example, laboratory microcosm experiments with rock and green crabs held together and offered prey of different sizes in four bivalve species, including *M. edulis*, showed that rock crabs captured fewer prey species than green crabs, therefore suggesting that rock crabs spend more time searching for particular prey than green crabs (Miron et al., 2005). Bélair and Miron (2009b) documented similar mussel consumptions in rock and green crabs foraging singly (in the absence of conspecifics and heterospecifics) and in the presence of one another at temperatures between 5 and 20°C. Overall, those studies have helped increase our understanding of how variation in prey availability and temperature may affect prey capture in rock and green crabs. However, the effect of temperature on prey size selection in both species remains largely unexplored.

According to optimal foraging theory, predators should select prey items based on prey and habitat characteristics to maximize energy intake (Charnov, 1976; Emlen, 1966; Pulliam, 1974). Therefore, optimal foraging theory predicts that prey selection should follow quantitative rules based on whether prey types should or should not be included in an optimal diet (Pulliam, 1974; Werner and Hall, 1974). Many factors influence prey selection, including relative abundance and nutritional value of prey, distance to prey, prey handling time, and environmental variables such as temperature (Burch and Seed, 2000; Juanes and Hartwick, 1990; Mascaró and Seed, 2001; Miron et al., 2005; Sanchez-Salazar et al., 1987; Werner and Hall, 1974). Prey size and predator physiology can markedly affect the foraging strategy of a predator, especially when the prey has hard body parts (e.g. mussel shells) that require longer handling time, and hence higher predator energy expenditure (Barbeau and Scheibling, 1994a; Hughes and Elner, 1979). A few experimental studies investigating prey selection suggest green crabs select prey sizes that provides the highest energy per unit of handling time (Ameyaw-Akumfi and Hughes, 1987; Hughes and Elner, 1979). However, other studies also indicate that green crabs (and other decapods) select suboptimal prey sizes to avoid damaging predatory limbs (chelae) when attempting to crush larger, harder shelled prey (Juanes, 1992; Juanes and Hartwick, 1990; Smallegange and Van Der Meer, 2003).

Crabs rely on their chelae to crush or open hard-shelled prey (Elner, 1978) and chelae morphology and the speed and force at which dactyls (chelae parts) collapse vary among species (Seed and Hughes, 1995). Rock crab has one pair of monomorphic chelae that produce similar crushing forces (Pattinson et al., 2003). In contrast, green crab has one pair of dimorphic chelae: one relatively large 'crusher' chela used primarily to crush prey and one smaller, faster 'cutter' chela to grasp and control prey movement (Elner, 1978; Smallegange and Van Der Meer, 2003). As reviewed by Juanes and Smith (1995), limb damage and autotomy (induced severance) in decapod crustaceans is common, with up to 55 and 60% of *Cancer* spp. and *C. maenas* individuals missing at least one limb in populations of the northeast Pacific and northern Europe, respectively. Autotomy most frequently involves chelae and results from inter- and intraspecific encounters (Juanes and Smith, 1995; Smith and Hines, 1991). Matthews et al. (1999) showed that of male green crabs collected from four sites along southern New England and missing at least one limb, nearly half missed one or both chelae. Autotomy can negatively affect crabs by reducing intermoult growth (Smith, 1990), mating success (Abello et al., 1994), and strength of regenerating chelae (Brock and Smith, 1998). Chela loss and damage can reduce prey capture and alter prey preference (species and size), but this pattern varies with crab species and the severity and number of limbs lost (Davis et al., 2009; Juanes and Hartwick, 1990; Mathews et al., 1999; Smith and Hines, 1991). Individual and combined effects of chela loss and temperature on foraging in both rock and green crab are not well understood.

Many crustacean predators rely on chemical cues in their environment to assess the presence of prey, competitors, and other predators at distances that often exceed visual detection (Lee and Meyers, 1996; Rebach, 1996; Weissburg and Zimmer-Faust, 1994). While cues from prey can stimulate foraging, cues from predators and competitors can reduce and even terminate foraging (Hazlett, 1997; 1999), especially in small individuals that are more vulnerable to predation or less competitive (Stein, 1977; Wahle, 1992). Therefore, predators with chemosensory organs such as rock and green crabs should be able to alter foraging based on the presence or absence of cues from prey, predators, or competitors. Combinations of cues can also lead to trade-offs between foraging and avoidance behaviors (Hazlett, 2003; Lima and Dill, 1990). For example, crayfish often respond to cues from predators by reducing feeding (Hazlett, 1999), whereas chemical cues from bodily fluids in lethally injured blue crabs (*Callinectes sapidus*) can increase avoidance by conspecifics (Ferner et al., 2005). Further research is required to better understand effects of temperature and chemical cues on foraging in rock crabs.

In this study, we use two laboratory microcosm experiments with rock and green crabs from Newfoundland and Labrador held individually and offered blue mussels (*Mytilus edulis*) to test hypotheses that: 1) mussel capture in rock and green crabs increases with increasing body size, 2) large rock and green crabs select larger mussels than small crabs, 3) chela loss in both species decreases mussel capture while altering mussel size selection, and 4) chemical cues from conspecifics and heterospecifics alter mussel capture and size selection in rock crabs. We test each hypothesis in cold (4°C) and warm (12°C) water to determine how patterns are affected by temperature representative of the current northern limit of the green crab distribution in the northwest Atlantic.

2.2 MATERIALS AND METHODS

2.2.1 Collection and selection of crabs for experimentation

Our study was conducted with rock and green crabs hand collected by divers or captured with Fukui traps (baited with herring) between late May and November 2009, and in June 2010. Crabs were collected from the upper subtidal zone at sites along the western (Bonne Bay), southern (North Harbor), and eastern (Petty Harbour, Bay Bulls, Tors Cove, Bauline East) shores of Newfoundland. Crabs were transported in containers with seawater to the Ocean Sciences Centre (OSC) where they were placed in 330-L holding tanks supplied with seawater pumped in from a depth of ~5 m in the adjacent embayment, Logy Bay. Only male crabs were used (females in both species were discarded at collection sites) to eliminate potential variation in foraging that could result from morphological and behavioral differences between the sexes (Abello et al., 1994; Elner and Hughes, 1978). Green crabs with a slightly red or orange carapace were also discarded at the collection site because this coloration may be indicative of a stronger, thicker carapace (and hence potentially stronger chelae) resulting from a prolonged intermolt period (Reid et al., 1997).

Crabs from each species were divided in experimental groups based on commonly captured sizes (carapace width). Three and two groups were formed for rock and green crabs, respectively. Carapace widths in small (RS), medium (RM), and large (RL) rock crabs were 48.5 (± 5.8), 67.9 (± 5.2), and 93.9 (± 6.0) (SD) mm, respectively, whereas carapace widths in small (GS) and large (GL) green crabs were 40.2 (± 4.2) and 60.5 (± 4.5) mm, respectively (see Appendix A for additional morphological data). Large rock crabs were, on average, ~33 mm larger than green crabs. This difference resulted from the intentional use of the largest individuals in each species to allow comparisons with other studies that used the same approach. The medium size category in rock crabs was added to allow comparisons of individuals of approximately equal sizes in the two species (RM versus GL; these differed by less than 7.5 mm on average). Crabs in holding tanks were fed twice a week with live blue mussels, *Mytilus edulis*, maintained in separate holding tanks supplied with running seawater. Crabs and mussels in holding tanks were exposed to ambient temperatures of water pumped in from Logy Bay and to natural light entering the laboratory through large windows.

2.2.2 Experimental tanks and acclimation of crabs prior to experimentation

Trials were conducted in glass aquaria (62 [length] x 31 [width] x 43 [height] cm) supplied with flow-through seawater. Water flow in each tank was set at ~1 L min^{-1} to ensure consistency in water conditions among trials. Water depth in each tank was approximately 40 cm. To mimic natural substratum the bottom of each tank was covered with a 3-cm layer of sediments collected from the upper intertidal zone near the OSC.

Small rocks (~5-10 cm in diameter) and a 15-cm diameter plastic pot cut in half and placed atop the sediments in the middle of each tank further mimicked crab habitat and provided crabs with the opportunity to bury and move into a protective shelter (Fig. 2.1). Each tank was surrounded by a thick, opaque canvas to eliminate any light or visual stimuli from the lab. An incandescent, 100-watt light bulb (Soft White, General Electric) was positioned 45 cm above the water surface and controlled with dimmers and timers to create the desired light environment (see below).

Crabs were maintained in holding tanks for a minimum of one week prior to acclimation to experimental conditions. Acclimation took place within glass aquaria similar to those used during experimental trials and consisted of exposing each crab for 72 h to the same water temperature (cold [4°C] or warm [12°C], see below) and photoperiod (held constant among temperature treatments, with 12 h of light followed by 12 h of darkness) as in the experimental treatment they were assigned to. Light intensity was kept relatively low, 90 to 100 lux as measured at the air-water interface with a handheld photometer (Smart Sensor RDI-AR823), to reduce physiological stress and behavioral modification that may result from shifts in light intensity every 12 h when light bulbs automatically turned on or off. Simulated daylight occurred between 07h00 and 19h00 every day and all trials were conducted between 10h00 and 17h00 to facilitate crab observations. Crabs were not fed during the acclimation period to standardize hunger levels.

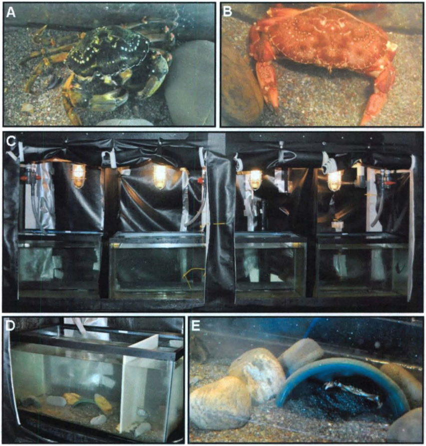

Figure 2.1. Photographs showing specimens of (A) green crab, *Carcinus maenas,* and (B) rock crab, *Cancer irroratus*, (C) four of the tanks used in Experiments 1 and 2, (D) one of the plastic dividers used during acclimation to separate crabs from mussels in Experiments 1 and 2 [a similar divider was placed at the other end of the tank to physically isolate crabs used to produce chemical cues in Experiment 2], and (E) rocks and one of the plastic pots used to mimic natural habitat [note the presence of a rock crab inside the pot].

2.2.3 Experimental approach

In this study, we defined prey capture as any crab-mussel interaction that resulted in the crushing or opening of shells of one mussel individual. In two experiments, Experiment 1 and Experiment 2, we investigated the impact that temperature, crab size, chela loss, and chemical cues from crabs have on the ability of rock and green crabs to capture mussels (*M. edulis*) of different sizes. Experiment 1 was designed to test hypotheses that: 1) mussel capture in rock and green crabs increases with increasing body size, 2) large rock and green crabs select larger mussels than small crabs, and 3) chela loss in both species decreases mussel capture while altering mussel size selection. We used crabs of all size classes (RS, RM, RL, GS, and GL) to test the first two hypotheses, whereas large crabs in each species (RL and GL) were used to test the third hypothesis. The average size of rock and green crabs missing one chela (RLi: 96.7 ± 7.0 mm and GLi: 65.3 ± 3.2 mm) was comparable to that of large conspecifics with both chelae present (RL and GL, see above). We used intact crabs in which we induced chela loss (as opposed to using crabs that already lacked one chela) to ensure that crabs lacking one chela experienced comparable stress while benefiting from the same amount of time and environmental conditions to adapt to chela loss. Chela loss was induced by gripping tightly with pliers the midpoint of the merus until the chela detached from the crab. Because both chelae in rock crab are similar in size and strength, we removed the right or left chela randomly. The small chela (cutter) was removed in green crabs to ensure that each individual had a chela capable of crushing mussels. Crabs with one chela missing were maintained in holding tanks for one week prior to the 72-h acclimation period and discarded if they showed reduced physical activity compared to the other with one chela missing. Experiment 2 tested the hypothesis that 4) chemical cues from conspecifics and heterospecifics alter mussel capture and size selection in rock crabs. Small (RS) and large (RL) rock crabs, as well as large rock crabs missing one chela (RLi) were individually exposed to one of the three following chemical cues: large, live rock (RL) and green (GL) crabs and large, dead (lethally injured) rock crabs (RLd). A fourth treatment with no cue (N) was used as a control.

To provide details on behaviors of crabs that lead to the observed patterns of prey capture we also recorded the occurrence of the five following behaviors at 5-min intervals in each trial of each experiment (experimental setup is described below): 1) handling prey, 2) feeding on prey, 3) sitting [stationary on tank bottom with no or minimal movement of limbs], 4) moving [displacing on tank bottom], and 5) burying in sediments or located within the pot (Table 2.1). The two experiments were conducted at two temperatures approximating spring (or fall) and summer averages in shallow coastal areas of southern Newfoundland: 4°C (cold) and 12°C (warm) (Methven and Piatt, 1991). In each experiment, we randomly assigned treatments to tanks and conducted one replicate of each treatment each day we performed trials between July and September 2009, when water temperature was 12°C, and between late November and December 2009 and in early June 2010, when water temperature was 4°C. A water chiller was used, as required, to help maintain stability of water temperature in the tanks. Each treatment was replicated seven to ten times.

In each trial crabs were offered one aggregate of mussels in the centre of the tank. The aggregate consisted of 60 individuals, 10 in each of the following six size classes (shell length, measured in millimeters, with a caliper): 10-15, 15-20, 20-25, 25-30, 30-35,

Table 2.1. Summary of five crab behaviors recorded at 5-min intervals during each trial in Experiments 1 and 2 (see Materials and methods for a description of each experiment).

Behavior	**Description**
Handling	- Crab is touching or moving the mussel with legs or chelae (mussel shell closed)
Feeding	- Crab is using chelae, legs, or mouthparts to tear off and ingest mussel flesh
Sitting	- Crab is stationary on tank bottom with no or minimal limb movement
Moving	- Crab displaces with legs on tank bottom
Burying or in the pot	- Crab is partly or completely underneath the sediment layer or digging sediments with legs (or chelae) or inside the pot

and 35-40 mm. Mussels were distributed homogeneously on a thin layer of sediments in a Petri dish. The dish was used to contain mussels in a tight cluster to mimic a natural mussel patch. Each mussel was marked individually with liquid whitener and colored sharpie markers for quick visual identification of the size of mussels captured by crabs. Preliminary trials with marked and unmarked mussels (25-30 mm) indicated that prey capture in both crab species was not affected by marking (Appendix B). To ensure that the number of mussels used in the two experiments (10 individuals in each of the six size classes) was not limiting, we also tested Hypothesis 1 (see above) with half the number of mussels (5 individuals in each size class) in cold water. The total number of prey captured did not differ between the two groups of trials (Appendix C), and we therefore concluded that prey capture in both species was unaffected by the number of mussels offered. We used the highest number of mussels (60) to offset the anticipated increase in prey capture in warm water.

At the end of the 72-h acclimation (see above), each crab was moved to one of the two ends (determined randomly for Experiment 1) of an experimental tank where it was physically isolated from the mussels and rest of the tank by an opaque plastic divider. Each divider had two horizontal rows of four perforations (5 mm in diameter) every 10 cm. The lowest perforations were 15 cm above the tank bottom to prevent visual assessment of the tank environment on the other side of the divider by the crab. In Experiment 2, the crab used to release the chemical cue was transferred to that end of the tank with inflowing seawater and was physically separated from the foraging crab and mussels for the entire trial. The crab foraging on the other side of the divider was always downstream of cue release. Crabs used for cue release were introduced to the tanks

15 min before foraging crabs to allow chemical cues to diffuse throughout the tank (trials with food dye indicated complete diffusion occurred within 15 min, Appendix D). Foraging crabs were allowed to acclimate 15 min to their new environment prior to the start of each trial.

Each trial lasted 4 hours and began with the removal of the divider from the tank to expose mussels to foraging crabs. Crab behaviors (Table 2.1) were assessed every 5 min in the first three hours for a total of 36 observations per crab. The number of mussels captured in each size class was determined by subtracting the number of intact mussels at the end of the trial from the initial number of mussels. After each trial, mussels (intact or crushed), and the top layer (~1 cm) of sediments were removed from the tank and replaced with fresh mussels and sediments. We excluded trials in which the foraging crab molted in the week following experimentation to further minimize variation in the data that could have resulted from any associated physiological stress and behavioral modification. Logistical constraints sometimes limited access to rock crabs, which we circumvented by selecting individuals randomly from a pool of crabs used in previous trials. Complementary trials showed that prey capture did not vary between rock crabs that had not been used yet and crabs that had been used once ($t_{0.05(2),15}=0.83$, $p=0.42$). Therefore, we assumed that reusing a few rock crabs (<20% were used twice) had no effect on the observed patterns. Green crabs were always readily available, and hence each green crab was used only once.

2.2.4 Statistical analysis

2.2.4.1 *Experiment 1*

We used a three-way ANOVA with the factors Temperature (cold and warm), Species (rock and green crabs), and Size (small and large crabs) to analyze effects of temperature, crab species, and crab size on the proportion of mussels captured, i.e. the number of mussels crushed or opened relative to the total number of mussels offered (Hypothesis 1). Data were square-root transformed to correct for heteroscedasticity and normality of the residuals. We used this approach instead of the particular case of the generalized linear model that assumes a binomial distribution of the response variable since every binary decision to capture or reject a mussel could not be considered totally independent from decisions in previous observations, which were likely influenced by increasing satiation (Manly, 2006). We used a two-way ANOVA with the factors Temperature (cold and warm) and Species (rock and green crabs) to analyze effects of temperature and crab species on the proportion of mussels captured in crabs of equal size (RM and GL). The analysis was applied to the square-root transformed data to correct the lack of normality of the residuals.

We used a three-way MANOVA (Schneiner and Gurevitch, 2001) with the factors Temperature (cold and warm), Species (rock and green crabs), and Size (small and large crabs) to examine effects of temperature, crab species, and crab size on the proportion of mussels captured in each of the six mussel size classes (Hypothesis 2). Although the analysis was applied to the square-root transformed data to correct for heteroscedasticity, not all residuals in each mussel size classes were normally distributed. We reported the results from the analyses on square-root transformed data since the MANOVA is robust to deviations from normality (Huberty and Olejnik, 2006). We used a two-way MANOVA with the factors Temperature (cold and warm) and Species (rock and green crabs) to analyze effects of temperature and crab species on the proportion of mussels captured in each of the six mussel size classes in crabs of equal size (RM and GL). Data were square-root transformed to obtain homoscedasticity, which also improved normality of the residuals.

We used a three-way ANOVA with the factors Temperature (cold and warm), Chela (both chelae present and one chela missing), and Species (rock and green crabs) to investigate effects of temperature, chela loss, and crab species on the proportion of mussels captured in large crabs (Hypothesis 3). Data were square-root transformed to obtain normality of the residuals. We used a three-way MANOVA with the factors Temperature (cold and warm), Chela (both chelae present and one chela missing), and Species (rock and green crabs) to examine effects of temperature, chela loss, and crab species on the proportion of mussels captured in each of the six mussel size classes in large crabs. Data were square-root transformed, which improved the normality of the residuals.

To supplement the MANOVAs described above, we also analyzed the proportion of mussels captured in each mussel size class with the particular case of the Manly-Chesson selection index that accounts for prey depletion since mussels captured were not replenished during trials (Chesson, 1978; Manly, 1972). The following equation was used to calculate an alpha value, α_i, for each of the six mussel size classes in each trial:

$$\alpha_i = \frac{\ln((n_{io} - r_i)/n_{io})}{\sum_{j=1}^{m} \ln((n_{jo} - r_j)/n_{jo})}, i = 1, \ldots, m$$

where n_{io} and n_{jo} are the numbers of mussels in size classes i and j at the beginning of each trial, r_i and r_j are the numbers of mussels captured in size classes i and j, and m is the number of mussel size classes used. The α_i value lies between zero (no mussel captured in a given size class) and one (all mussels captured in a given size class). We calculated the mean α_i and associated 95% confidence interval (CI) across trials in each experimental treatment and compared it to the theoretical proportion of mussels captured in each size class: $k = 1/m = 1/6 = 0.17$. If k was contained within the mean $\alpha \pm 95\%$ CI of a given mussel size class, that class was considered to be used randomly by crabs. However, if k was above or below the mean $\alpha \pm 95\%$ CI of a given mussel size class, that class was considered to be avoided or selected by crabs, respectively (Manly, 1972; Manly, 1995).

2.2.4.2 *Experiment 2*

We used three two-way ANOVAs with the factors Temperature (cold and warm) and Cue (no cue [N], large rock crab [RL], large green crab [GL], and large dead rock crab [RLd]) to determine effects of temperature and chemical cues on the proportion of mussels captured in small rock crabs (RS) (1st ANOVA), large rock crabs (RL) (2nd ANOVA), and large rock crabs missing one chela (RLi) (3rd ANOVA) (Hypothesis 4). We applied each analysis to the raw data, which were homoscedastic and produced normally distributed residuals. We used two two-way MANOVAs with the factors Temperature (cold and warm) and Cue (N, RL, GL, and RLd) to examine effects of temperature and chemical cues on the proportion of mussels captured in each of the six mussel size classes in RL (1st MANOVA) and RLi crabs (2nd MANOVA) (Hypothesis 4). The absence of prey capture in a large proportion of trials with RS crabs exposed to RLd cues in cold water forced the use of a two-way MANOVA with the factors Temperature (cold and warm) and Cues with three levels only (N, RL, and GL) to analyze effects of temperature and chemical cues on the proportion of mussels captured in each of the six mussel size classes in RS crabs. To gain a fuller understanding of effects of chemical cues on the proportion of mussels captured in each mussel size class in RS crabs, we also conducted a one-way MANOVA with the factor Cue (N, RL, GL, and RLd) in warm water. We applied analyses to the raw data in RS and RLi crabs, whereas data were square-root transformed in RL crabs to correct for heteroscedasticity and lack of normality of the residuals. The Manly-Chesson selection index (see above) was also used to supplement MANOVA results.

2.2.4.3 *Behavioral repertoire*

We used a three-way MANOVA with the factors Temperature (cold and warm), Species (rock and green crabs), and Size (small and large crabs) to examine effects of temperature, crab species, and crab size on frequencies of each of the five crab behaviors we monitored (handling prey, feeding on prey, sitting, moving, and burying in sediments or in the pot) relative to the total number of observations (36) in each trial (Hypothesis 1). Data were square-root transformed to obtain homoscedasticity in all but one of the five crab behaviors (burying in sediments or in the pot). We used a two-way MANOVA with the factors Temperature (cold and warm) and Species (rock and green crabs) to examine effects of temperature and crab species on the frequency of crab behaviors in crabs of similar size (RM and GL). Data were square-root transformed which improved homoscedasticity and the normality of the residuals. We used a three-way MANOVA with the factors Temperature (cold and warm), Chela (both chelae present and one chela missing), and Species (rock and green crabs) to analyze effects of temperature, chela loss, and crab species on the frequency of crab behaviors (Hypothesis 3). The analysis was applied to the raw data. Lastly, we used three two-way MANOVAs with the factors Temperature (cold and warm) and Cue (no cue [N], large rock crab [RL], large green crab [GL], and large dead rock crab [RLd]) to determine effects of temperature and chemical cues on frequencies of behaviors in small rock crabs (RS) (1st MANOVA), large rock crabs (RL) (2nd MANOVA), and large rock crabs missing one chela (RLi) (3rd MANOVA) (Hypothesis 4). Analyses were applied to the raw data for RL and to the square-root transformed data for RS and RLi crabs.

In all analyses, normality was verified using Shapiro-Wilk's statistic and homogeneity of variance by using Levene tests and examining the graphical distribution of the residuals. All factors in each analysis were considered fixed because we were only concerned with the effects of the specific levels within each factor we tested. To detect differences among levels within a factor we used least-square means multiple comparison tests (ANOVAs) and multivariate contrasts with Bonferonni correction of probabilities (MANOVAs). When a factor or interaction between factors was significant in any MANOVA, we examined the univariate model for each response variable (the six mussel size classes or five behaviors) to identify which one(s) contributed to the multivariate effect. This was done by conducting an ANOVA for each response variable with the same factors as in the corresponding MANOVA. The Pillai's trace multivariate statistic, which is more robust than other multivariate statistics to deviations from homoscedasticty and normality of the residuals as well as more conservative with small and uneven sample sizes, was used in MANOVAs to determine which factor(s) with more than two levels were statistically significant (Schneiner and Gurevitch, 2001). A significance threshold of 0.05 was used for all statistical tests. All the analyses were conducted with JMP 7.0.

2.3 RESULTS

2.3.1 Mussel capture and size selection in intact rock and green crabs

Analysis of data from Experiment 1 with intact (both chelae present) rock and green crabs indicated that numbers of mussels captured were similar between species, though varied with crab size and temperature (Table 2.2). Large crabs (RL and GL altogether) captured three times more mussels than small crabs (RS and GS) (Fig. 2.2), whereas mussel capture was almost three times higher in warm (12°C) than cold (4°C) water (Fig. 2.3). Likewise, rock and green crabs of comparable size (RM and GL) captured similar numbers of mussels, yet nearly three times as many in warm than cold water (Table 2.3).

The MANOVA examining effects of temperature, crab species, and crab size, on the proportion of mussels captured in each of the six mussel size classes showed that

Table 2.2. Summary of three-way ANOVA (applied to square-root transformed data) showing the effect of Temperature (cold and warm), Species (rock and green crabs), and Size (small and large crabs) on the proportion of mussels captured (see Hypothesis 1 in Materials and methods).

Source of variation	***df***	**MS**	***F*-value**	***P***
Temperature	1	0.43	24.49	< 0.01
Species	1	< 0.01	0.25	0.62
Size	1	0.43	24.39	< 0.01
Temperature x Species	1	< 0.01	0.13	0.72
Temperature x Size	1	0.03	1.68	0.20
Species x Size	1	0.01	0.41	0.53
Temperature x Species x Size	1	0.01	0.66	0.42
Error	56	0.13		
Corrected total	63			

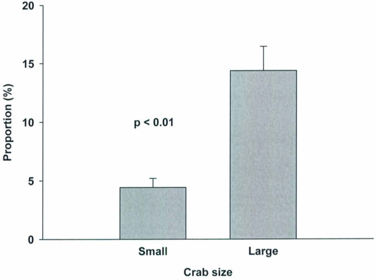

Figure 2.2. Mean proportion (+SE) of mussels captured by small and large crabs. Data were pooled across Temperature (cold and warm) and Species (rock and green crabs) treatments. (n=8 [64 in total] for each combination of Temperature x Species x Size).

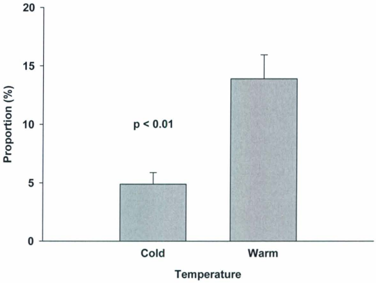

Figure 2.3. Mean proportion (+ SE) of mussels captured by crabs in cold and warm water. Data were pooled across Species (rock and green crabs) and Size (small and large crabs) treatments (n=8 [64 in total] for each combination of Temperature x Species x Size).

Table 2.3. Summary of two-way ANOVA (applied to square-root transformed data) showing the effect of Temperature (cold and warm) and Species (rock and green crabs) on the proportion of mussels captured in crabs of similar size (RM and GL) (see Hypothesis 1 in Materials and methods).

Source of variation	***df***	**MS**	***F*-value**	***P***
Temperature	1	0.23	10.64	<0.01
Species	1	0.032	1.48	0.23
Temperature x Species	1	0.023	1.07	0.31
Error	28	0.021		
Corrected total	31			

temperature had no effect on mussel size selection in both crab species (Table 2.4). However, crabs of different size within and between species used mussel classes differently as shown by the significant interaction between factors Species and Size (Table 2.4). For example, in each species large crabs captured a higher proportion (up to 46%) of large (>30 mm) mussels than small crabs (up to 20%) (LS means, $p < 0.01$), whereas small crabs captured the smallest (10-15 mm) mussels at least seven times more frequently as large crabs (LS means, $p < 0.01$) (Table 2.5 and Fig. 2.4). Mussel size selection did not differ between large rock and green crabs, though small and large green crabs altogether captured a significantly larger proportion of small (<20 mm) mussels than rock crabs (LS means, $p < 0.035$), a result largely attributable to the marked preference of small green crabs for those mussels (76% of the mussels captured by small green crabs were <20 mm) (Table 2.5 and Fig. 2.4). Interestingly, small rock (RS) crabs captured medium-sized mussels (25-30 mm) more frequently than any other size class and nearly four times as often as small green (GS) crabs (LS means, $p < 0.01$) (Fig. 2.4). Mussel size selection did not differ between rock and green crabs of comparable size (RM and GL) (two-way MANOVA, Factor Species: $F_{6,18} = 1.94$, $p = 0.13$). Examination of Manly-Chesson indices indicated that small green (GS) crabs selected mussels <20 mm while avoiding mussels >25 mm, whereas small rock (RS) crabs avoided only the largest (35-40 mm) mussels while using all the other size classes equally (Table 2.6). Moreover, large rock (RL) and green (GL) crabs avoided mussels smaller than 20 and 15 mm, respectively (Table 2.6). Such results are consistent with those of the MANOVA (see above), which reinforces the notion that rock and green crabs of different size can use mussel resources in a different way.

Table 2.4. Summary of three-way MANOVA (applied to square-root transformed data) showing the effect of Temperature (cold and warm), Species (rock and green crabs), and Size (small and large crabs) on the proportion of mussels captured in each of the six mussel size classes (see Hypothesis 2 in Materials and methods).

Source of variation	**F-Test**	***F*-value**	**NumDF**	**DenDF**	***p***
Temperature	0.23	1.47	6	39	0.22
Species	0.90	5.82	6	39	< 0.01
Size	3.25	21.11	6	39	< 0.01
Temperature x Species	0.058	0.38	6	39	0.89
Temperature x Size	0.11	0.74	6	39	0.63
Species x Size	0.39	2.52	6	39	0.037
Temperature x Species x Size	0.11	0.73	6	39	0.63

Table 2.5. Summary of three-way ANOVAs (applied to square-root transformed data) showing the effect of Temperature (cold and warm), Species (rock and green crabs), and Size (small and large crabs) on the proportion of mussels captured in each of the six mussel size classes (see Hypothesis 2 in Materials and methods).

Mussel size class (mm)	Source of variation	*df*	MS	*F*-value	*p*
10-15	Temperature	1	0.023	0.33	0.57
	Species	1	0.33	4.74	0.035
	Size	1	0.93	13.46	< 0.01
	Temperature x Species	1	< 0.01	< 0.01	1.00
	Temperature x Size	1	< 0.01	< 0.01	0.97
	Species x Size	1	0.24	3.41	0.072
	Temperature x Species x Size	1	< 0.01	0.017	0.90
	Error	44	0.069		
	Corrected total	51			
15-20	Temperature	1	0.093	1.19	0.28
	Species	1	0.48	6.20	0.017
	Size	1	0.18	2.36	0.13
	Temperature x Species	1	< 0.01	0.031	0.86
	Temperature x Size	1	0.24	3.03	0.089
	Species x Size	1	0.12	1.55	0.22
	Temperature x Species x Size	1	0.14	1.82	0.18
	Error	44	0.078		
	Corrected total	51			
20-25	Temperature	1	< 0.01	0.022	0.88
	Species	1	0.15	2.14	0.15
	Size	1	0.21	3.01	0.09
	Temperature x Species	1	0.074	1.05	0.31
	Temperature x Size	1	0.087	1.23	0.27
	Species x Size	1	0.042	0.59	0.45
	Temperature x Species x Size	1	0.037	0.52	0.48
	Error	44	0.071		
	Corrected total	51			

Table 2.5. (continued)

Mussel size class (mm)	Source of variation	*df*	MS	F-value	*p*
25-30	Temperature	1	0.027	0.37	0.55
	Species	1	0.58	7.94	< 0.01
	Size	1	0.17	2.29	0.14
	Temperature x Species	1	< 0.01	< 0.01	0.97
	Temperature x Size	1	0.026	0.36	0.55
	Species x Size	1	0.45	6.18	0.017
	Temperature x Species x Size	1	< 0.01	< 0.01	0.94
	Error	44	0.073		
	Corrected total	51			
30-35	Temperature	1	< 0.01	0.046	0.83
	Species	1	0.16	3.55	0.066
	Size	1	0.38	8.69	< 0.01
	Temperature x Species	1	0.015	0.33	0.57
	Temperature x Size	1	0.019	0.45	0.51
	Species x Size	1	0.020	0.46	0.50
	Temperature x Species x Size	1	0.046	1.06	0.31
	Error	44	0.044		
	Corrected total	51			
35-40	Temperature	1	0.16	4.16	0.047
	Species	1	< 0.01	0.024	0.88
	Size	1	1.34	34.82	< 0.01
	Temperature x Species	1	0.033	0.85	0.36
	Temperature x Size	1	< 0.01	0.055	0.82
	Species x Size	1	0.014	0.37	0.55
	Temperature x Species x Size	1	< 0.01	0.027	0.87
	Error	44	0.039		
	Corrected total	51			

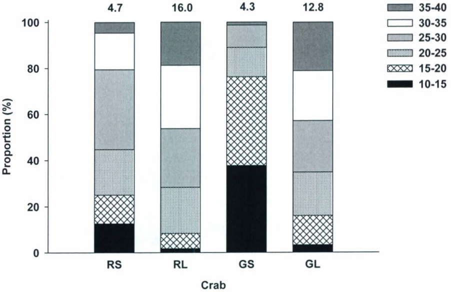

Figure 2.4. Standardized proportion (error bars not shown for clarity) of mussels captured in each of six mussel size classes (10-15, 15-20, 20-25, 25-30, 30-35, 35-40 mm) in small and large rock (RS and RL) and green (GS and GL) crabs. Values above bars represent mean proportions of mussels captured relative to the total number of mussels (60) offered. Data were pooled across Temperature (cold and warm) treatments (n=4 and 7 [RS], 6 and 8 [RL], 6 and 6 [GS], and 8 and 7 [GL] in cold and warm treatments, respectively [52 in total]).

Table 2.6. Summary of Manly-Chesson selection indices showing the effect of Temperature (cold and warm), Species (rock [R] and green [G] crabs), Size (small [S], medium [M], and large [L] crabs), Chelae (both chelae present and one chela missing [denoted by the letter "i"]), and Cue (no cue [N], large rock crab [RL], large green crab [GL], and large dead rock crab [RLd]) on mussel selection in each of the six mussel size classes. Indices in bold indicate mussel size classes that were avoided (A) or selected (S) by crabs (see Hypothesis 2, 3, and 4, and statistical details in Materials and methods). Data were pooled across cold and warm water treatments when Temperature had no significant effect.

					Mussel size class (mm)					
Hypothesis	**Temperature**	**Crab**	**Cue**	**n**	**10-15**	**15-20**	**20-25**	**25-30**	**30-35**	**35-40**
2	Pooled	RS	N	10	0.13	0.15	0.19	0.28	0.18	**0.07 (A)**
	Pooled	RM	N	14	0.011	**0.075 (A)**	0.19	0.11	0.32	0.19
	Pooled	RL	N	13	**0.014 (A)**	**0.044 (A)**	0.20	0.26	**0.30 (S)**	0.18
	Pooled	GL	N	17	**0.029 (A)**	0.122	0.20	0.22	0.23	0.21
	Pooled	GS	N	10	**0.42 (S)**	**0.43 (S)**	0.12	**0.023 (A)**	**< 0.01 (A)**	**0.016 (A)**
3	Cold	RLi	N	4	0.13	**< 0.01 (A)**	0.50	0.13	0.25	**< 0.01 (A)**
	Cold	GLi	N	6	0.13	0.086	0.24	0.26	**0.053 (A)**	0.24
	Warm	RLi	N	7	0.044	0.12	0.18	0.27	0.17	0.22
	Warm	GLi	N	8	**< 0.01 (A)**	**0.080 (A)**	0.25	0.14	**0.29 (S)**	0.24
4	Cold	RS	RL	5	**0.038 (A)**	**0.58 (S)**	0.18	**< 0.01 (A)**	**< 0.01 (A)**	0.20
	Cold	RS	GL	6	0.30	**< 0.01 (A)**	**0.70 (S)**	**< 0.01 (A)**	**< 0.01 (A)**	**< 0.01 (A)**
	Warm	RS	RL	6	0.13	0.18	0.18	0.15	0.28	0.074
	Warm	RS	GL	7	0.12	0.090	0.16	0.31	0.19	0.14
	Warm	RS	RLd	6	0.080	0.12	0.39	0.10	0.15	0.094

Table 2.6 (continued)

					Mussel size class (mm)					
Hypothesis	**Temperature**	**Crab**	**Cue**	**n**	**10-15**	**15-20**	**20-25**	**25-30**	**30-35**	**35-40**
4	Pooled	RL	RL	14	**0.041 (A)**	**0.084 (A)**	**0.11 (A)**	0.28	0.18	**0.31 (S)**
	Pooled	RL	GL	16	**0.033 (A)**	**0.073 (A)**	0.15	0.23	0.19	**0.32 (S)**
	Pooled	RL	RLd	13	**< 0.01 (A)**	**0.037 (A)**	0.17	0.18	**0.34 (S)**	**0.26 (S)**
4	Cold	RLi	RL	7	**0.018 (A)**	0.16	0.18	0.33	0.13	0.18
	Cold	RLi	GL	7	**< 0.01 (A)**	**0.022 (A)**	0.26	0.19	0.13	0.40
	Cold	RLi	RLd	7	**0.011 (A)**	0.24	0.079	0.37	0.12	0.18
	Warm	RLi	RL	6	**0.073 (A)**	0.095	0.17	0.24	0.23	0.19
	Warm	RLi	GL	6	0.20	0.23	0.13	0.19	0.15	**0.09 (A)**
	Warm	RLi	RLd	4	0.20	0.078	0.15	0.20	0.22	0.15

The MANOVA examining effects of temperature, crab size, and crab species on frequencies of the five crab behaviors indicated that each factor affected behaviors independently (Table 2.7). Handling and feeding frequencies increased twofold, while sitting decreased by more than threefold in warm compared to cold water (Table 2.8 and Fig. 2.5). Handling occurred almost twice as often in large than small rock crabs (LS means, $p = 0.027$), yet was observed as frequently in small than large green crabs (LS means, $p = 0.31$) (Fig. 2.6). Even though rock and green crabs captured similar numbers of mussels (see above), the frequency of behaviors differed between species. For example, small green (GS) crabs handled mussels three times more frequently than small rock (RS) crabs (LS means, $p < 0.01$) but there was no difference in handling frequencies between large rock (RL) and green (GL) crabs (Fig. 2.6). Overall, feeding occurred twice as often in large than small crabs (Table 2.8 and Fig. 2.6). Interestingly, the frequency of occurrence of crabs burying in sediments or in the pot differed between rock and green crabs of different size as indicated by the significant interaction between Species and Size factors (Table 2.8 and Fig. 2.6). Small rock (RS) and green (GS) crabs buried in sediments or were in the pot more often than large conspecifics (LS means, $p < 0.01$ and 0.046 for rock and green crabs, respectively). We noted small rock (RS) crabs buried in sediments or were in the pot nearly five times more often than small green (GS) crabs (LS means, $p < 0.01$; Fig. 2.6). These behaviors were also more frequent in rock than green crabs of similar size (RM and GL) ($F_{1,31} = 12.37$, $p < 0.01$). Large crabs in both species buried in sediments or were in the pot only very rarely, if at all (Fig. 2.6).

Table 2.7. Summary of three-way MANOVA (applied to square-root transformed data) showing the effect of Temperature (cold and warm), Species (rock and green crabs), and Size (small and large crabs) on the frequency of crab behaviors (see Hypothesis 1 in Materials and methods).

Source of variation	**F-Test**	***F*-value**	**NumDF**	**DenDF**	***P***
Temperature	0.69	7.16	5	52	< 0.01
Species	0.37	3.84	5	52	< 0.01
Size	0.79	8.24	5	52	< 0.01
Temperature x Species	0.087	0.91	5	52	0.48
Temperature x Size	0.13	1.34	5	52	0.26
Species x Size	0.20	2.09	5	52	0.082
Temperature x Species x Size	0.044	0.46	5	52	0.81

Table 2.8. Summary of three-way ANOVAs (applied to square-root transformed data) showing the effect of Temperature (cold and warm), Species (rock and green crabs), and Size (small and large crabs) on the frequency of crab behaviors (see Hypothesis 1 in Materials and methods).

Behavior	**Source of variation**	***df***	**MS**	***F*-value**	***p***
Handling	Temperature	1	0.99	21.84	< 0.01
	Species	1	0.67	14.82	< 0.01
	Size	1	0.035	0.77	0.39
	Temperature x Species	1	< 0.01	0.12	0.73
	Temperature x Size	1	0.11	2.40	0.13
	Species x Size	1	0.25	5.42	0.024
	Temperature x Species x Size	1	0.088	1.94	0.17
	Error	56	0.045		
	Corrected total	63			
Feeding	Temperature	1	0.55	9.89	< 0.01
	Species	1	0.012	0.22	0.64
	Size	1	0.60	10.76	< 0.01
	Temperature x Species	1	0.049	0.89	0.35
	Temperature x Size	1	0.13	2.40	0.13
	Species x Size	1	0.020	0.35	0.56
	Temperature x Species x Size	1	< 0.01	< 0.01	0.98
	Error	56	0.056		
	Corrected total	63			
Sitting	Temperature	1	1.50	20.14	< 0.01
	Species	1	0.074	0.99	0.32
	Size	1	0.017	0.23	0.63
	Temperature x Species	1	0.17	2.29	0.14
	Temperature x Size	1	0.25	3.36	0.07
	Species x Size	1	0.13	1.80	0.19
	Temperature x Species x Size	1	< 0.01	0.014	0.91
	Error	56	0.074		
	Corrected total	63			

Table 2.8. (continued)

Behavior	Source of variation	*df*	MS	*F*-value	*p*
Moving	Temperature	1	0.078	2.29	0.14
	Species	1	< 0.01	0.17	0.68
	Size	1	< 0.01	0.045	0.83
	Temperature x Species	1	0.033	0.97	0.33
	Temperature x Size	1	0.040	1.13	0.29
	Species x Size	1	< 0.01	0.071	0.79
	Temperature x Species x Size	1	< 0.01	0.014	0.91
	Error	56	0.034		
	Corrected total	63			
Burying or in the pot	Temperature	1	< 0.01	< 0.01	0.94
	Species	1	0.67	11.14	< 0.01
	Size	1	1.50	24.78	< 0.01
	Temperature x Species	1	0.013	0.22	0.64
	Temperature x Size	1	0.014	0.24	0.63
	Species x Size	1	0.27	4.40	0.04
	Temperature x Species x Size	1	0.064	1.07	0.31
	Error	56	0.060		
	Corrected total	63			

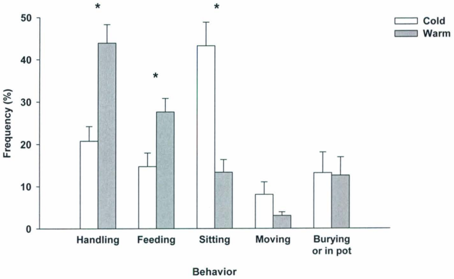

Figure 2.5. Mean frequency (+ SE) of occurrence of five crab behaviors during trials in cold and warm water. Data were pooled across Species (rock and green crabs) and Size (small and large crabs). Asterisks indicate significant differences between frequencies for a given behavior (LS means, $p<0.05$; n=8 [64 in total] for each combination of Temperature x Species x Size).

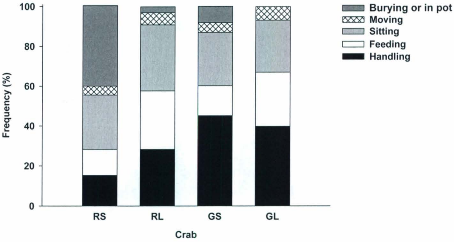

Figure 2.6. Mean frequency (error bars not shown for clarity) of occurrence of five crab behaviors during trials with small and large rock (RS and RL) and green (GS and GL) crabs. Data were pooled across Temperature (cold and warm) treatments (n=8 [64 in total] for each combination of Temperature x Species x Size).

2.3.2 Effect of chela loss on mussel capture and size selection in rock and green crabs

Analysis of data from Experiment 1 with crabs missing one chela indicated that the effect of chela loss on mussel capture varied between rock and green crabs (Table 2.9). Indeed, mussel capture was twice as high in rock crabs with both chelae (RL) than rock crabs missing one chela (RLi) (LS means, $p < 0.01$), yet did not differ in green crabs (Fig. 2.7). As seen with intact crabs (see above), temperature had a strong effect on mussel capture, which was four times higher in warm than cold water (data pooled across factors Species and Chela, Table 2.9).

The MANOVA testing for effects of temperature, crab species, and chela loss on the proportion of mussels captured in each of the six mussel size classes showed that mussel size selection varied with temperature between species, yet was not influenced by chela loss in both species (Table 2.10). Even though mussel size selection was similar between the two temperature treatments in both small (RS and GS) and large (RL and GL) crabs (see above), rock crabs captured a significantly higher proportion (36%) of large (30-35 mm) mussels than green crabs (19%) in cold water only (LS means, $p < 0.01$; Table 2.11). The two crab species captured similar proportions of the largest (35-40 mm) mussels, though mussel capture occurred three times more often in warm than cold water (Table 2.11). Examination of Manly-Chesson indices suggested chela loss caused only subtle differences in the use of mussel resources. For example, large rock crabs missing one chela (RLi) did not select large (30-35 mm) mussels and avoided the largest (35-40 mm) mussels in cold water, while using all mussel size classes equally in

Table 2.9. Summary of three-way ANOVA (applied to square-root transformed data) showing the effect of Temperature (cold and warm), Species (rock and green crabs), and Chela (both chelae present and one chela missing) on the proportion of mussels captured (see Hypothesis 3 in Materials and methods).

Source of variation	***df***	**MS**	***F*-value**	***p***
Temperature	1	1.18	65.92	< 0.01
Species	1	< 0.01	0.053	0.82
Chela	1	0.14	8.05	< 0.01
Temperature x Species	1	< 0.01	0.10	0.76
Temperature x Chela	1	0.016	0.91	0.35
Species x Chela	1	0.096	5.33	0.025
Temperature x Species x Chela	1	< 0.01	0.034	0.85
Error	57	0.018		
Corrected total	64			

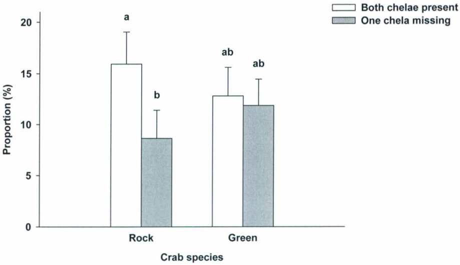

Figure 2.7. Mean proportion (+ SE) of mussels captured in rock and green crabs with both chelae present and one chela missing. Data were pooled across Temperature (cold and warm) treatments. Bars not sharing the same letters are different (LS means, $p<0.05$; ($n=8$ for each combination of Temperature x Species x Chela, with the exception of 9 in green crabs with one chela missing in cold water [65 in total]).

Table 2.10. Summary of three-way MANOVA (applied to square-root transformed data) showing the effect of Temperature (cold and warm), Species (rock and green crabs), and Chela (both chelae present and one chela missing) on the proportion of mussels captured in each of the six mussel size classes (see Hypothesis 3 in Materials and methods).

Source of variation	**F-Test**	***F*-value**	**NumDF**	**DenDF**	*p*
Temperature	0.78	5.07	6	39	< 0.01
Species	0.23	1.50	6	39	0.20
Chela	0.18	1.15	6	39	0.35
Temperature x Species	0.48	3.11	6	39	0.014
Temperature x Chela	0.30	1.95	6	39	0.098
Species x Chela	0.087	0.57	6	39	0.76
Temperature x Species x Chela	0.17	1.07	6	39	0.40

Table 2.11. Summary of three-way ANOVAs (applied to square-root transformed data) showing the effect of Temperature (cold and warm), Species (rock and green crabs), and Chela (both chelae present and one chela missing) on the proportion of mussels captured in each of the six mussel size classes (see Hypothesis 3 in Materials and methods).

Mussel size class (mm)	**Source of variation**	***df***	**MS**	***F*-value**	***p***
10-15	Temperature	1	< 0.01	0.032	0.86
	Species	1	0.021	0.71	0.41
	Chela	1	< 0.01	0.028	0.87
	Temperature x Species	1	0.052	1.77	0.19
	Temperature x Chela	1	0.016	0.54	0.47
	Species x Chela	1	< 0.01	0.12	0.73
	Temperature x Species x Chela	1	0.068	2.33	0.13
	Error	44	0.029		
	Corrected total	51			
15-20	Temperature	1	0.088	1.90	0.18
	Species	1	0.067	1.43	0.24
	Chela	1	0.031	0.67	0.42
	Temperature x Species	1	0.075	1.62	0.21
	Temperature x Chela	1	0.23	4.84	0.033
	Species x Chela	1	< 0.01	0.14	0.71
	Temperature x Species x Chela	1	< 0.01	0.045	0.83
	Error	44	0.046		
	Corrected total	51			
20-25	Temperature	1	0.013	0.20	0.65
	Species	1	0.045	0.72	0.40
	Chelae	1	0.039	0.62	0.43
	Temperature x Species	1	0.068	1.10	0.30
	Temperature x Chela	1	0.019	0.31	0.58
	Species x Chela	1	< 0.01	0.016	0.90
	Temperature x Species x Chela	1	0.12	1.86	0.18
	Error	44	0.062		
	Corrected total	51			

Table 2.11. (continued)

Mussel size class (mm)	Source of variation	*df*	MS	*F*-value	*p*
25-30	Temperature	1	0.019	0.27	0.60
	Species	1	< 0.01	0.022	0.88
	Chela	1	0.095	1.40	0.24
	Temperature x Species	1	0.054	0.80	0.38
	Temperature x Chela	1	0.019	0.28	0.60
	Species x Chela	1	< 0.01	0.035	0.85
	Temperature x Species x Chela	1	0.070	1.03	0.32
	Error	44	0.068		
	Corrected total	51			
30-35	Temperature	1	0.041	0.74	0.40
	Species	1	0.14	2.48	0.12
	Chela	1	0.035	0.65	0.43
	Temperature x Species	1	0.48	8.82	< 0.01
	Temperature x Chela	1	0.081	1.48	0.23
	Species x Chela	1	< 0.01	0.04	0.84
	Temperature x Species x Chela	1	0.021	0.38	0.54
	Error	44	0.055		
	Corrected total	51			
35-40	Temperature	1	0.42	8.64	< 0.01
	Species	1	0.15	3.14	0.083
	Chela	1	0.042	0.87	0.36
	Temperature x Species	1	0.18	3.79	0.058
	Temperature x Chela	1	0.044	0.92	0.34
	Species x Chela	1	0.092	1.91	0.18
	Temperature x Species x Chela	1	0.049	1.00	0.32
	Error	44	0.048		
	Corrected total	51			

warm water (Table 2.6). Likewise, green crabs missing one chela (GLi) avoided large (30-35 mm) mussels in cold water, yet selected them in warm water (Table 2.6).

Results of the MANOVA testing the effect of temperature, crab species, and chela loss on frequencies of the five crab behaviors indicated that the occurrence of behaviors between crabs with both chelae present and one chela missing differed between the two temperature treatments (Table 2.12). In cold water, large green crabs missing one chela (GLi) handled mussels nearly three times more frequently as both large green crabs with both chelae (GL) and large rock crabs missing one chela (RLi) (LS means, $p < 0.016$; Table 2.13). Yet, there was no difference in handling frequencies at either temperature between large rock crabs with both chelae (RL) and those with one chela missing (RLi). Overall feeding frequencies (data pooled across factors Species and Chela) increased nearly sixfold, while sitting decreased almost fourfold, in warm compared to cold water. Even though mussel capture in the absence of one chela decreased only in rock crabs (see above), feeding frequencies in each species missing one chela decreased by at least 5% compared to individuals with both chelae (Table 2.13). Crabs missing one or no chela buried in sediments or remained inside the pot equally frequently (Table 2.13).

2.3.3 Effect of chemical cues on mussel capture and size selection in rock crabs

Analysis of data from Experiment 2 with rock crabs missing or not one chela indicated that mussel capture in rock crabs was unaffected by the presence of any of the chemical cues tested (Table 2.14). However, rock crabs captured up to four times as many mussels in warm than cold water (Table 2.14), a pattern similar to that shown in

Table 2.12. Summary of three-way MANOVA (applied to raw data) showing the effect of Temperature (cold and warm), Species (rock and green crabs), and Chela (both chelae present and one chela missing) on the frequency of crab behaviors (see Hypothesis 3 in Materials and methods).

Source of variation	**F-Test**	***F*-value**	**NumDF**	**DenDF**	***p***
Temperature	1.26	13.39	5	53	< 0.01
Species	0.19	2.00	5	53	0.094
Chela	0.15	1.64	5	53	0.17
Temperature x Species	< 0.01	0.034	5	53	1.00
Temperature x Chela	0.32	3.37	5	53	0.010
Species x Chela	0.12	1.27	5	53	0.29
Temperature x Species x Chela	0.16	1.67	5	53	0.16

Table 2.13. Summary of three-way ANOVAs (applied to raw data) showing the effect of Temperature (cold and warm), Species (rock and green crabs), and Chela (both chelae present and one chela missing) on the frequency of crab behaviors (see Hypothesis 3 in Materials and methods).

Behavior	Source of variation	*df*	MS	*F*-value	*P*
Handling	Temperature	1	0.51	10.17	< 0.01
	Species	1	0.46	9.32	< 0.01
	Chela	1	< 0.01	0.011	0.92
	Temperature x Species	1	< 0.01	0.058	0.81
	Temperature x Chela	1	0.24	4.87	0.031
	Species x Chela	1	0.048	0.97	0.33
	Temperature x Species x Chela	1	0.22	4.33	0.042
	Error	57	0.050		
	Corrected total	64			
Feeding	Temperature	1	1.00	42.94	< 0.01
	Species	1	0.049	2.11	0.15
	Chela	1	0.10	4.28	0.043
	Temperature x Species	1	< 0.01	0.010	0.92
	Temperature x Chela	1	0.031	1.33	0.25
	Species x Chela	1	0.094	4.01	0.050
	Temperature x Species x Chela	1	0.045	1.91	0.17
	Error	57	0.023		
	Corrected total	64			
Sitting	Temperature	1	3.13	37.78	< 0.01
	Species	1	0.73	8.83	< 0.01
	Chela	1	0.11	1.35	0.25
	Temperature x Species	1	< 0.01	< 0.01	0.97
	Temperature x Chela	1	< 0.01	< 0.01	0.93
	Species x Chela	1	0.323	3.90	0.053
	Temperature x Species x Chela	1	0.042	0.51	0.48
	Error	57	0.083		
	Corrected total	64			

Table 2.13. (continued)

Behavior	**Source of variation**	***df***	**MS**	***F*-value**	***p***
Moving	Temperature	1	0.036	2.44	0.12
	Species	1	< 0.01	< 0.01	1.00
	Chela	1	0.035	2.40	0.13
	Temperature x Species	1	< 0.01	0.12	0.73
	Temperature x Chela	1	0.041	2.77	0.10
	Species x Chela	1	< 0.01	0.050	0.82
	Temperature x Species x Chela	1	< 0.01	0.056	0.81
	Error	57	0.015		
	Corrected total	64			
Burying or in the pot	Temperature	1	0.057	2.60	0.11
	Species	1	< 0.01	0.11	0.74
	Chela	1	0.024	1.09	0.30
	Temperature x Species	1	< 0.01	< 0.01	0.93
	Temperature x Chela	1	0.022	0.99	0.32
	Species x Chela	1	< 0.01	0.23	0.64
	Temperature x Species x Chela	1	< 0.01	0.27	0.60
	Error	57	0.022		
	Corrected total	64			

Table 2.14. Summary of two-way ANOVAs (applied to raw data in large rock [RL] crabs and to square-root transformed data in small rock [RS] crabs and large rock crabs missing a chela [RLi]) showing the effect of Temperature (cold and warm) and Cue (no cue [N], large rock crab [RL], large green crab [GL], and large dead rock crab [RLd]) on the proportion of mussels captured (see Hypothesis 4 in Materials and methods).

Crab	**Source of variation**	***df***	**MS**	***F*-value**	***p***
RS	Temperature	1	0.28	20.89	< 0.01
	Cue	3	0.018	1.39	0.26
	Temperature x Cue	3	0.024	1.82	0.15
	Error	59	0.013		
	Corrected total	66			
RL	Temperature	1	0.56	62.22	< 0.01
	Cue	3	0.011	1.22	0.31
	Temperature x Cue	3	< 0.01	0.86	0.47
	Error	56	< 0.01		
	Corrected total	63			
RLi	Temperature	1	0.34	10.88	< 0.01
	Cue	3	0.031	0.99	0.40
	Temperature x Cue	3	0.065	2.08	0.11
	Error	60	0.031		
	Corrected total	67			

Experiment 1 (see above). The MANOVAs examining effects of temperature and chemical cues on proportions of mussels captured in each of the six mussel size classes showed that mussel size selection varied with: 1) temperature and the nature of the chemical cues in small rock (RS) crabs, 2) temperature only in large rock crabs missing one chela (RLi), and 3) chemical cue only in large intact rock crabs (RL) (Table 2.15). Indeed, small rock crabs captured a larger proportion of medium (25-30 mm) mussels at each temperature in the control treatment (N, up to 46%) than in the presence of cues from large rock (RL, up to 15%) and green (GL, up to 31%) crabs (LS means, $p < 0.01$ and 0.041, respectively, Fig. 2.8). In the absence of cues small rock crabs captured medium-large (25-35 mm) mussels nearly three times more frequently in warm than cold water (LS means, $p < 0.023$). In warm water, size selection was similar in small rock crabs exposed to no cue and to cues from large dead rock crabs (RLd) (one-way MANOVA, $F_{18,57} = 0.85$, $p = 0.64$). Interestingly, large rock (RL) crabs captured the largest (35-40 mm) mussels nearly twice as often when exposed to cues from large green crabs (GL) than in the absence of cues (N) (LS means, $p = 0.02$). Manly-Chesson indices indicated that in warm water small rock (RS) crabs used all mussel size classes equally regardless of chemical cues (Table 2.6). However, in cold water these crabs avoided most mussel size classes, selecting only small (15-20 mm) and medium (20-25 mm) mussels in the presence of cues from large rock (RL) and green (GL) crabs, respectively. Large rock (RL) crabs selected the largest (35-40 mm) mussels when exposed to any of the chemical cues (Table 2.6). Large rock crabs missing one chela (RLi) generally used all mussel size classes equally regardless of chemical cues and temperature. The only exceptions to this pattern were the smallest (10-15 mm) and largest (35-40 mm) mussels which they

Table 2.15. Summary of two-way MANOVAs (applied to square-root transformed data in small rock [RS] crabs, large rock [RL] crabs, and large rock crabs missing a chela [RLi]) showing the effect of Temperature (cold and warm) and Cue (no cue [N], large rock crab [RL], large green crab [GL], and large dead rock crab [RLd]) on the proportion of mussels captured in each of the six mussel size classes (see Hypothesis 4 in Materials and methods).

Crab	Source of variation	Pillai's Trace	*F*-value	NumDF	DenDF	*p*
RS	Temperature	2.28	8.72	6	23	< 0.01
	Cue	0.73	2.31	12	48	0.020
	Temperature x Cue	0.76	2.43	12	48	0.015
RL	Temperature	0.18	1.61	6	44	0.17
	Cue	0.63	2.05	18	138	0.011
	Temperature x Cue	0.37	1.09	18	138	0.37
RLi	Temperature	0.86	4.85	6	34	< 0.01
	Cue	0.46	1.09	18	108	0.37
	Temperature x Cue	0.44	1.02	18	108	0.44

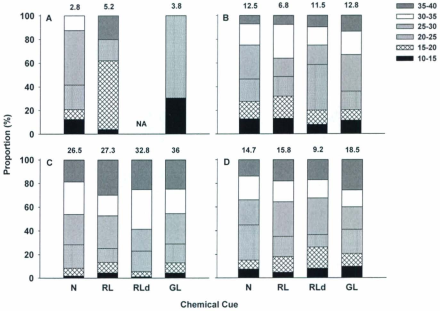

Figure 2.8. Standardized proportion (error bars not shown for clarity) of mussels captured in each of six mussel size classes (10-15, 15-20, 20-25, 25-30, 30-35, 35-40 mm) in (A) small rock [RS] crabs in cold water, (B) small rock crabs in warm water, (C) large intact rock [RL] crabs, and (D) large rock crabs missing a chela [RLi], exposed to either of four chemical cues: no cue [N], large rock [RL] crab, large dead rock [RLd] crab, and large green [GL] crabs. Values above bars represent mean proportions of mussels captured relative to the total number of mussels (60) offered. Data were pooled across Temperature (cold and warm) treatments in panels (C) and (D) due to a non-significant interaction between factors Temperature and Cue (n = 4-6 [A], 6-7 [B], 5-8 [C], 4-8 [D] [or 14, 20, 57, and 47 in total, respectively] for each combination of Temperature x Species x Size).

avoided in cold water with any cue, and in warm water in the presence of cues from large green crabs, respectively (Table 2.6). Therefore, Manly-Chesson indices were also in agreement with results from the MANOVAs.

The MANOVA examining effects of temperature and chemical cues on frequencies of the five crab behaviors indicated that temperature affected behaviors in both small (RS) and large (RL) rock crabs, whereas chemical cues affected behaviors only in small rock crabs (Table 2.16). Feeding in small and large rock crabs increased as much as threefold, while sitting decreased more than twofold in warm compared to cold water (LS means, $p < 0.021$). In small rock crabs, handling decreased fourfold, while burial in sediments or use of the pot increased twofold, in the presence of cues from large dead rock crab (RLd) compared to no cue (N) (LS means, $p = 0.038$ and 0.029, respectively; Table 2.17 and Fig. 2.9). Small rock (RS) crabs rarely moved in the absence of cues, yet moved even less when exposed to cues from large rock crab (RL) and large dead rock crab (RLd) (LS means, $p = 0.023$ and 0.047, respectively). Frequencies of each behavior in small rock crabs were similar in the absence of cues and presence of cues from large green crabs (Fig. 2.9).

2.4 DISCUSSION

We used two laboratory experiments to determine effects of changes in water temperature, body size, chela loss, and chemical cues on capture and size selection of blue mussels (*Mytilus edulis*) and associated behaviors in rock (*Cancer irroratus*) and green (*Carcinus maenas*) crabs from Newfoundland and Labrador held individually in

Table 2.16. Summary of two-way MANOVAs (applied to raw data in large rock [RL] crabs and to square-root transformed data in small rock [RS] crabs and large rock crabs missing a chela [RLi]) showing the effect of Temperature (cold and warm) and Cue (no cue [N], large rock crab [RL], large green crab [GL], and large dead rock crab [RLd]) on the frequency of rock crab behaviors (see Hypothesis 4 in Materials and methods).

Crab	**Source of variation**	**Test**	**Value**	***F*-value**	**NumDF**	**DenDF**	***P***
RS	Temperature	F Test	0.24	2.62	5	55	0.034
	Cue	Pillai's Trace	0.53	2.46	15	171	< 0.01
	Temperature x Cue	Pillai's Trace	0.15	0.59	15	171	0.88
RL	Temperature	F Test	0.49	5.09	5	52	< 0.01
	Cue	Pillai's Trace	0.31	1.23	15	162	0.26
	Temperature x Cue	Pillai's Trace	0.30	1.20	15	162	0.28
RLi	Temperature	F Test	0.19	2.17	5	56	0.070
	Cue	Pillai's Trace	0.12	0.47	15	174	0.96
	Temperature x Cue	Pillai's Trace	0.14	0.57	15	174	0.90

Table 2.17. Summary of two-way ANOVAs (applied to square-root transformed data) showing the effect of Temperature (cold and warm) and Cue (no cue [N], large rock crab [RL], large green crab [GL], and large dead rock crab [RLd]) on the frequency of behaviors in small rock crabs (see Hypothesis 4 in Materials and methods).

Behavior	**Source of variation**	***df***	**MS**	***F*-value**	***p***
Handling	Temperature	1	13.59	5.78	0.019
	Cue	3	7.14	3.04	0.036
	Temperature x Cue	3	1.56	0.66	0.58
	Error	59	2.35		
	Corrected total	66			
Feeding	Temperature	1	7.03	4.91	0.031
	Cue	3	2.97	2.08	0.11
	Temperature x Cue	3	1.37	0.96	0.42
	Error	59	1.43		
	Corrected total	66			
Sitting	Temperature	1	19.97	6.06	0.017
	Cue	3	8.80	2.67	0.056
	Temperature x Cue	3	2.97	0.90	0.45
	Error	59	3.30		
	Corrected total	66			
Moving	Temperature	1	1.17	2.69	0.11
	Cue	3	1.52	3.49	0.021
	Temperature x Cue	3	0.24	0.54	0.66
	Error	59	0.44		
	Corrected total	66			
Burying or in the pot	Temperature	1	1.70	0.37	0.55
	Cue	3	16.39	3.54	0.02
	Temperature x Cue	3	6.09	1.31	0.28
	Error	59	4.63		
	Corrected total	66			

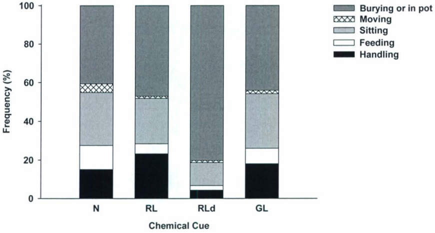

Figure 2.9. Mean frequency (error bars not shown for clarity) of occurrence of five crab behaviors during trials with small rock (RS) crabs exposed to either of four chemical cues: no cue (N), large rock (RL) crab, large dead rock (RLd) crab, and large green (GL) crab. Data were pooled across Temperature (cold and warm) treatments (n=8 for each combination of Temperature x Species x Chela, with the exception of 10 with RLd cue in cold water and 9 with RL cue in warm water [67 in total]).

microcosm tanks. Results from the first experiment, which addressed effects of changes in water temperature, body size, and chela loss indicated that overall, rock and green crabs captured (i.e. crushed or opened the shells of mussel individuals) nearly three times more mussels in warm (12ºC) than cold (4ºC) water, while handling and feeding upon them more frequently in warm than cold water. Those results reinforce the paradigm that food consumption in marine invertebrates generally increases with temperature due, in part, to associated higher metabolic demand (Barbeau and Scheibling, 1994b; Elner, 1980; Gooding et al., 2009; Murray et al., 2007; Wallace, 1973). Movement (and hence foraging) in both rock and green crabs decreased with lower temperature as notably indicated by the higher proportion of time crabs were motionless in cold than warm water.

Recent studies with rock and green crabs from Prince Edward Island showed that foraging (including mussel capture) in both species generally decreased with temperature below 20°C and virtually ceased around 5°C (Bélair and Miron, 2009a; b). Likewise, other studies showed that feeding in green crabs decreases with decreasing temperature and may actually stop below 7°C (Eriksson and Edlund, 1977; Ropes, 1968). In our study, rock and green crabs still captured and consumed relatively high numbers of mussels (up to 13 in 4 hours) at 4°C and that mussel capture and frequencies of handling and feeding did not differ between species when looking at a given temperature (4 or 12°C). These findings somewhat deviate from those of Bélair & Miron (2009b) who reported mussel capture varied differently in rock and green crabs with changes in temperature, which they attributed to seasonal changes in thermal tolerance (crabs in their experiments were exposed to each of three temperature treatments: 5, 12, and 20°C in each of two different seasons). Crabs can remain physiologically and behaviorally conditioned to seasonal patterns of water temperature despite extended periods of acclimation to different thermal conditions (Cuculescu et al., 1998; Hopkin et al., 2006). In this study, warm water trials were all conducted between July and September 2009, when sea temperature (and hence the water flowing in the tanks) was at 12°C, whereas cold water trials were conducted between November and December 2009 and early June 2010, when sea temperature was at 4°C. This approach was used to try to minimize changes between temperatures at which crabs were accustomed to in their natural habitats and those used during trials, and may explain part of the variation between our results and those of Bélair and Miron (2009b). While in using this approach temperature treatments are confounded by time, it is arguably a better representation of likely seasonal variation in crab behavior. Temperature generally had no effect on mussel size selection in individuals of either species, which is consistent with previous findings (Elner, 1980; Sanchez-Salazar et al., 1987). Overall, our results indicated that low (4°C) temperature exerts a marked, yet similar influence on mussel capture in rock and green crabs from Newfoundland and Labrador. These results also suggested that green crab populations in this region are more tolerant to cold water than those in southernmost regions of eastern Canada, which also differ slightly from one another genetically (Roman, 2006, Blakeslee et al., 2010).

Mussel capture and the occurrence of mussel consumption (referred to as "feeding" behavior in this study) in both rock and green crabs were higher in large than small individuals, which supports Hypothesis 1 that mussel capture in rock and green crabs increases with increasing body size. This finding is consistent with other studies on prey capture in crabs (Dudas et al., 2005; Murray et al., 2007; Pickering and Quijón, 2011). Higher mussel capture in large individuals likely resulted from higher energy requirements and increased chela strength and gape compared to smaller individuals (Boulding, 1984). Interestingly, we found that prey capture was similar between rock and green crabs in each crab size category (small and large). However, frequencies of the five monitored behaviors (handling, feeding, sitting, moving, and burying in sediments or located within the pot) generally differed between small rock and green crabs. This was well demonstrated by burial in sediments or use of the pot, which occurred nearly five times more frequently in small rock than green crabs. Breen & Metaxas (2008) documented generally lower prey consumption in juvenile green than rock crabs, though crabs in their study were smaller than the smallest crabs in our study. In Atlantic Canada adult rock crabs typically attain a larger size than adult green crabs (Drummond-Davis et al., 1982; Klassen and Locke, 2007; this study). Other studies that reported similar mussel capture rates in rock and green crabs of Atlantic Canada used "large" individuals where rock crabs were 30 to 40 mm larger than green crabs (Bélair and Miron, 2009b; Miron et al., 2005). In this study we also compared mussel capture in rock and green crabs of comparable size (medium rock crabs versus large green crabs) and found no difference in prey capture between the two. This finding suggests that rock crabs do not need to attain a larger size than the largest green crabs to achieve similar predation on mussels. Chelae in adult rock and green crabs can produce comparable crushing force (Block and Rebach, 1998; Elner, 1978; Warner et al., 1982), which may partly explain why large individuals in both species were equally successful in capturing mussels in this study. Further research is required to better understand how relative abundances of rock and green crabs may affect natural mussel populations.

The time required by a crab to crush a prey typically increases exponentially with prey size, and hence capturing large prey requires more energy and likely stronger chelae than smaller prey (e.g. Elner and Hughes, 1978; Juanes and Hartwick, 1990; Sanchez-Salazar et al., 1987). We found that large rock and green crabs both predominantly captured large (>30 mm) mussels, whereas small individuals more frequently captured the smallest (10-15 mm) mussels. This finding which supports Hypothesis 2, that large rock and green crabs select larger mussels than small crabs. This preference is consistent with the idea that large crabs are better adapted and more likely to use larger prey than smaller crabs (Dudas et al., 2005; Murray et al., 2007). Miron et al (2005) suggested that blue mussels with a shell length >25 mm attain a partial size refuge from predation by rock and green crabs since mussels of this size were rarely consumed. Other studies also indicate that crabs often select hard-shelled prey smaller than those that would provide a higher net energy intake (Ameyaw-Akumfi and Hughes, 1987; Elner and Hughes, 1978; Sanchez-Salazar et al., 1987) likely to reduce the risks of damaging chelae while handling larger, harder prey (Juanes, 1992; Smallegange and Van Der Meer, 2003). In our experiments, large crabs consistently selected prey with shells >25 mm, which is larger than the mussels used in the above mentioned studies. Yet, none of the crabs we used damaged their chelae.

Mussels are typically scattered in studies of mussel size selection in crabs (e.g. Burch and Seed, 2000; Elner and Hughes, 1978; Mascaró and Seed, 2001). However, blue mussels usually form compact aggregations (patches) in natural habitats.

The likelihood of encounters between crabs and small mussels in such aggregations may be reduced by larger mussels that partly or completely protect small mussels from the reach of crabs (Barbeau and Scheibling, 1994a; Elner and Hughes, 1978). Interestingly, we found that mussel size selection was similar between large rock and green crabs, though small green crabs captured more of the smallest (<20 mm) mussels than small rock crabs. Common preference for a given mussel size can increase the occurrence of aggressive encounters in large crabs (Wong et al., 2010). Our data indicated that rock and green crabs alter mussel size selection according to their own size and, presumably, their ability to crush shells. The data also suggest that large rock and green crabs may compete for prey and that small green crabs may decrease mussel populations by exerting higher predation on the smaller, more vulnerable mussels. Overall, the use of mussel aggregations in our experiments indicated that rock and green crabs can readily use mussels that are larger than previously suggested and that mussel selection is partly influenced by the likelihood of encounters between crabs and mussels of different sizes.

Mussel capture decreased in the absence of one chela in rock, though not green crabs, which partly refutes the first part of Hypothesis 3 that chela loss in both species decreases mussel capture. In fact, rock crabs missing one chela consistently captured mussels, which again differs from studies showing virtually no capture of hard-shelled prey in other species of *Cancer* crabs (*C. magister* and *C. pagarus*) with one damaged or missing chela (Juanes and Hartwick, 1990; Patterson et al., 2009). Food ingestion can decrease with the loss of a chela due to reduced ability to crush hard-shelled prey. However, this pattern is not consistent across crab species and often depends on the type of chela that is lost (Davis et al., 2009; Elner, 1980; Juanes and Hartwick, 1990; Mathews et al., 1999; Smith and Hines, 1991). In this study we systematically removed the small (cutter) chela in green crabs as opposed to the large (crusher) chela normally used to capture prey since we anticipated high fluctuation in the data had we randomly removed either chela (Elner and Hughes, 1978; Smallegange and Van Der Meer, 2003). This strategy meant each rock and green crab retained a chela capable of crushing mussels, which allowed us to compare the ability of each species to capture mussels with only one chela. Logistical considerations prevented us from testing both the effects of loss of small and large chelae. Nevertheless, the loss of the small chela in green crab had no perceptible effect on prey capture compared to conspecifics with both chelae intact. The loss of the large chela in green crabs may only slightly reduce mussel capture (Delaney et al., 2011). We found that in both crab species individuals lacking one chela fed less than those with both chelae intact. Mussel handling was more frequent (by 30%) in green crabs missing one chela than those missing no chela in cold water only (there was no difference in warm water), though handling occurred equally frequently in rock crabs regardless of chela loss and water temperature. All patterns above support the contention that green crabs must use their two chelae together to capture mussels efficiently (with the small chela grasping and holding the mussel while the large chela crushes it). In contrast rock crabs can use either chela because they are equally strong and agile at both grasping and crushing mussels. Chela loss only had a negligible effect on mussel size selection in rock and green crabs, which lends weak support to the second part of Hypothesis 3 that chela loss in both species alters mussel size selection. In both species, individuals missing one chela showed preferred large (>30 mm) mussels less than intact crabs in cold water only. Possibly, the negative effect of low temperature on muscle functions in crabs

(Blundon, 1989) combined with a decreased ability to crush hard-shelled mussels in the absence of one chela contributed to the observed reduction in capture of large mussels.

Chemicals released from prey, predators, and competitors can represent cues that alter predation and associated behaviors in marine crustaceans, including crabs (Ferner et al., 2005; Hazlett, 1997; 1999). Accordingly, the decision to search for and capture prey often reflects a trade-off between the risk of being preyed on and the benefit of capturing prey (Lima and Dill, 1990). Our second experiment, which addressed effects of changes in water temperature and chemical cues, indicated that rock crabs, regardless of water temperature, captured similar proportions of mussels with and without chemical cues from intact and dead rock crabs and intact green crabs. This pattern refutes the first part of Hypothesis 4, that chemical cues from conspecifics and heterospecifics alter mussel capture. We propose that in the absence of visual or tactile alarm cues from conspecifics and heterospecifics, rock crabs maintained capture rates irrespective of present chemical cues, which they may not perceive as a threat or as a minimal threat that only requires increased vigilance, as seen in some other aquatic species (Brown et al., 2004; Hazlett and McLay, 2000). The three types of cues we used were strong enough to be perceived by rock crabs, as clearly shown by resulting shifts in the size of mussels captured by small rock crabs and, to a lesser extent, large rock crabs with missing or intact chelae. These findings generally support the second part of Hypothesis 4 that chemical cues from conspecifics and heterospecifics alter size selection in rock crabs. In particular, small rock crabs exposed to cues from intact rock and green crabs captured a narrower range of mussel sizes with fewer medium-sized (25-30 mm) mussels than in the absence of cues (control) in cold water only (there was no difference in warm water). Other experimental studies showed that the presence of conspecifics did not alter prey size selection in green and blue crabs (*Callinectes sapidus*), though used large individuals only (Smallegange et al., 2008; Wong et al., 2010). Ours is the first study to explore effects of chemical cues from crabs on mussel predation in rock crabs. Further studies are required to determine how these sorts of chemical cues affect preferences in rock crabs offered multiple prey species.

In crustaceans, small individuals are generally more vulnerable to predation than large individuals, but exhibit lower activity and increased defensive behaviors in the presence of a potential threat relative to their larger counterpart (Smith and Hines, 1991; Stein, 1977). Our results are consistent with this paradigm in that the presence of cues from only large, dead rock crabs significantly decreased mussel handling while increasing frequencies of burial in sediments or use of pot but only in small rock crabs in both cold and warm water. We suggest that small rock crabs systematically perceived this cue as a potential threat of predation and therefore hid in sediments or moved inside the pot. This pattern along with the absence of change in mussel handling and burial or use of the pot in the presence of cues from green crabs is also consistent with studies suggesting cues from conspecifics affect feeding and habitat selection in crustaceans more adversely than heterospecifics (Hazlett, 2000; Tanner, 2007). Rock crabs used in this study were collected at sites with no confirmed occurrence of the green crab. Therefore, it is also possible that rock crabs had no prior interactions with green crabs, and hence were not responsive to the unfamiliar cues released by green crabs during trials.

In summary, these experiments demonstrate that: 1) mussel capture in rock and green crabs was higher in large than small individuals, 2) large crabs in each species selected larger mussels than small crabs, 3) chela loss decreased mussel capture uniquely in rock crabs and caused only subtle changes in mussel size selection in both species, and 4) chemical cues from other crabs did not affect mussel capture in rock crabs, yet altered mussel size selection and the frequency of foraging behaviors in small rock crabs only. Increasing temperature from 4 to 12°C generally exacerbated these patterns by significantly increasing mussel capture in both species, which highlights the importance of considering changes in the thermal environment in studies of predation in crabs and other related taxa. Our findings are based on laboratory microcosm experiments that mimicked natural conditions. We used this approach to control temperature and light, while eliminating potential effects of other environmental variables such as wave and current energy and the chemical environment. Our goal was to examine how rock and green crabs respond to different treatments related to foraging, and hence did not allow any interactions between them. Results presented here provide a framework to examine physical interactions between rock and green crabs competing for a common, limited prey (see Chapter III). These are the first experiments to compare predation between rock and green crabs using green crabs from Newfoundland and Labrador, currently the northern limit of the species distribution in the northwest Atlantic (DFO, 2011). Our findings suggest that the recent introduction of the green crab to this region may have a greater impact on foraging in small than large rock crabs and those missing one chela, while altering mussel populations through marked preference by small green crabs for small mussels.

CHAPTER III

Effects of temperature, body size, and chela loss on competition for a limited food source between indigenous rock (*Cancer irroratus* Say) and recently introduced green (*Carcinus maenas* L.) crabs

3.1 INTRODUCTION

The European green crab, *Carcinus maenas*, is one of the most successful marine invasive species worldwide (Audet et al., 2003; Cohen et al., 1995; Klassen and Locke, 2007; Lowe et al., 2000). The green crab is tolerant of diverse environmental conditions, especially temperature and salinity (Beukema, 1991; Eriksson and Edlund, 1977), and has a generalist diet that includes bivalves, gastropods, polychaetes, crustaceans, and seaweeds (Cohen et al., 1995; Elner, 1981; Ropes, 1968). These characteristics suggest high adaptive potential that likely contributed to significant alteration of many shallow subtidal communities by green crab throughout its distribution range (Grosholz et al., 2000; Rochette et al., 1998; Trussell et al., 2002; Walton et al., 2002; Whitlow, 2010).

The high agility and aggressiveness of green crabs may enable more efficient foraging, and hence the capacity to outcompete other crustaceans for space and food resources (Lohrer and Whitlatch, 2002; Sneddon et al., 1997a; Williams et al., 2006). For example, laboratory microcosm experiments measuring competition for food between green and Dungeness (*Cancer magister*) crabs and between green and blue (*Callinectes sapidus*) crabs showed that green crabs initially contacted food items (the venus clam, *Venerupis philippinarum*, and the ribbed mussel, *Geukensia demissa*) more frequently and spent more time feeding upon them than the two other species (MacDonald et al., 2007; McDonald et al., 2001). Rossong et al. (2011) reported that the presence of an adult green crab led juvenile American lobsters, *Homarus americanus*, to decrease feeding and increase time within a shelter. These studies improved understanding about the ability of green crabs to compete with other crustaceans. Nonetheless, little is known about the capacity of indigenous species to limit or slow down the establishment of new populations of green crabs (i.e. biotic resistance; Elton, 1958), beyond a few studies showing that large individuals in a few crab species can prey upon green crabs or attenuate effects of green crab on prey (deRivera et al., 2005; Gregory and Quijon, 2011; Hunt and Yamada, 2003; Jensen et al., 2007). Moreover, prey capture and frequencies of associated foraging behaviors in green crab generally decrease with decreasing water temperature (Bélair and Miron, 2009a; Elner, 1980; Sanchez-Salazar et al., 1987; Wallace, 1973; Chapter II), which suggests that the ability of this species to compete for food may decrease as it approaches its northern, colder distribution limit.

The recent (2007) discovery and rapid explosion of populations of green crab in predominantly cold marine ecosystems of Newfoundland and Labrador (eastern Canada) raises concerns about its impact on populations of indigenous species and associated fisheries. For example, green crab abundance in some areas of Placentia Bay are currently several orders of magnitude higher than in other parts of eastern and western Canada and the USA; (DFO, 2011; McKenzie et al., 2010). Rock crab, *Cancer irroratus*, is a dominant, indigenous, crustacean predator in subtidal ecosystems in eastern Canada, including Newfoundland and Labrador (Caddy and Chandler, 1976; Drummond-Davis et al., 1982; Squires, 1990). In Newfoundland, rock and green crabs can coexist in sandy and rocky habitats (Drummond-Davis et al., 1982; Grosholz and Ruiz, 1995; Musick and McEachran, 1972; Winget et al., 1974) with substantial dietary overlap (Cohen et al., 1995; Elner, 1981; Miron et al., 2005; Ropes, 1968). In Chapter II, we used laboratory microcosm experiments with rock and green crabs from Newfoundland and Labrador held separately and offered aggregates of 60 variably sized (10 to 40 mm in shell length) blue mussels, *Mytilus edulis*. Results showed that individuals in both species captured similar numbers of mussels of comparable sizes in both cold (4°C) and warm (12°C) water, whereas mussel capture in rock crabs was unaffected by exposure to chemical cues from conspecifics and green crabs. These patterns suggest interspecific competition for food and shelter, regardless of water temperature. This idea is reinforced by extensive field surveys indicating declines in the abundance of rock crabs in areas of southern Newfoundland now populated by green crab (DFO 2011). Other microcosm experiments with rock and green crabs from Prince Edward Island held together and offered smaller numbers (up to 30) of blue mussels showed that competition can affect foraging, including prey capture, in rock crabs (Bélair and Miron, 2009a; b). Yet, the outcome of contests between rock and green crabs for an even more limited prey resource remains largely unexplored. This is especially the case at low water temperatures characteristic of subarctic and temperate marine habitats of Newfoundland and Labrador and with green crab populations that only recently invaded habitats. Green crabs may not have had sufficient time to adapt behaviorally and physiologically to their new environment (both individually and as a population).

In crustaceans, contests for food, shelter, and mates can increase when these resources are limited (Jachowski, 1974; Sneddon et al., 1997a; Williams et al., 2006). Conflicts between competing crabs can be resolved through behaviors that range from escape of one crab in response to aggressive displays of chelae (i.e. meral spread) by the other crab, to escalating contests between the two crabs that can cause injury and even death. Encounters between crabs can begin with threatening signals that evolve into physical interactions in sustained competitive situations (Glass and Huntingford, 1988).

Interactions that could potentially cause injury should be resolved faster than those that are nonthreatening (Maynard Smith, 1974). In general, large individuals are better than smaller individuals at stealing or monopolizing a resource (Huntingford et al., 1995; Smith et al., 1994; Thorpe et al., 1994). Consequently, the ability to maintain possession of a resource is often positively related to body size (Archer, 1988; Parker, 1974) and differences in body size and other morphological asymmetries between competing crabs often influence the outcome of contests (Maynard Smith, 1979; Sneddon and Swaddle, 1999).

Crabs use their chelae to show aggressive warning signals and strike or grasp opponents (Juanes and Smith, 1995) and relative chela size can influence the outcome of contests for food resources between crabs of similar body size (Sneddon et al., 1997a). The intentional severance (autotomy) of chelae or other limbs in response to potential injury or predation is a frequent phenomenon in crabs, and can adversely affect prey capture (Abello et al., 1994; Sekkelsten, 1988; Smith et al., 1994). The likelihood of losing a chela generally increases with body size (Abello et al., 1994; Mathews et al., 1999), due to more intense physical interactions between large individuals. Chapter II showed that mussel capture in rock crabs held individually was 50% less in individuals that lost one chela compared to individuals with both chelae intact. Testing how the presence of green crabs affects the ability of rock crabs with one or both chelae to capture prey when prey items are limited would help further characterize competitive abilities in rock crab and how its populations may respond to biological invasions.

In this study, we use one laboratory microcosm experiment with rock and green crabs from Newfoundland and Labrador to determine how changes in body size and the loss of one chela affects the ability of one rock crab to compete with one large green crab for a single prey item, the blue mussel, *Mytilus edulis*. Specifically, we test hypotheses that: 1) the ability of the rock crab to grasp the mussel before the green crab decreases with decreasing body size and chela loss, 2) the proportion of time the rock crab holds the mussel decreases with decreasing body size and chela loss, 3) the number of contests and associated degree of physical interactions between rock and green crabs decrease with decreasing body size and chela loss, 4) the likelihood that the rock crab initiates and wins contests with the green crab decreases with decreasing body size and chela loss, and 5) the proportion of time the rock crab is buried in sediments or within a cavity increases with decreasing body size and chela loss. We test each hypothesis in cold (4°C) and warm (12°C) water to determine how a temperature representative of spring (or fall) and summer in Newfoundland affects patterns.

3.2 MATERIALS AND METHODS

3.2.1 Collection, maintenance, and acclimation of crabs prior to experimentation

This study was part of a research project examining mussel capture and size selection in rock and green crabs of Newfoundland and Labrador. A comprehensive description of crab collection, maintenance, and acclimation prior to experimentation, as well as experimental tank set-up is provided in Chapter II. Rock and green crabs were hand collected by divers or captured with baited (herring) Fukui traps in shallow (<10 m deep) water at sites in eastern and southern Newfoundland between late May and

November 2009 and in June 2010. Only male crabs with no red/orange coloration (indicative of stronger, thicker carapace and chelae; Reid et al., 1997) were transported to the Ocean Sciences Centre where they were maintained in large holding tanks supplied with flow-through seawater. Rock crabs were selected and grouped in three size classes according to carapace width: small (RS; 49.57 ± 4.62 mm), medium (RM; 68.98 ± 4.96 mm), and large (RL; 91.19 ± 6.02 mm), whereas only large (61.05 ± 4.51 mm) green crabs were selected. All crabs were fed twice a week with live, blue mussels (*Mytilus edulis*) maintained in separate tanks until the start of the acclimation period (see below).

The experiment was conducted in glass tanks (62x31x43 cm [L, W, H]) supplied with ~1 L min^{-1} of flow-through seawater. The bottom of each tank was covered with a 3-cm thick layer of sediments on top of which 10 to 15 small (<10 cm in diameter) rocks were scattered haphazardly and a plastic pot (15 cm in diameter) cut in half and deposited in the middle of the tank to mimic crab habitat and provide crabs with the opportunity to bury and move into a protective shelter. Each tank was surrounded by an opaque canvas to avoid visual external stimuli. An incandescent, 100-watt light bulb (Soft White, General Electric) located at 45 cm above each tank was set with dimmers and timers to expose crabs to continuous cycles of 12 h of low light intensity (90-100 lux) followed by 12 h of darkness. Crabs were maintained in holding tanks for a minimum of one week prior to acclimation to experimental conditions. The acclimation consisted of exposing each crab for 72 h to the same water temperature (one of two levels) and photoperiod (held constant among temperature treatments) used in the corresponding experimental treatment in glass aquaria similar to those used during trials (see below). To standardize hunger levels we did not feed crabs during the acclimation period.

3.2.2 Experimental approach

We define "contest" as any interaction between rock and green crabs ranging from simple display of chelae (i.e. meral spread) with no physical contact, to the use of chelae to strike or grasp each other. A contest begins when an interaction occurs, regardless of whether one or no crab holds the mussel at the start of the contest, and ends either when a crab takes the mussel away from the other crab (if the contest involves a mussel) or when the interaction forces one crab to move away (if the contest involves no mussel). Accordingly, a crab wins a contest if it takes the mussel away from the other crab or if the other crab retreats in apparent response to the interaction. We used a laboratory microcosm experiment to investigate effects of temperature, body size, and chela loss on the ability of one rock crab to compete with one green crab for a single prey, the blue mussel, *Mytilus edulis.* The experiment was designed to test hypotheses that: 1) the ability of the rock crab to grasp the mussel before the green crab decreases with decreasing body size and chela loss, 2) the proportion of time the rock crab holds the mussel decreases with decreasing body size and chela loss, 3) the number of contests and associated degree of physical interactions between rock and green crabs decrease with decreasing body size and chela loss, 4) the likelihood that the rock crab initiates and wins contests with the green crab decreases with decreasing body size and chela loss, and 5) the proportion of time the rock crab is buried in sediments or inside the pot increases with decreasing body size and chela loss. The average size of rock crabs missing one chela (RLi, 90.71 ± 4.51

mm) was comparable to that of large rock crabs with both chelae present (RL, see above). We used intact crabs in which we induced chela loss (as opposed to using crabs that already lacked one chela) to ensure that crabs with one chela missing experienced comparable stress while benefiting from the same amount of time and environmental conditions to adapt to the loss of a chela (refer to Chapter II for a description of the procedure used to induce chela loss). Crabs with one chela missing were maintained in holding tanks for one week prior to the 72-h acclimation period (see above) and discarded if physical activity levels decreased compared to the other individuals with one chela missing. The experiment was conducted at two temperatures approximating spring (and fall) and summer averages in shallow coastal areas of southern Newfoundland: 4°C (cold) and 12°C (warm) (Methven and Piatt, 1991). Treatments were randomly assigned to tanks and one replicate of each treatment was conducted each day we performed trials in July 2009, when water in the tanks was 12°C, and in November 2009, when water in the tanks was 4°C. Each treatment was replicated seven or eight times. To increase sample size we replicated treatments an additional seven or eight times in early June and July 2010, when water was again at 4 and 12°C, respectively.

In each trial, crabs were offered one blue mussel with a shell length between 25 and 30 mm (measured with a vernier caliper) placed in the centre of the tank. This mussel size was selected based on our previous experiments that showed it was frequently captured by both crab species (see Chapter II). Contrary to some other studies of competition in crabs (e.g. Jensen et al., 2002; Williams et al., 2006), we did not artificially anchor (e.g. with cable ties) the mussel to the substrate. Anchoring the mussel can increase competition between crabs (which was not our goal), but we left the mussel unanchored to allow crabs to interact with it freely like in natural habitats. After the acclimation period (see above), one rock and one green crab were moved to opposite ends (determined randomly) of one experimental tank and physically isolated from one another and the mussel by two perforated, opaque plastic dividers (details in Chapter II). Crabs were allowed to acclimate 15 min to their new environment before the start of each trial. Each trial lasted 45 min and began when we removed the plastic dividers from the tank to expose the mussel to the two crabs, which could then physically interact.

We observed the two crabs continuously during each trial and recorded which of them: 1) grasped the mussel first [recorded once], 2) held the mussel with chelae or legs [recorded every minute], 3) initiated and won each contest, and 4) was buried in sediments or inside the pot [recorded every minute]. For each contest, whether the mussel was involved or not, we determined the maximum degree of physical interaction that occurred between crabs using the following interaction scale (adapted from Sneddon et al., 1997a): 1) "Very weak": one crab approached the other one with or without displaying its chelae in meral spread and the other crab responded by retreating without physical contact, 2) "Weak": only one crab used its chelae or legs to push the other crab or both crabs displayed their chelae [i.e. meral spread] but did not establish physical contact, 3) "Moderate": both crabs displayed chelae and used them or their legs to push each other, and 4) "Strong": crabs struck or grasped each other with chelae. We used only the highest degree of interaction to characterize those contests that involved multiple interactions. We also recorded limb loss or fatality in crabs during trials. At the end of each trial we removed the mussel from the tank and replaced the top layer (~1 cm) of sediments with fresh sediments. We discarded trials in which any of the crabs molted in the week following experimentation to further minimize variation in the data that could have arisen from any physiological stress and behavioral modification. Each trial was conducted with crabs not used previously.

3.2.3. Statistical Analysis

We used a two-way ANOVA with the factors Temperature (cold and warm) and Size/Chela (small [RS], medium [RM], and large [RL] intact rock crabs, and large rock crabs missing one chela [RLi]) to examine effects of temperature, crab size, and chela loss on the proportion of trials in which rock crabs grasped the mussel before green crabs (Hypothesis 1). We treated this analysis as a particular case of the generalized linear models (McCullagh and Nelder, 1989), which assumed a binomial distribution of the response variable (ratio of number of trials where the rock crab grasped the mussel first relative to total number of trials), and hence did not test for homoscedasticity and normality in the data. The observed proportions were also compared with proportions expected by chance assuming a binomial distribution (i.e. a 50/50 chance) to determine if one crab species grasped the mussel first more frequently than the other species in each crab treatment. Crab treatments were pooled if the ANOVA described above indicated that crab treatments did not differ between each other. We excluded from the analysis trials in which no crab grasped the mussel.

We used a two-way ANOVA with the factors Temperature (cold and warm) and Size/Chela (RS, RM, RL, and RLi) to investigate effects of temperature, crab size, and chela loss on the proportion of observations in which rock crabs held the mussel relative to the total number of observations in which any of the two crabs held the mussel

(Hypothesis 2). Data were square-root transformed to correct for heteroscedasticity. We used this approach instead of the particular case of the generalized linear model that assumes a binomial distribution of the response variable because each binary decision to hold or release the mussel could not be considered totally independent from decisions in previous observations, which were likely influenced by satiation and interactions between crabs (Manly, 2006). We used two-tailed paired t-tests to determine if rock and green crabs held the mussel equally frequently in each rock crab treatment.

We used a two-way ANOVA with the factors Temperature (cold and warm) and Size/Chela (RS, RM, RL, and RLi) to examine effects of temperature, crab size, and chela loss on the number of contests that occurred between rock and green crabs in each trial (Hypothesis 3). We applied the analyses to the square-root transformed data to correct for the lack of normality of the residuals. We used a two-way MANOVA (Schneiner and Gurevitch, 2001) with the factors Temperature (cold and warm) and Size/Chela (RS, RM, RL, and RLi) to further examine effects of temperature, crab size, and chela loss on the proportion of contests assigned to each of four degrees of physical interactions (Very weak, Weak, Moderate, Strong) between crabs (Hypothesis 3). Although we square-root transformed data to correct for heteroscedasticity not all residuals in each category of physical interaction was normally distributed. We reported the results from the analyses on square-root transformed data since the MANOVA is robust to deviations from normality (Huberty and Olejnik, 2006).

We used two two-way ANOVAs with the factors Temperature (cold and warm) and Size/Chela (RS, RM, RL, and RLi) to determine effects of temperature, crab size, and chela loss on the proportion of contests initiated and won by rock crabs (Hypothesis 4).

We used this approach instead of a generalized linear model for the same reasons explained above. We applied each analysis to the raw data even though residuals in the proportion of contests won were still not normally distributed after data transformation (ANOVA is robust to deviations from normality; Underwood, 1997). We used paired t-tests (two-tailed) to determine whether the proportion of contests initiated and won differed between rock and green crabs in each rock crab treatment. The ability of a green crab to win a contest involving a prey with a crustacean competitor may depend on which individual holds the prey at the onset of the contest and the difference in size between individuals (Williams et al., 2006; Williams et al., 2009), and, presumably, the loss of a chela. Therefore, we conducted two additional sets of analyses to further investigate whether holding the mussel at the onset of a contest, the difference in size between crabs, and the loss of a chela influenced the likelihood that rock and green crabs win contests. First, we used two one-way ANCOVAs with the factor Temperature (cold and warm) and the covariate Carapace Width (difference in carapace width between rock and green crabs in each trial) to examine effects of temperature and relative body size on the proportion of contests starting with the green crab holding the mussel that ended with the rock crab holding the mussel (i.e. the rock crab won the contest by taking the mussel from the green crab) and vice versa. The use of the covariate necessitated pooling data across all rock crab sizes (RS, RM, and RL) to increase sample size. No transformation corrected the lack of normality in the residuals, and hence we applied each analysis to the raw data, which were homoscedastic. Secondly, we used a two-way ANOVA with the factors Temperature (cold and warm) and Chela (both chelae present and one chela missing) to investigate effects of temperature and chela loss on the proportion of contests starting with the green crab holding the mussel that ended with the large rock crab holding the mussel. The analysis was applied to square-root transformed data to correct for heteroscedasticity.

We used a two-way ANOVA with the factors Temperature (cold and warm) and Size/Chela (RS, RM, RL, and RLi) to investigate effects of temperature, crab size, and chela loss on the proportion of observations (out of a total of 45 observations per trial) in which rock crabs were buried in sediments or located in the pot (Hypothesis 5). We considered crab burial and displacement to inside the pot as analogous behaviors (see discussion), and hence we summed observations (as opposed to treating each separately) of crabs buried in sediments and inside the pot in each trial. We applied the analysis to the raw data because they met the assumptions of the ANOVA. We used two-tailed paired t-tests to determine whether frequencies of burial and use of the pot differed between rock and green crabs in each rock crab treatment.

The factor Year (2009 and 2010) was initially included in all analyses to determine whether results from experiments conducted in 2009 differed from those in 2010. Results did not differ, and hence were pooled. In all analyses, normality was verified using Shapiro-Wilk's statistic and homogeneity of variance by using Levene tests and examining the graphical distribution of the residuals. All factors in each analysis were considered fixed because we were only concerned with the effects of the specific levels within each factor we tested. To detect differences among levels within a factor we used least-square means multiple comparison tests (ANOVAs and ANCOVAs) and multivariate contrasts with Bonferonni correction of probabilities (MANOVA). When a factor or interaction between factors was significant in the MANOVA we examined the univariate model for each response variable (the four degrees of physical interactions) to identify, which contributed to the multivariate effect. This comparison was achieved by conducting an ANOVA for each response variable with the same factors as in the corresponding MANOVA. We used Pillai's trace multivariate statistic, which is more robust than other multivariate statistics to deviations from homoscedasticity and normality of the residuals and more conservative with small and uneven sample sizes, to determine which factor(s) in the MANOVA with more than two levels were statistically significant (Schneiner and Gurevitch, 2001). A significance threshold of 0.05 was used for all statistical tests. All the analyses were conducted with JMP 7.0.

3.3 RESULTS

3.3.1 Interactions between crabs and mussels

Temperature (warm and cold), body size (small, medium, and large), and the loss of a chela did not affect the ability of the rock crab to grasp the mussel before a large, intact green crab (Table 3.1). In fact, green crabs were consistently more successful than rock crabs as indicated by >90% of the trials (79 out of 87, data pooled across temperature and crab treatments) in which the green crab grasped the mussel first (comparison with proportions expected by chance assuming a binomial distribution, $p < 0.01$). The proportion of time the rock crab held the mussel varied with temperature and crab treatments (body size and chela loss) altogether (Table 3.2). For example, small rock (RS) crabs spent a smaller proportion of time holding the mussel in cold (2%) than warm (24%) water, whereas large rock (RL) crabs spent a greater

Table 3.1. Summary of two-way ANOVA (generalized linear model) showing the effect of Temperature (cold and warm) and Size/Chela (small [RS], medium [RM], and large [RL] intact rock crabs, and large rock crabs missing one chela [RLi]) on the proportion of trials in which the rock crab grasped the mussel before the green crab (see Hypothesis 1 in Materials and methods).

Source of variation	*df*	χ^2	*p*
Temperature	1	< 0.01	1.00
Size/Chela	3	7.46	0.059
Temperature x Size/Chela	3	6.63	0.085

Table 3.2. Summary of two-way ANOVA (applied to square-root transformed data) showing the effect of Temperature (cold and warm) and Size/Chela (small [RS], medium [RM], and large [RL] intact rock crabs, and large rock crabs missing one chela [RLi]) on the proportion of observations in which rock crabs held the mussel (see Hypothesis 2 in Materials and methods).

Source of variation	***df***	**MS**	***F*-value**	***p***
Temperature	1	0.031	0.38	0.54
Size/Chela	3	0.47	5.89	< 0.01
Temperature x Size/Chela	3	0.28	3.46	0.021
Error	68	0.080		
Corrected total	75			

proportion of time holding the mussel in cold (50%) than warm (17%) water (LS means, $p = 0.049$ and 0.016, respectively; Fig. 3.1). In cold water, large rock (RL) crabs held the mussel twenty five and three times more frequently than small (RS) (LS means, $p < 0.01$) and medium (RM) (LS means, $p < 0.01$) rock crabs, respectively (Fig. 3.1). However, in warm water, small rock (RS) crabs held the mussel as often as large rock (RL) crabs and seven times more frequently than medium rock (RM) crabs (LS means, $p = 0.86$ and 0.031, respectively; Fig. 3.1). Large intact rock crabs held the mussel 12-fold more frequently than large rock crabs missing one chela in cold water (LS means, $p < 0.01$) though there was no difference in warm water (Fig. 3.1). Green crabs held the mussel more often (between 76 and 98% of the time) than rock crabs in all combinations of temperature and crab treatments (paired t-tests, $p < 0.036$), except in cold water where medium and large rock crabs held the mussel as frequently as green crabs ($p = 0.068$ and 0.98, respectively).

3.3.2 Frequency and intensity of contests between rock and green crabs

The number of contests during trials (between 0 and 17 or 3.97 ± 3.85 contests on average per trial) was unaffected by changes in Temperature and Size/Chela treatments (Table 3.3, Fig. 3.2). The MANOVA examining the effect of temperature, crab size, and chela loss on the proportion of contests assigned to each of four degrees of physical interactions (very weak to strong) indicated the degree of physical interactions varied separately with temperature and crab treatments (Table 3.4). Indeed, there was nearly a twofold increase in the proportion of contests with very weak physical interactions in warm compared to cold water (LS means, $p < 0.01$; Table 3.5, Fig. 3.2). Contests with

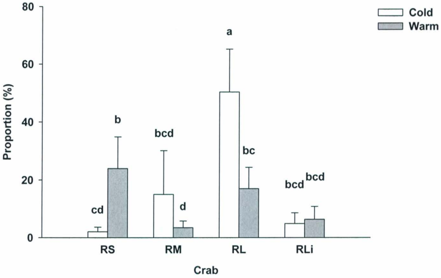

Figure 3.1. Mean proportion (+SE) of observations in which small (RS), medium (RM), and large (RL) intact rock crabs, and large rock crabs missing one chela (RLi) held the mussel in cold and warm water. Bars not sharing the same letters are different (LS means, $p < 0.05$; n=6 to 14).

Table 3.3. Summary of two-way ANOVA (applied to square-root transformed data) showing the effect of Temperature (cold and warm) and Size/Chela (small [RS], medium [RM], and large [RL] intact rock crabs, and large rock crabs missing one chela [RLi]) on the total number of contests in each trial between rock and green crabs (see Hypothesis 3 in Materials and methods).

Source of variation	***df***	**MS**	***F*-value**	***P***
Temperature	1	4.49	3.74	0.056
Size/Chela	3	0.98	0.82	0.49
Temperature x Size/Chela	3	2.14	1.78	0.15
Error	119	1.20		
Corrected total	126			

Table 3.4. Summary of two-way MANOVA (applied to square-root transformed data) showing the effect of Temperature (cold and warm) and Size/Chela (small [RS], medium [RM], and large [RL] intact rock crabs, and large rock crabs missing one chela [RLi]) on the proportion of contests between rock and green crabs assigned to each of four degrees of physical interactions (Very weak, Weak, Moderate, and Strong) (see Hypothesis 3 in Materials and methods).

Source of variation	**Pillai's Trace**	***F*-value**	**NumDF**	**DenDF**	***p***
Temperature	0.17	3.77	4	88	< 0.01
Size/Chela	0.26	2.16	12	270	0.014
Temperature x Size/Chela	0.19	1.51	12	270	0.12

Table 3.5. Summary of two-way ANOVAs (applied to square-root transformed data) showing the effect of Temperature (cold and warm) and Size/Chela (small [RS], medium [RM], and large [RL] intact rock crabs, and large rock crabs missing one chela [RLi]) on the proportion of contests between rock and green crabs assigned to each of four degrees of physical interactions (see Hypothesis 3 in Materials and methods).

Degree	**Source of variation**	***df***	**MS**	***F*-value**	***p***
Very weak	Temperature	1	1.62	13.79	< 0.01
	Size/Chela	3	0.61	5.19	< 0.01
	Temperature x Size/Chela	3	0.042	0.36	0.78
	Error	91	0.12		
	Corrected total	98			
Weak	Temperature	1	0.65	6.40	0.013
	Size/Chela	3	0.035	0.34	0.79
	Temperature x Size/Chela	3	0.22	2.18	0.10
	Error	91	0.10		
	Corrected total	98			
Moderate	Temperature	1	0.17	1.82	0.18
	Size/Chela	3	0.29	3.22	0.026
	Temperature x Size/Chela	3	0.054	0.59	0.62
	Error	91	0.091		
	Corrected total	98			
Strong	Temperature	1	0.034	0.36	0.55
	Size/Chela	3	0.35	3.74	0.014
	Temperature x Size/Chela	3	0.16	1.68	0.18
	Error	91	0.094		
	Corrected total	98			

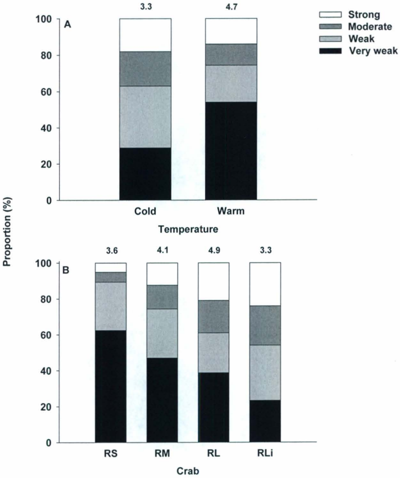

Figure 3.2. Standardized proportion (error bars not shown for clarity) of contests between rock and green crabs assigned to each of four degrees of physical interactions (Very weak, Weak, Moderate, and Strong) in (A) cold and warm water with data pooled across Size/Chela [RS, RM, RL, and RLi] treatments and (B) small [RS], medium [RM], and large [RL] intact rock crabs, and large rock crabs missing one chela [RLi] with data pooled across Temperature (cold and warm) treatments ([A] n=31 [RS] and 32 [each other crab category] and [B] n=64 [cold] and 63 [warm]). Values above bars represent the mean number of contests per trial.

weak physical interactions occurred twice as frequently in cold than warm water (LS means, $p = 0.013$), whereas the frequency of moderate and strong physical interactions did not differ with temperature (Fig. 3.2). The proportion of contests with very weak physical interactions was 24 % greater in small (RS) than large (RL) rock crabs, though this difference was marginally non significant (LS means, $p = 0.057$, Fig. 3.2). The proportions of contests with moderate and strong physical interactions were respectively 14 and 19% higher in large (RL) than small (RS) rock crabs (LS means, $p < 0.01$ for both comparisons, Table 3.5, Fig. 3.2). Each degree of physical interactions with the green crab occurred as often in large rock crabs with two chelae (RL) as those missing one chela (RLi), with the exception that very weak interactions were more frequent in rock crabs with two chelae (LS means, $p = 0.049$; Fig. 3.2). There was no incident of limb loss or fatality in crabs during any trial.

The proportion of contests initiated by rock crabs varied with Temperature and Size/Chela treatments altogether (Table 3.6). In cold water, rock crabs initiated contests equally frequently regardless of size and chela loss (Fig. 3.3). However, in warm water, large rock crabs with both chelae present (RL) and missing one chela (RLi) initiated a significantly higher proportion of contests (up to 62%) than small rock (RS) crabs (18%) (Fig. 3.3). Rock crabs in each category initiated a similar proportion of contests as green crabs in cold water (paired t-tests, $p < 0.11$ for all paired treatments). However, in warm water, green crabs initiated a higher proportion of contests (76 to 80%) than small (RS) and medium (RM) rock crabs (paired t-tests, $p = 0.021$ and 0.018, respectively). The proportion of contests won by the rock crab was not affected by temperature, but differed

Table 3.6. Summary of two-way ANOVA (applied to raw data) showing the effect of Temperature (cold and warm) and Size/Chela (small [RS], medium [RM], and large [RL] intact rock crabs, and large rock crabs missing one chela [RLi]) on the proportion of contests initiated by the rock crab (see Hypothesis 4 in Materials and methods).

Source of variation	***df***	**MS**	***F*-value**	***p***
Temperature	1	0.092	0.69	0.41
Size/Chela	3	0.27	2.01	0.12
Temperature x Size/Chela	3	0.38	2.83	0.043
Error	92	0.13		
Corrected total	99			

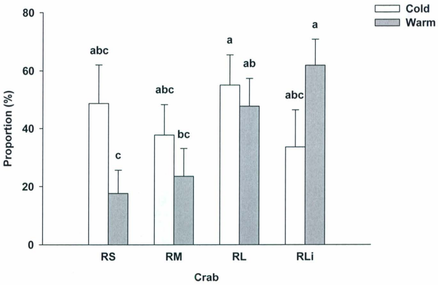

Figure 3.3. Mean proportion (+SE) of contests initiated by small (RS), medium (RM), and large (RL) intact rock crabs, and large rock crabs missing one chela (RLi). Bars not sharing the same letters are different (LS means, $p < 0.05$; n=21 [RS] and 25 [each other crab category]).

between Size/Chela treatments (Table 3.7). For example, large, intact rock (RL) crabs won a significantly higher proportion of contests (50%) than small (9%) and medium (18%) rock (RS and RM) crabs (LS means, $p < 0.01$; Fig. 3.4). Large rock (RL) crabs won a similar proportion of contests as green crabs (paired t-test, $p = 0.12$), whereas green crabs won a greater proportion of contests (up to 91%) than small and medium rock (RS and RM) crabs (paired t-tests, $p < 0.01$; Fig. 3.4). Interestingly, rock crabs missing one chela (RLi) won as many contests as large, intact rock crabs (RL) (Fig. 3.4).

The proportion of contests that the rock crab won by taking the mussel from the green crab was low (11% of all contests) and increased with increases in rock crab size (carapace width) relative green crab size, but in cold water only (Table 3.8). Conversely, the proportion of contests that green crab won by taking the mussel from the rock crab was only slightly higher (17% of all contests) and did not vary with changes in temperature and size difference between crabs (Table 3.9). When the green crab held the mussel at the beginning of the contest, large intact rock crabs (RL) were fivefold more successful in taking the mussel from the green crab compared to large rock crabs missing one chela (RLi) (26 and 5% respectively; Table 3.10).

3.3.3 Use of sediments and pot by crabs

Results of the ANOVA examining effects of temperature, body size, and chela loss on the proportion of observations in which rock crabs were buried in sediments or located in the pot indicated that such behaviors were not influenced by temperature and the loss of a chela, yet decreased with increasing size in rock crabs with both chelae (Table 3.11, Fig. 3.5). Indeed, small (RS) and medium (RM) rock crabs were buried in

Table 3.7. Summary of two-way ANOVA (applied to raw data) showing the effect of Temperature (cold and warm) and Size/Chela (small [RS], medium [RM], and large [RL] intact rock crabs, and large rock crabs missing one chela [RLi]) on the proportion of contests won by the rock crab (see Hypothesis 4 in Materials and methods).

Source of variation	***df***	**MS**	***F*-value**	***p***
Temperature	1	0.13	1.23	0.27
Size/Chela	3	1.096	10.61	< 0.01
Temperature x Size/Chela	3	0.13	1.24	0.30
Error	92	0.10		
Corrected total	99			

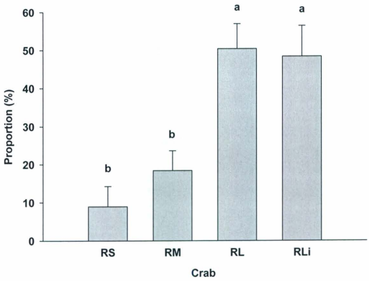

Figure 3.4. Mean proportion (+SE) of contests won by small (RS), medium (RM), and large (RL) intact rock crabs, and large rock crabs missing one chela (RLi). Data were pooled across Temperature (cold and warm) treatments. Bars not sharing the same letters are different (LS means, $p < 0.05$; n=22 [RS] and 26 [each other crab category]).

Table 3.8. Summary of one-way ANCOVA (applied to raw data) showing the effect of Temperature (cold and warm) and Carapace Width (the difference in carapace width between the rock and green crab in each trial, which is used as a covariate in the model) on the proportion of contests starting with the green crab holding the mussel that ended with the rock crab holding the mussel (see Hypothesis 4 in Materials and methods).

Source of variation	***df***	**MS**	***F*-value**	***p***
Temperature	1	0.020	0.25	0.63
Carapace Width	1	0.35	4.34	0.046
Temperature x Carapace Width	1	0.44	5.40	0.027
Error	29	0.081		
Corrected total	32			

Table 3.9. Summary of one-way ANCOVA (applied to raw data) showing the effect of Temperature (cold and warm) and Carapace Width (the difference in carapace width between the rock and green crab in each trial, which is used as a covariate in the model) on the proportion of contests starting with the rock crab holding the mussel that ended with the green crab holding the mussel (see Hypothesis 4 in Materials and methods).

Source of variation	***df***	**MS**	***F*-value**	***p***
Temperature	1	0.032	0.23	0.64
Carapace Width	1	0.37	2.69	0.14
Temperature x Carapace Width	1	0.52	3.71	0.086
Error	9	0.14		
Corrected total	12			

Table 3.10. Summary of two-way ANOVA (applied to square-root transformed data) showing the effect of Temperature (cold and warm) and Chela (both chelae present and one chela missing) on the proportion of contests starting with the green crab holding the mussel that ended with the large rock crab holding the mussel (see Hypothesis 4 in Materials and methods).

Source of variation	***df***	**MS**	***F*-value**	***p***
Temperature	1	0.11	1.20	0.29
Chela	1	0.59	6.35	0.021
Temperature x Chela	1	0.31	3.32	0.084
Error	19	0.093		
Corrected total	22			

Table 3.11. Summary of two-way ANOVA (applied to raw data) showing the effect of Temperature (cold and warm) and Size/Chela (small [RS], medium [RM], and large [RL] intact rock crabs, and large rock crabs missing one chela [RLi]) on the proportion of observations in which rock crabs were buried in sediments or located in the pot (see Hypothesis 5 in Materials and methods).

Source of variation	***df***	**MS**	***F*-value**	***p***
Temperature	1	0.12	1.18	0.28
Size/Chela	3	0.81	7.82	< 0.01
Temperature x Size/Chela	3	0.11	1.04	0.38
Error	119	0.10		
Corrected total	126			

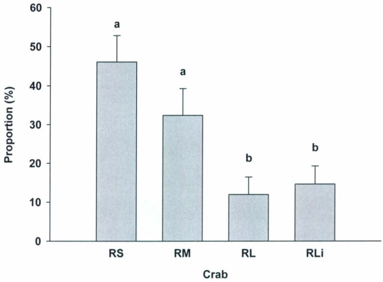

Figure 3.5. Mean proportion (+SE) of observations in which small (RS), medium (RM), and large (RL) intact rock crabs, and large rock crabs missing one chela (RLi), were buried in sediments or inside the pot. Data were pooled across Temperature (cold and warm) treatments. Bars not sharing the same letters are different (LS means, $p < 0.05$; n=31 [RS] and 32 [each other crab category]).

sediments or in the pot at least three times more frequently than large rock (RL) crabs (LS means, $p < 0.01$ and 0.013, respectively; Fig. 3.5). In all crab treatments, rock crabs were buried in sediments or located in the pot more often than green crabs (paired t-tests, $p < 0.029$ for all paired treatments), which rarely exhibited (<2% of all observations) such behaviors.

3.4 DISCUSSION

We used rock (*Cancer irroratus*) and recently introduced green (*Carcinus maenas*) crabs from Newfoundland and Labrador to determine experimentally how changes in water temperature (4°C versus 12°C), body size (small, medium, and large), and the loss of one chela affects the ability of one rock crab to compete with one large green crab for a single prey item, the blue mussel, *Mytilus edulis*. ANOVA results indicated temperature, body size, and chela loss had no effect on the ability of rock crabs to grasp the mussel before the green crab, which refutes our hypothesis that the ability of the rock crab to grasp the mussel before the green crab decreases with decreasing body size and chela loss (Hypothesis 1). In fact, green crabs grasped the mussel before rock crabs in >90% of all trials, hence providing a first indication of competitive dominance by green crabs. This finding suggests that green crabs have a greater ability to visually or chemically detect a mussel prey or are more inclined to forage in open habitats than rocks crabs (the mussel was always located in the centre of experimental tanks with no visual or physical obstruction). It also complements other studies showing that green crabs most often found a prey item first when interacting with Asian shore crabs (*Hemigrapsus sanguineus*) or blue crabs (*Callinectes sapidus*) of similar size or larger, sub-adult American lobsters (*Homarus americanus*) (Jensen et al., 2002; MacDonald et al., 2007; Williams et al., 2006).

In competitive foraging conditions, an individual that is first to contact a prey is likely to spend more time with it than its opponent(s) if it can defend the prey successfully (Archer, 1988; Williams et al., 2006). Large rock crabs in our experiment were on average 30 mm larger than green crabs. Interestingly, large rock crabs spent an equal proportion of time holding the mussel than green crabs in cold water, though not in warm water in which green crabs held the mussel at least 76% of the time regardless of rock crab size and chela loss. These results indicate that at low (~4°C) temperature large rock crabs can reverse the initial dominance that green crabs exhibit by grasping the mussel first, while suggesting that competitive abilities of green crabs recently introduced to Newfoundland and Labrador increase with increasing temperature (up to at least 12°C). Experiments with green crabs and American lobsters from other ecosystems of the northwest Atlantic where green crab invaded more than a decade ago showed that lobsters can reverse competitive dominance by green crabs when they become substantially larger in size and mass (Rossong et al., 2006; Williams et al., 2006; Williams et al., 2009), though the effect of temperature on this pattern was not examined.

In this study, large rock crabs spent at least 46% more time holding the mussel than small rock crabs and large rock crabs missing one chela in cold water only (there was no difference in warm water). However, increasing temperature increased and decreased mussel holding times in small and large rock crabs, respectively. Interestingly, in warm water, ~50% of the small rock crabs that took possession of the mussel moved the mussel to inside the pot, whereas green crabs never attempted to enter the pot to take the mussel from those rock crabs. These two behaviors suggest that small rock crabs can take advantage of habitat complexity to create spatial refuges that reduce confrontations with potential competitors. Overall, these results partly refute our hypothesis that the proportion of time the rock crab holds the mussel decreases with decreasing body size and chela loss (Hypothesis 2), while highlighting the importance of considering water temperature in studies of crab foraging. In metazoans, metabolism and the need to ingest food generally increase with temperature, which, along with the presence of predators, ultimately affect foraging strategies (Gooding et al., 2009; Lima and Dill, 1990; Murray et al., 2007; Sih, 1980; Wallace, 1973; Chapter II). We suggest that greater energetic demands in warm water pushed small rock crabs to forage despite greater risks associated with the presence of large green crabs, which may have been perceived by rock crabs as a potential predator more than a competitor. Also, crabs of different size may respond differently to the thermal environment and could explain why large rock crabs (which used the pot only in 10% of all trials involving them) held the mussel less frequently in cold than warm water. Alternatively, low temperature could limit the ability of green crabs recently introduced to cold water ecosystems of Newfoundland and Labrador to compete for resources, which may explain why large rock crabs held the mussel as frequently as the green crab in cold water, but less frequently in warm water. Further research is needed to elucidate the exact nature of relationships between rock crab size and water temperature as it affects competitive interactions with green crabs (and other crustacean species) when food resources are both limiting (this study) and non-limiting.

Water temperature, rock crab size, and chela loss did not affect the number of contests between rock and green crabs, which refutes the first part of our hypothesis that the number of contests and associated degree of physical interactions (very weak, weak, moderate, and strong) between rock and green crabs decrease with decreasing body size and chela loss (Hypothesis 3). This finding contradicts other studies of competition for food that showed greater numbers of contests between rock and green crabs in warm (20°C) than cold (5°C) water (Bélair and Miron, 2009a), and an increase in the number of contests between green crabs with increasingly large size differences at relatively high (18 to 21°C) temperature (Smallegange et al., 2007). Such discrepancies may be due to acclimation of crabs to different temperature regimes in their natural habitats and use of a higher prey density (4 and 30 mussels) in trials (Bélair and Miron, 2009a), or use of higher (at least 6°C) temperature and a coarser classification of physical interactions (Smallegange et al., 2007) than in this study, which ultimately affected classification and interpretation of crab behaviors. Theoretical models suggest that individuals decide to pursue a contest, engage in escalating physical interactions, or retreat based on their perception of competitive abilities of their opponent (Enquist and Leimar, 1987; Maynard Smith, 1982). In crustaceans, body size is considered to be a reliable indicator of fighting abilities, with greater physical strength, experience, and potential to cause injury in large than small individuals (Archer, 1988). Such contention was supported by our finding that large rock crabs engaged with green crabs in a smaller proportion of contests with very weak physical interactions and a larger proportion of contests with strong physical interactions than small rock crabs. However, the second part of our Hypothesis 3 was weakly supported by our data showing only a higher frequency of very weak physical interactions in rock crabs with two chelae than those missing one chela (frequencies of weak, moderate, and strong interactions were not affected by chela loss).

Physical interactions sometimes are more frequent in large than small crabs (Glass and Huntingford, 1988; Smallegange et al., 2006), though the strongest physical interactions during intraspecific contests may occur between crabs of similar size (Archer, 1988; Maynard Smith, 1982). Moreover, levels of intrinsic aggression may well vary between crab species (Hazlett, 1971). For example, green crabs often initiate contests with competitors by establishing physical contact (i.e. use of chelae to strike or grasp) rather than by displaying signals (e.g. meral spread) to warn competitors (Sneddon et al., 1997a; Williams et al., 2006; this study). In this study, moderate and strong physical interactions were frequent (at least 40% of all interactions altogether) between large green and rock crabs whether the latter had one or two chelae. Presumably, large rock crabs perceived their own size (rock crabs were larger than green crabs) as an advantage that offset the loss of one chela. To our knowledge this is the first study to examine the effect of chela loss on the frequency and degree of physical interactions between rock and green crabs competing for food. Further research is required to understand how physical interactions may influence spatial and temporal changes in the structure of natural crab populations.

Crabs may decide whether to initiate a contest with another crab based on their perceived likelihood of winning the contest. Typically, in crustaceans, the largest of two or more competing individuals wins the contest (Glass and Huntingford, 1988; Pavey and Fielder, 1996; Richards and Cobb, 1986; Thorpe et al., 1994). We found that large rock crabs initiated more contests than small rock crabs in warm water only (no difference in cold water), while large rock crabs won more contests than small rock crabs, regardless of water temperature. These results support the first part of our hypothesis that the likelihood that the rock crab initiates and wins contests with the green crab decreases with decreasing body size and chela loss (Hypothesis 4). Interestingly, small rock crabs initiated 18 and 51% of the contests in warm and cold water, respectively, while winning only 9% of all contests (temperature treatments pooled). Conceivably, such a high inclination by small rock crabs to initiate contests with a much larger opponent resulted from their incapacity to assess the fighting ability of another crab species based uniquely on visual or chemical stimuli (the latter may be harder to interpret in cold than warm water), as seen in the swimming crab, *Liocarcinus depurator* (Glass and Huntingford, 1988). We noted that small rock crabs often approached green crab only to retreat immediately following the display of chelae or physical attack by the green crab. Medium-sized rock crabs (which were equally as large as large green crabs) won only 18% of their contests with large green crabs, while large rock crabs won no more than an equal number of contests than large green crabs. This finding, coupled with others outlined above, indicates that large green crabs still exert competitive dominance even when smaller than rock crabs.

In addition to differences in body size, relative chela length and other morphological asymmetries between individuals can influence the outcome of intraspecific contests in green crabs (Sneddon et al., 1997b; Sneddon and Swaddle, 1999).

Chelae of comparable size in rock and green crabs can produce similar crushing forces (Block and Rebach, 1998; Elner, 1978; Warner et al., 1982). Chelae of large rock and green crabs used in this study were very similar in size, which helps explain why these crabs won an equal proportion of contests, despite uneven body size. The loss of one chela can decrease prey capture and feeding frequencies in rock crabs (Chapter II) and reduce the ability of male green crabs to compete for or defend mates (Abello et al., 1994). Yet, in our experiment, chela loss did not affect the likelihood that the rock crab would initiate or win contests with the green crab, which does not support the second part of Hypothesis 4. Overall, our results indicated that body size in rock crabs exerts a marked influence on their ability to win contests with green crab, while suggesting that green crabs may show increased aggression in warm than cold water through the initiation of more contests.

The ability of rock crab to win a contest by taking the mussel from the green crab increased with increases in rock crab size in cold water only. However, both rock and green crabs were relatively unsuccessful in taking the mussel away from the other crab, which occurred in only 11 and 17% of all attempts, respectively. This result supports the idea that the crab in possession of a resource (in this study the crab that holds the mussel) likely knows more about its value than the intruder (in this study the crab that tries to take the mussel from the other crab). The intruder may not be as motivated to attempt to steal the resource as if it had spent some time with it to better judge its value (Enquist and Leimar, 1987). Rock and green crabs both exhibited defensive behaviors and vigilance while holding the mussel. For example, large individuals in each species often temporarily discarded the mussel to initiate physical contact with the other crab, presumably to protect the mussel when the other crab came too close. Small rock crabs frequently withdrew from the centre of the tank with the mussel before the green crab could initiate any physical contact. Interestingly, the ability of large rock crab to take the mussel from green crab decreased fivefold following chela loss. This finding suggests that chela loss substantially decreases the likelihood that rock crabs win a contest when food resources are scarce, presumably in part because the intensity of a contest can be higher in the presence than absence of food as seen in intraspecific contests among green crabs (Sneddon et al., 1997a). Contests between crustaceans for especially valuable resources such as mates and burrows can lead to injuries or fatalities (Dingle, 1983; Jones, 1980). None of the rock and green crabs used in this study inflicted apparent injuries to any of their opponents. Overall, rock and green crabs were able to successfully defend the mussel from stealing attempts by the other crab, which further supports our contention that both crab species are at an advantage when they grasp the mussel first.

Animals exposed to predation and competition may increase shelter use (Lima and Dill, 1990; Richards, 1992; Spanier et al., 1998). In crustaceans vulnerability to predation generally increases with decreasing body size (Stein, 1977), which can lead to size-dependant behavioral shifts, including shelter use (Wahle, 1992; Chapter II). Our results were consistent with this as small rock crabs spent more time burying in sediments or in the pot (used to mimic a cavity) than large rock crabs, regardless of water temperature, and hence support the first part of our hypothesis that the proportion of time the rock crab is buried in sediments or inside the pot increases with decreasing body size and chela loss (Hypothesis 5). Small rock crabs most likely behaved this way to minimize possible encounters with the green crab. However, the amount of time that rock crabs spent burying in sediments or in the pot did not change with the loss of one chela, which does not support the second part of Hypothesis 5. A laboratory experiment by McDonald et al. (2001) showed that juvenile green crabs were able to displace juvenile Dungeness crabs from their shelters. In our experiment we observed very few interactions between rock and green crabs for the pot. In fact, large green crabs never displaced small rock crabs from inside the pot and only used it on very rare occasions, as seen in green crabs foraging singly in non-competitive conditions (Rossong et al., 2006; Chapter II). Juvenile rock and green crabs inhabit spaces between rocks and under seaweeds and move inside shelters when disturbed (Breen and Metaxas, 2009; McVean and Findlay, 1979; K. Matheson personal observations). We did not examine competition in small green crabs in this study, but small rock and green crabs likely compete for shelters in natural habitats as well.

In summary, we showed that: 1) green crabs primarily grasped the mussel before rock crabs regardless of temperature and body size and chela loss in rock crabs, 2) large rock crabs spent more time holding the mussel than small rock crabs and rock crabs missing one chela in cold water only, 3) the number of contests between rock and green crabs was not affected by temperature and body size and chela loss in rock crabs though the frequency of strong physical interactions was higher in contests with large than small rock crabs, 4) large rock crabs initiated contests with green crabs more frequently than smaller conspecifics in warm water only while winning more contests than small rock crabs regardless of temperature, and 5) small rock crabs spent more time burying in sediments or in the pot than large rock crabs whereas chela loss had no perceptible effect on the frequency of those two behaviors regardless of temperature. In a companion study we showed that increasing temperature from 4 to 12°C significantly increased mussel (*M. edulis*) capture while altering patterns of mussel size selection and foraging behaviors in rock and recently introduced green crabs from Newfoundland and Labrador foraging on mussel aggregates under non-competitive conditions (Chapter II). This study further demonstrates that a similar increase in temperature alters the behavioral repertoire of rock crabs of different sizes while improving the ability of green crabs to compete with rock crabs of a larger size for a limited food source. We used a single mussel prey in all trials to determine more accurately the relative ability of rock crabs of different body size and prey handling capacity (one versus two chelae) to compete with some of the largest green crabs in Newfoundland and Labrador than would have been possible had we used more than one prey item. Prey diversity and abundance may not be as limiting and rock crabs may also compete with smaller green crabs in natural habitats. We therefore recommend future research on competitive interactions between rock and green crabs across a broader spectrum of prey availability and competitor abundance. Our findings suggest that the recent introduction of green crab to Newfoundland and Labrador may negatively affect foraging in rock crabs of similar or larger size than the largest green crabs and that this pattern may be exacerbated in competitive interactions with smaller rock crabs and those missing one chela, especially in warm water.

CHAPTER IV

SUMMARY

4.1 Overall objective of the study

In the past few decades coastal marine ecosystems worldwide have been increasingly impacted by biological invasions. When introduced to new habitats, non-indigenous species may experience different physicochemical conditions and biological interactions than in their native range. The capacity of an introduced species to adapt to new conditions and interactions determine its ability to invade the habitat. For many marine predatory metazoans, predation success (the number of prey captured per unit time) is largely dictated by the diversity and abundance of competitors and prey. Dietary overlaps between indigenous and non-indigenous predators can increase the frequency and magnitude of competitive interactions, which ultimately affects foraging strategies. Therefore, studying how environmental variability affects predation success in non-indigenous, predatory species is a key step towards understanding and predicting their ecological and socioeconomic consequences. The overall objective of this research was to determine experimentally how water temperature (cold [4ºC] versus warm [12ºC]) affects predation success in indigenous rock (*Cancer irroratus*) and recently introduced green (*Carcinus maenas*) crabs from Newfoundland and Labrador (currently the northern distribution limit of green crab) under non-competitive and competitive conditions. Prey (the blue mussel, *Mytilus edulis*) capture and size selection as well as associated foraging behaviors (feeding, handling, sitting, moving, and burying in sediments or inside a pot mimicking shelter) were measured in both crab species. Additional factors (crab size, prey size, chela loss, and chemical cues from conspecifics and heterospecifics) were included to gain further insights about how this introduction may alter the structure of shallow benthic ecosystems in this region.

4.2 Predation under non-competitive conditions

Chapter II used two laboratory experiments to determine effects of changes in water temperature, body size, chela loss, and chemical cues on capture and size selection of blue mussels and associated foraging behaviors in rock and green crabs held individually (in the absence of competition) in microcosm tanks. We showed that 1) mussel capture in rock and green crabs was higher in large than small individuals, 2) large crabs in each species selected larger mussels than small crabs, 3) chela loss decreased mussel capture uniquely in rock crabs while causing only subtle changes in mussel size selection in both species, and 4) chemical cues from other crabs did not affect mussel capture in rock crabs, but they altered mussel size selection and the frequency of foraging behaviors in small rock crabs only. Increasing temperature from 4 to 12°C generally exacerbated these patterns by markedly increasing mussel capture in both species. Specifically, numbers of mussels captured in each size category were similar in rock and green crabs. Yet, small green crabs showed marked preference for small (<20 mm) mussels, while small rock crabs captured medium (25-30 mm) mussels most frequently. Frequencies of the five behaviors we monitored differed between crab species. Most notably, small rock crabs buried in sediments or were in the pot fivefold more than small green crabs. Prey capture also decreased twofold with chela loss in rock crabs only, indicating that the loss of the small chela in green crabs had no perceptible effect on prey capture. However, in cold water only mussel handling increased by 30% in green crabs missing one chela. In the presence of chemical cues from large, dead rock crabs handling decreased fourfold while frequencies of burying in sediments or use of the pot increased twofold in small rock crabs, regardless of water temperature, which suggests that small rock crabs systematically perceived this cue as a potential threat.

4.3 Predation under competitive conditions

Chapter III determined experimentally how changes in water temperature, body size, and the loss of one chela affects the ability of rock crab to compete with large green crab for blue mussel prey. We showed that: 1) green crabs primarily grasped the mussel before rock crabs regardless of temperature and body size and chela loss in rock crabs, 2) large rock crabs spent more time holding the mussel than small rock crabs and rock crabs missing one chela in cold water only, 3) the number of contests between rock and green crabs was not affected by temperature and body size and chela loss in rock crabs though the frequency of strong physical interactions was higher in contests with large than small rock crabs, 4) large rock crabs initiated contests with green crabs more frequently than smaller conspecifics in warm water only while winning more contests than small rock crabs regardless of temperature, and 5) small rock crabs spent more time burying in sediments or in the pot than large rock crabs, whereas chela loss had no perceptible effect on the frequency of those two behaviors regardless of temperature. Interestingly, the time spent with the mussel increased twelve times in small rock crabs, but decreased threefold in large rock crabs in cold versus warm water suggesting that crabs of different size respond differently to changes in temperature. Moreover, in cold water only, large rock crabs held the mussel as frequently as the green crab and small and medium rock crabs initiated a similar number of contests as the green crab. These findings indicate that low temperature may limit the ability of green crabs recently introduced to the cold water ecosystems of Newfoundland and Labrador to compete with native crustaceans for food resources. Lastly, both rock and green crabs showed limited success in stealing the mussel from the other crab suggesting that crabs that grasp the mussel first have an advantage.

4.4 Importance of study

This is the first study to examine predation success and associated foraging behaviors in rock and green crabs from Newfoundland and Labrador at different temperatures and in the presence and absence of competition. Results increase our knowledge of marine predator-predator-prey interactions while underscoring the importance of considering the thermal environment in studies of predation and competition in decapod crustaceans. Chapter II showed that in the absence of competition, prey capture in both rock and green crabs increase markedly in warm compared to cold water. Similar predation rates in rock and green crabs in both cold and warm water indicate that changes in temperature affected predation success in both species equally. Similar prey size selection in rock and green crabs indicated that interspecific competition likely exists in natural habitats. This suggestion was confirmed in Chapter III, where rock crabs were rarely first (<10% of the time) to grasp the mussel in the presence of a green crab. However, large rock crabs were able to hold the mussel for as long as the green crabs, though only in cold water (green crabs held the mussel more frequently than rock crabs in warm water). These patterns suggest that predominantly cold water environments of Newfoundland and Labrador reduce the ability of green crab to compete with rock crab. Nevertheless, the recent introduction of green crab to this region may negatively impact foraging in rock crabs, whether the latter are equal or larger in size than the largest green crabs. This pattern may be exacerbated in competitive interactions with smaller rock crabs and those missing one chela, especially in warm water. The marked preference by small green crabs for small mussels suggests that green crabs may alter mussel populations in Newfoundland and Labrador, which could affect interactions with other species that rely on mussels as a food source.

4.5 Future directions

This study provides a framework for further studies of interactions between rock (and other invertebrates) and green crabs from Newfoundland and Labrador. It is based on laboratory microcosm experiments controlling effects of temperature and light while eliminating variation in other environmental variables such as wave and current energy. Although these controlled experiments allowed comparisons of predation and competitive abilities between individual rock and green crabs, *in situ* observations and experiments are required to determine the real impact of the introduction of green crab on populations of indigenous species. Results presented in this thesis support the idea that foraging in small rock crabs and those missing one chela is most likely to be impacted by this introduction, which may lead to the reported decreases in rock crab abundance in Newfoundland after green crab introduction. It was shown that low water temperatures representative of Newfoundland and Labrador decrease the ability of green crab to compete with rock crab for a common, limited food source. Research is required to further increase our understanding of how thermal and hydrodynamic environments affect predation in green crabs exposed to a higher diversity and abundance of competitors and prey species (this study examined one-on-one interactions for a unique and limited prey source). Without such knowledge, our capacity to predict and mitigate changes in the distribution and abundance of indigenous species that are directly or indirectly impacted by the presence of green crab will remain limited.

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Appendix A

Table A.1. Mean values (and associated standard deviations in parentheses) of morphological characteristics of rock crabs (small [RS], medium [RM], and large [RL] individuals with two chelae, and large individuals with one chela missing [RLi]) and green crabs (small [GS] and large [GL] individuals with two chelae, and large individuals with one chela missing [GLi]) used in Experiments 1 and 2 (Chapter II).

Crab	n	Carapace width (mm)	Mass (g)	1st Chela (mm)[a]	2nd Chela (mm)[a]
RS	66	48.5 (5.8)	20.5 (7.1)	9.6 (1.4)	9.6 (1.4)
RM	17	67.9 (5.2)	50.5 (11.9)	13.8 (1.5)	13.7 (1.4)
RL	65	93.9 (6.0)	151.2 (30.2)	21.3 (2.2)	21.4 (2.2)
RLi	66	96.7 (7.0)	148.3 (31.5)	22.7 (2.0)	na
GS	17	40.2 (4.2)	16.8 (5.4)	9.4 (1.6)	7.7 (1.3)
GL	17	60.5 (4.5)	81.4 (15.9)	21.0 (2.0)	16.0 (1.6)
GLi	16	65.3 (3.2)	79.8 (13.6)	22.5 (2.1)	na

[a] Distance across the midpoint of the propodus

Appendix B

Table B.1. Summary of two-way ANOVA (applied to raw data) showing the effect of Marking (with [M+] and without [M-] liquid whitener) and Species (rock [R] and green [G] crabs) on the proportion of mussels captured (out of 10 individuals) in 1-h trials (n=6 [M+R], 6 [M-R], 5 [M+G], and 5 [M-G]).

Source of variation	*df*	MS	*F*-value	*p*
Marking	1	0.010	0.19	0.67
Species	1	0.051	0.92	0.35
Marking x Species	1	0.032	0.58	0.46
Error	18	0.055		
Corrected total	21			

Appendix C

Table C.1. Summary of three-way ANOVA (applied to square-root transformed data) showing the effect of the number of Mussels (5 and 10 mussels in each of six size classes), Species (rock [R] and green [G] crabs), and Size (small [S] and large [L] crabs) on the proportion of mussels captured (n=8 [5RS], 8 [10RS], 8 [5RL], 8 [10RL], 9 [5GS], 8 [10GS], 9 [5GL], 8 [10GL]).

Source of variation	*df*	MS	*F*-value	*p*
Mussels	1	0.40	0.41	0.52
Species	1	0.60	0.62	0.43
Size	1	21.60	22.33	<0.01
Mussels x Species	1	0.85	0.88	0.35
Mussels x Size	1	0.75	0.77	0.38
Species x Size	1	0.17	0.18	0.68
Mussels x Species x Size	1	3.68	3.81	0.056
Error	58	0.97		
Corrected Total	65			

Appendix D

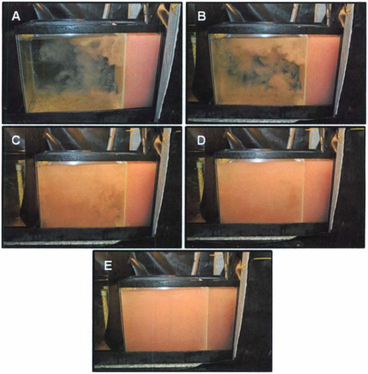

Figure D.1. Diffusion of a solution of red food dye at (A) 1, (B) 2, (C) 3, (D) 5, and E) 15 minutes following the addition of the solution to the right side of the vertical divider used to separate crabs releasing chemical cues from those foraging on mussels in Experiment 2 (Chapter II). In the experiment, mussels and foraging crabs were introduced to the left side of the vertical divider, whereas crabs releasing chemical cues were introduced to the right side, which received inflowing seawater that diffused throughout the rest of the tank before exiting the tank through a hole in the upper portion of the left tank panel.