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

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**A R T I C L E   I N F O**

Article history:
Received 21 January 2012
Received in revised form 5 June 2012
Accepted 6 June 2012
Available online xxxx

Keywords:
Behavior
Competition and predation
Green crab and rock crab
Invasive species
Mussels
Temperature

**A B S T R A C T**

The green crab, *Carcinus maenas*, is one of the most successful marine invasive species worldwide. The recent (2007) discovery and rapid explosion of populations of green crab in predominantly cold water ecosystems of Newfoundland and Labrador (NL) provided an opportunity to investigate interactions with a potential, indigenous competitor, the rock crab, *Cancer irroratus*, under presumably adverse thermal conditions for green crab. We used a laboratory microcosm experiment with rock crab and green crab from NL to determine how changes in temperature (4 °C and 12 °C), body size (small, medium, and large), and the loss of one chela affect the ability of one rock crab to compete with one large, intact green crab for one blue mussel, *Mytilus edulis*. Green crab was first to grasp the mussel in >90% of trials, regardless of temperature. In cold water, large, intact rock crab held the mussel as frequently as green crab and 25- and 12-fold more frequently than small, intact rock crab and large rock crab missing one chela, respectively. Changes in temperature and relative body size did not affect the number of contests between species, although strong physical interactions occurred ~20% more often in contests with large than small rock crab. Large, intact rock crab initiated contests with green crab more frequently than smaller conspecifics in warm water only, while winning 5-fold more contests than small rock crab, regardless of temperature. The ability of large rock crab to win contests was not affected by chela loss. Small and medium rock crab spent at least threefold more time buried in sediments or inside a shelter than large crab, regardless of chela loss. This study suggests that the recent introduction of green crab to NL reduces foraging in rock crab, especially in competitive interactions between green crab and smaller rock crab, and that this effect is exacerbated during warmer times of year.

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1. Introduction

The European green crab, *Carcinus maenas* L., is one of the most successful marine invasive species worldwide (Audet et al., 2003; Cohen et al., 1995; Lowe et al., 2000). Green crab exhibits a broad tolerance to variation in environmental conditions, especially temperature and salinity (Beukema, 1991; Eriksson and Edlund, 1977), as well as a generalist diet that includes bivalves, gastropods, polychaetes, crustaceans, and seaweeds (Cohen et al., 1995; Elner, 1981; Ropes, 1968). These characteristics and the relatively high agility and aggressiveness of green crab 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 experiments measuring competition for food between green crab and Dungeness, *Cancer magister*, or blue, *Callinectes sapidus*, crabs showed that green crab was more frequently first to contact bivalve prey, while spending more time feeding upon them, than their opponents (MacDonald et al., 2007; McDonald et al., 2001). Likewise, Rossong et al. (2011) found that the presence of an adult green crab can reduce feeding and increase the time spent in a shelter in juvenile American lobster, *Homarus americanus*. These studies helped clarify the ability of green crab to compete with other crustaceans. However, prey capture and frequencies of associated foraging behaviors in green crab have been shown to generally decrease with decreasing water temperature (Bélair and Miron, 2009a; Matheson and Gagnon, 2012; Wallace, 1973), which suggests that the ability of this species to compete for food may decrease as it reaches its northern, colder distribution limit.

The recent (2007) discovery and rapid explosion of populations of green crab in predominantly cold marine habitats of Newfoundland and Labrador (NL, eastern Canada) raises concerns about its impact on populations of indigenous species and associated fisheries. Green crab abundance in some areas of Placentia Bay (southern Newfoundland) is 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* Say, is a dominant,
indigenous, crustacean predator in subtidal ecosystems in eastern Canada (Caddy and Chandler, 1976; Drummond-Davis et al., 1982; Squires, 1990). In this region, rock crab and green crab coexist in shallow (<10 m depth) sandy and rocky habitats (DOF, 2011; Drummond-Davis et al., 1982; Grosholz and Ruiz, 1995; Matheson and Gagnon, 2012), while exhibiting substantial dietary overlap (Cohen et al., 1995; Elner, 1981; Miron et al., 2005; Ropes, 1968).

Understanding of competitive interactions between rock crab and green crab in natural habitats in NL is limited to anecdotal evidence. However, laboratory microcosm experiments with individuals from southern Newfoundland held separately showed both species can capture similar numbers of blue mussel, Mytilus edulis L., of comparable sizes in both cold (4 °C) and warm (12 °C) water (Matheson and Gagnon, 2012). These experiments also demonstrated that mussel capture in rock crab was unaffected by exposure to chemical cues from conspecifics of green crab (Matheson and Gagnon, 2012). Such patterns suggest that interspecific competition for food and shelter exist, regardless of water temperature. This idea is reinforced by extensive field surveys showing a gradual replacement, over the last few years, of rock crab by green crab in shallow (<5 m depth) habitats in southern Newfoundland (DOF, 2011). Microcosm experiments with rock crab and green crab from Prince Edward Island held in sympathy and offered smaller numbers (up to 30) of blue mussels showed that competition can affect foraging, including prey capture, in rock crab (Bélair and Miron, 2009a,b). Yet, competition between rock crab and green crab for even more limited prey resources remains largely unexplored, especially at low water temperatures characteristic of subarctic and temperate marine habitats in NL.

In crustaceans, the frequency of contests can increase when food, shelter, and mates are limited (Jachowski, 1974; Sneddon et al., 1997a; Williams et al., 2006). Conflicts between two competing crabs can be resolved through behaviors that range from escape of one crab in response to aggressive displays of chela (i.e. meral spread) by the other crab, to escalating contests between the two crabs that involve the use of chela to strike or grasp the opponent and which can cause injury or death. In general, large individuals are better than smaller ones at stealing or monopolizing a resource (Smith et al., 1994; Thorpe et al., 1994). Accordingly, morphological asymmetries such as chela size are often used to predict the outcome of contests (Sneddon and Swaddle, 1999; Sneddon et al., 1997b). Crabs can intentionally sever (autotomize) chela or other limbs in response to threatening conditions, despite potentially adverse effects on prey capture (Abello et al., 1994; Smith et al., 1994). The likelihood of losing a chela generally increases with body size (Abello et al., 1994), possibly as a result of more intense physical interactions between large individuals. Matheson and Gagnon (2012) show that mussel capture in rock crab held individually was 50% lower in individuals that missed one chela, compared to individuals with both chela. Testing how the presence of green crab affects the ability of rock crab with one or two chela to capture prey when prey are extremely limited would help further characterize competitive abilities in rock crab and how its populations may respond to biological invasions. In this study, we use a laboratory microcosm experiment with rock crab and green crab from southern Newfoundland to test five hypotheses about effects of body size and chela loss on the ability of one rock crab to compete with one large green crab for a single prey item, the blue mussel, M. edulis. We test each hypothesis in cold (4 °C) and warm (12 °C) water to determine how temperatures representative of NL affect foraging behaviors.

2. Materials and methods

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 crab and green crab from 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 Matheson and Gagnon (2012). Essentially, hard-shelled, male rock crab and green crab with no red/orange coloration 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 in May, June, and September 2009, as well as in June 2010. Crabs were transported to the Ocean Sciences Centre where they were maintained in large holding tanks (up to 20 crabs of the same species in each tank) supplied with flow-through seawater pumped directly in from a depth of ~5 m in the adjacent embayment, Logy Bay. Rock crab 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 crab were selected. All crabs were fed twice a week with live blue mussels, M. edulis, free of epibionts until the start of the acclimation period (see below). Mussels were collected by hand from the intertidal zone at Bellevue (northwestern side of the Avalon Peninsula).

The experiment was conducted in glass tanks (62 L x 31 W x 43 H cm) supplied with ~1 L min⁻¹ of flow-through seawater. To mimic crab habitat, the bottom of each tank was covered with a 3-cm thick layer of sediments and 10 to 15 small (<10 cm in diameter) rocks scattered haphazardly throughout. The bottom of a dome-shaped shelter (plastic pot of 15 cm in diameter cut along the length) was placed against one of the two longest sides of the tank with the opening facing the tank center. Each tank was exposed to continuous cycles of 12 h of low light intensity (90–100 lx) followed by 12 h of darkness and was surrounded by an opaque canvas to avoid visual external stimuli. Acclimation of crabs consisted of exposing each individual for 72 h (as per Bélair and Miron, 2009a; Matheson and Gagnon, 2012; Rossong et al., 2006) 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 (see below). Crabs were not fed during acclimation to standardize hunger levels.

2.2. Hypotheses and experimental approach

In this study, we define a contest as any interaction between rock crab and green crab (whether one or no crab is holding the mussel) ranging from simple display of chela (i.e. meral spread) with no physical contact between crabs, to the use of chela to strike or grasp each other. Accordingly, a crab wins a contest if it takes the mussel away from the other crab or if the other crab chooses to retreat in 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, M. edulis. The experiment was designed to test the following five hypotheses (hereafter referred to as H1 to H5) based on current knowledge of interactions between rock crab, green crab, and the abiotic environment (see Introduction):

H1. The ability of rock crab to grasp the mussel before green crab decreases with decreasing body size and chela loss.
H2. The proportion of time rock crab holds the mussel decreases with decreasing body size and chela loss.
H3. The number of contests and associated degree of physical interactions between rock crab and green crab decrease with decreasing body size and chela loss.
H4. The likelihood that rock crab initiates and wins contests with green crab decreases with decreasing body size and chela loss.
H5. The proportion of time rock crab is buried in sediments or inside a shelter increases with decreasing body size and chela loss.
The average size of rock crab missing one chela (RL, 90.71 ± 4.51 mm) was comparable to that of large rock crab 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 Matheson and Gagnon, 2012 for a description of the procedure used to induce chela loss). Crabs with one chela missing were maintained in holding tanks for seven days prior to the 72-h acclimation (see above) and discarded if feeding and displacement decreased compared to those with two chelae.

The experiment was conducted at two temperatures approximating spring (and fall) and summer averages in shallow inshore habitats in southern Newfoundland: 4 °C (cold) and 12 °C (warm) (Methven and Platt, 1991). Treatments were randomly assigned to tanks. One replicate of each treatment was conducted each day we performed trials in July 2009 (with crabs collected in May and June 2009), when water in the tanks was 12 °C, and in November 2009 (with crabs collected in September 2009), when water in the tanks was 4 °C. Therefore, all crabs spent at least one week, but no more than two months, in the holding tanks prior to being used for trials. We chose this approach over running trials simultaneously at 4 °C and 12 °C to minimize changes between temperatures at which crabs were accustomed to in their natural habitats and those during trials. While in using this approach temperature treatments were confounded by time, it is arguably a better representation of likely seasonal variation in crab behavior given that crabs can be physiologically and behaviorally conditioned to seasonal patterns of water temperature despite extended periods of acclimation to new thermal conditions (Cuculescu et al., 1998; Hopkin et al., 2006; Matheson and Gagnon, 2012). Moreover, as shown by Matheson and Gagnon (2012), freshly collected rock crab and rock crab that had been maintained in the holding tanks for ~3 months exhibited similar mussel capture rates. Therefore, we assumed that varying the amount of time during which crabs were held in the tanks had no perceptible effect on the observed behaviors. Each crab was used only once. Each treatment was replicated seven or eight times in the July and November 2009 trials. To increase sample size we replicated each treatment an additional seven or eight times in early June and July 2010, when water was again at 4 °C and 12 °C, respectively. Therefore, each treatment was replicated 15 or 16 times in total.

In each trial, crabs were offered one blue mussel free of epibionts and 25–30 mm in shell length. We chose this size because rock crab and green crab exhibited common preference for it under non-competitive foraging conditions (Matheson and Gagnon, 2012). The mussel was placed in the center of the tank with no artificial attachment to the substratum and no visual or physical obstruction to allow crabs to interact with it freely, as they normally do in nature. After acclimation (see above), one rock crab and one green crab were moved to opposite ends (determined randomly) of one experimental tank and physically isolated from one another and from the mussel by two perforated, opaque plastic dividers (see details in Matheson and Gagnon, 2012). Both dividers were removed from the tank after 15 min, which marked the start of the trial. All trials lasted 45 min.

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 chela or legs [recorded every minute], 3) initiated and won each contest, and 4) was buried in sediments or inside the shelter [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 chela in meral spread and the other crab responded by retreating without physical contact, 2) “Weak”: only one crab used its chela or legs to push the other one 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 strongest interaction to characterize those contests that involved multiple interactions. We also recorded limb loss and mortality. 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.

### 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 crab, and large rock crab missing one chela [RLi]) to examine effects of temperature, crab size, and chela loss on the proportion of trials in which rock crab grasped the mussel before green crab (H1). We treated this analysis as a particular case of the generalized linear models (Bolker et al., 2008; 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 showed 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 crab held the mussel relative to the total number of observations in which any of the two crabs held the mussel (H2). 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 crab and green crab 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 crab and green crab in each trial (first part of H3). 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 (Scheiner 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, and strong) between crabs (second part of H3). Data were square-root transformed to correct for heteroscedasticity. However, not all residuals in each category of physical interactions 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 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 crab (H4). 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 crab and green crab 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 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 crab was buried in sediments or in the shelter (H5). We considered crab burial and displacement to inside the shelter as analogous behaviors (see Discussion), and hence we summed observations of crabs buried in sediments and inside the shelter 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 shelter differed between rock crab and green crab in each rock crab treatment.

The factor year (2009 and 2010) was initially included in all the analyses described above to determine whether results from experiments conducted in 2009 differed from those in 2010. Results did not differ, and hence data were pooled. In all analyses, normality was verified using Shapiro–Wilks’s statistic and homogeneity of variance by using Levene tests and examining the graphical distribution of the residuals. To detect differences among levels within a factor we used least-square means multiple comparison tests (ANOVAs) and multivariate contrasts with Bonferroni 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 (Scheiner 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. Results

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 large, intact green crab (two-way ANOVA [generalized linear model, see Statistical analysis]: Factor = temperature, χ² < 0.01, p = 1.00; Factor = size/chela, χ² = 7.46, p = 0.059; Factor = temperature x size/chela, χ² = 6.63, p = 0.085). In fact, green crab was consistently more successful than rock crab 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 1). For example, small rock (RS) crab spent a smaller proportion of time holding the mussel in cold (2%) than warm (24%) water, whereas large rock (RL) crab spent a greater proportion of time holding the mussel in cold (50%) than warm (17%) water (LS means, p = 0.049 and 0.016, respectively; Fig. 1). Large intact rock crab held the mussel 12-fold more frequently than large rock crab missing one chela in cold water (LS means, p < 0.01), though there was no difference in warm water (Fig. 1). Green crab held the mussel more often (between 76 and 98% of the time) than rock crab in all combinations of temperature and crab treatments (paired t-tests, p < 0.036), except in cold water where medium and large rock crab held the mussel as frequently as green crab (p = 0.068 and 0.98, respectively).

3.2. Frequency and intensity of contests between rock and green crabs

The number of contests (between 0 and 17 [mean = 3.9 ± 3.8] per trial) was unaffected by temperature and size/chela treatments and their interaction (two-way ANOVA: Factor = temperature, F₁,₁₁₀ = 3.74, p = 0.056; Factor = size/chela, F₂,₁₁₀ = 0.82, p = 0.49; Factor = temperature x size/chela, F₁,₁₁₀ = 1.78, p = 0.15) (Fig. 2). The MANOVA showed the intensity of physical interactions varied separately with temperature and crab treatments (Table 2). There was nearly a twofold increase in the proportion of contests with very weak physical interactions in warm compared to cold water (two-way ANOVA: Factor = temperature, F₁,₁₁₀ = 13.79, p < 0.01, Fig. 2). Contests with weak physical interactions occurred twice as frequently in cold than warm water (two-way ANOVA: Factor = temperature, F₁,₁₁₀ = 6.40, p = 0.013), whereas the frequency of moderate and strong physical interactions did not differ with temperature (Fig. 2). The proportions of contests with moderate and strong physical interactions were respectively 14 and 19% higher in large (RL) than small (RS) rock crab (LS means, p < 0.01 for both comparisons, Fig. 2). Each degree of physical interaction occurred as often in large rock crab with two chelae (RL) as those missing one chela (RLi), with the exception that very weak interactions were more frequent in rock crab with two chelae (LS means, p = 0.049; Fig. 2). There was no limb loss or mortality throughout the experiment.

![Fig. 1](image-url) Mean proportion (+ SE) of observations in which small (RS), medium (RM), and large (RL) intact rock crabs, as well as 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). [cold, warm.]
The proportion of contests initiated by rock crab varied with temperature and size/chela treatments (Table 3). In cold water, rock crab initiated contests equally frequently regardless of size and chela loss (Fig. 3). However, in warm water, large rock crab with two (RL) or one chela (RLi) initiated a significantly higher proportion of contests (up to 62%) than small rock (RS) crabs (18%) (Fig. 3). Rock crab in each category initiated a similar proportion of contests as green crab (paired t-tests, \( p > 0.11 \) for all paired treatments). However, in warm water, green crab initiated a higher proportion of contests (76 to 80%) than small and medium rock (RS and RM) crab (paired t-tests, \( p < 0.01 \); Fig. 4). Large rock (RL) crab won a similar proportion of contests as green crab (paired t-test, \( p = 0.12 \)), whereas green crab won a greater proportion of contests (up to 91%) than small and medium rock (RS and RM) crab (paired t-tests, \( p < 0.01 \); Fig. 4). Interestingly, rock crab missing one chela (RLi) won as many contests as large, intact rock crab (RL) (Fig. 4).

### Table 3

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 H4 in Materials and methods).

<table>
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<tr>
<th>Source of variation</th>
<th>df</th>
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<th>p</th>
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<td>2.01</td>
<td>0.12</td>
<td>0.41</td>
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<tr>
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</tr>
<tr>
<td>Error</td>
<td>92</td>
<td>0.13</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

ANOVA: Factor = temperature, \( F_{1,92} = 1.23, p = 0.27 \); Factor = size/chela, \( F_{3,92} = 10.61, p < 0.01 \); Factor = temperature × size/chela, \( F_{3,92} = 1.24, p = 0.30 \). For example, large, intact rock (RL) crab won a significantly higher proportion of contests (50%) than small (9%) and medium (18%) rock (RS and RM) crab (LS means, \( p < 0.01 \); Fig. 4). Large rock (RL) crab won a similar proportion of contests as green crab (paired t-test, \( p = 0.12 \)), whereas green crab won a greater proportion of contests (up to 91%) than small and medium rock (RS and RM) crab (paired t-tests, \( p < 0.01 \); Fig. 4). Interestingly, rock crab missing one chela (RLi) won as many contests as large, intact rock crab (RL) (Fig. 4).

#### 3.3. Use of sediments and shelter by crabs

The proportion of observations in which the rock crab was buried in sediments or in the shelter was not affected by temperature and chela loss, yet decreased with increasing size in rock crab with both chelae (two-way ANOVA: Factor = temperature, \( F_{1,119} = 1.18, p = 0.28 \); Factor = size/chela, \( F_{3,119} = 7.82, p < 0.01 \); Factor = temperature × size/chela, \( F_{3,119} = 1.04, p = 0.38 \) (Fig. 5)). Indeed, small (RS) and medium (RM) rock crabs buried in sediments or were inside the shelter at least three times more frequently than large rock (RL) crabs (LS means, \( p < 0.01 \) and 0.013, respectively; Fig. 5). In all crab treatments, rock crab buried in sediments or were located in the shelter more often than green crab (paired t-tests, \( p < 0.029 \) for all paired treatments), which rarely exhibited (<2% of all observations) such behaviors.

### 4. Discussion

Our experimental approach to the study of effects of body size and chela loss on the ability of indigenous rock crab, *C. maenas*, to compete with recently introduced green crab, *C. irroratus*, to compete with recently introduced green crab, *C. maenas*, from Newfoundland and Labrador (NL) for a limited prey resource, the blue mussel, *M. edulis*, demonstrated the strong impact that water temperature...
has on foraging in both crabs and a generally higher competitive ability in green crab.

4.1. Hypothesis 1

We showed that temperature, body size, and chela loss had virtually no effect on the ability of rock crab to grasp the mussel before green crab, which refuted H1 (Table 4). The finding that green crab grasped the mussel before rock crab in >90% of trials provides a first indication of competitive dominance by green crab, while suggesting a greater ability to visually or chemically detect a prey(8,624),(993,701) or inclination to forage in open habitats. It also supports studies showing that green crab is generally first to contact a prey when competing with crustaceans of similar or larger sizes (Jensen et al., 2002; MacDonald et al., 2007; Williams et al., 2006).

Under 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). In the present study, large rock crab (on average 30 mm larger than green crab) spent an equal amount of time holding the mussel as green crab in cold water, though in warm water green crab 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 crab can reverse the initial dominance by green crab, while suggesting that the ability of green crab from NL to compete for food increases with increasing temperature (up to at least 12 °C). Experiments with green crab and American lobster, H. americanus, from other regions of the northwestern Atlantic where green crab had been present for more than one decade also demonstrate that larger and heavier lobster can reverse competitive dominance by green crab (Rosssong et al., 2006; Williams et al., 2006, 2009), though the effect of temperature on this pattern was not examined.

4.2. Hypothesis 2

We found that large rock crab spent nearly 50% more time holding the mussel than small rock crab and large rock crab missing one chela in cold water only (holding times were similar across these crabs in warm water). Interestingly, in warm water, ~50% of small rock crab that took possession of the mussel moved with it inside the shelter and green crab never attempted to enter the shelter to steal the mussel. These results suggest that small rock crab use habitat complexity to reduce confrontations, and hence that coexistence with green crab (and other competing crustaceans) may exist, as seen in rock crab competing for space with the American lobster in kelp habitats (Wells et al., 2010). They also partly support H2 by demonstrating different effects of temperature on these interactions (Table 4). In view of these findings, we predict that rock crab will gradually seek alternative prey and habitat characteristics in shallow subtidal ecosystems of NL invaded by green crab, especially during warmer times of year. 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 crab (and other crustacean species) when food resources are both limiting (this study) and non-limiting.

4.3. Hypothesis 3

Water temperature, rock crab size, and chela loss did not affect the number of contests between rock crab and green crab, which, therefore, refutes the first part of H3 (Table 4). This finding contradicts other studies of competition for food showing a greater number of contests between rock crab and green crab in warm (20 °C) than cold (5 °C) water (Bélair and Miron, 2009b), as well as an increase in the number of contests between green crabs with increasingly large differences in size at high (18 to 21 °C) temperature (Smallegange et al., 2007). These discrepancies may result from acclimation of crabs to different temperature regimes than 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 our study.

A few studies show that physical interactions are more frequent in large than small crabs (Glass and Huntingford, 1988; Smallegange et al., 2006) and that strongest physical interactions during intraspecific contests may occur between crabs of similar size (Archer, 1988). This contention and the second part of H3 were supported by our observation that large rock crab engaged in a larger proportion of contests with strong physical interactions with green crab than small rock crab. Moderate and strong physical interactions were frequent (at least 40% of all interactions) between large rock crab and green crab, whether the former had one or two chelae. Presumably, large rock crabs perceived their own size as an advantage that offset the loss of one chela. The relatively small bottom of experimental tanks likely increased the frequency of physical interactions between...
crabs compared to natural habitats. Yet, spatial segregation between crab species likely exists in nature where prey abundance and diversity are higher than in this study. Further research, including field experiments, is required to understand how physical interactions may influence spatial and temporal changes in the structure of natural crab and prey populations in NL.

4.4. Hypothesis 4

Although crustaceans of any size can initiate contests, the larger of two competing individuals normally wins (Glass and Huntingford, 1988; Richards and Cobb, 1986; Thorpe et al., 1994). Our findings that large rock crab initiated more contests with large green crab than smaller conspecifics in warm water only, whereas large rock crab won more contests than small rock crab, regardless of temperature, partly support H4 (Table 4). Conceivably, the large number of contests initiated by small rock crab with a much larger green crab resulted from the incapacity of the former to assess the fighting ability of its opponent based on visual or chemical cues, as seen in the swimming crab, Liocarcinus depurator (Glass and Huntingford, 1988). Such cues may be harder to interpret in cold than warm water. We noted that small rock crab often approached green crab only to retreat immediately following the display of chelae or physical attack by green crab. This result and our observations that medium-sized rock crab (which was as big as large green crab) won less than 20% of their contests with large green crab, whereas large rock crab won as many contests as seen in small green crab, small rock crab and green crab in NL likely compete non-competitive conditions (Matheson and Gagnon, 2012; Rossong et al., 2011) may indirectly increase the vulnerability of rock crab to predation by reducing shelter availability.

4.5. Hypothesis 5

In crustaceans, vulnerability to predation generally increases with decreasing body size (Stein, 1977), which can lead to size-dependant behavioral shifts, including shelter use (Matheson and Gagnon, 2012; Wahle, 1992). Our finding that small rock crab spent more time buried in sediments or in the shelter than large rock crab, regardless of temperature, is consistent with this paradigm, while supporting the first part of H5 (Table 4). Small rock crabs most likely behaved this way to minimize potential encounters with green crab. However, the amount of time that rock crab spent buried in sediments or in the shelter did not change with the loss of one chela, which refutes the second part of H5 (Table 4). A laboratory experiment by McDonald et al. (2001) show that juvenile green crab were able to displace juvenile Dungeness crab from shelters. We witnessed only a few competitive interactions for the shelter between rock crab and green crab. In fact, large green crab never displaced small rock crab from inside the shelter and used it only on rare occasions as seen in green crab foraging singly under non-competitive conditions (Matheson and Gagnon, 2012; Rossong et al., 2006). In natural habitats, juvenile rock crab and green crab frequently inhabit spaces between rocks and underneath seaweeds and move inside shelters when disturbed (Breen and Metaxas, 2009; McVean and Findlay, 1979). Although we did not examine competition in small green crab, small rock crab and green crab in NL likely compete for shelters. High densities of green crab in certain areas of southern Newfoundland (DFO, 2011) may indirectly increase the vulnerability of rock crab to predation by reducing shelter availability.

5. Conclusion

In a companion study, we showed that increasing temperature from 4 to 12 °C significantly increases mussel (M. edulis) capture, while altering patterns of mussel size selection and foraging behaviors in rock crab and green crab from NL foraging under non-competitive conditions (Matheson and Gagnon, 2012). The present study further suggests that the recent introduction of green crab to NL reduces foraging in rock crab, especially in competitive interactions between green crab and smaller rock crab, and that this effect is exacerbated during warmer times of year. We used a single mussel prey to determine, with greater accuracy, the ability of rock crab of different sizes and prey handling capacity to compete with some of the largest green crab in NL, than would have been possible had crabs competed for more than one prey item. Conceivably, prey diversity and abundance in natural habitats may not be as limiting as in this study, and rock crab may compete with smaller green crab. Accordingly, we recommend that future studies examine competitive interactions between rock crab and green crab in natural habitats and across broader spectra of prey availability and competitor abundance.
Acknowledgments
We are grateful to S. Caines, A. Robar, and M. Stapleton for assistance with collection of organisms and laboratory work as well as C. McKenzie for use of Fukui traps. We thank P. Snelgrove, C. McKenzie, and three anonymous reviewers for constructive comments that helped improve the manuscript. This research was funded by Natural Sciences and Engineering Research Council of Canada (NSERC Discovery Grant) and Canada Foundation for Innovation (CFI-Leaders Opportunity Funds) to P. Gagnon. [SS]

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