

Regional differences in foraging behaviour of invasive green crab (*Carcinus maenas*) populations in Atlantic Canada

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Received: 18 April 2011 / Accepted: 14 September 2011 / Published online: 25 September 2011
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Abstract Invasive green crab populations initially established in Canada within the Bay of Fundy, New Brunswick in the 1950s and were present in all five Atlantic provinces by 2007. Genetic evidence suggests that the Atlantic Canadian populations originated from two separate introductions with differences in time of establishment among regions and possible population-level behavioural differences. In this study, we examine intraspecific foraging behaviour among crabs from different populations, and interspecific foraging behaviour between genetically similar crabs and juvenile lobsters. Both sets of foraging experiments

involved competition for a limited food source over a 1-h period. In intraspecific match-ups, recent invaders from Newfoundland (NL) were significantly superior foragers than long-established invaders from Nova Scotia (NS) and New Brunswick (NB) populations; however, we found no differences between NL and Prince Edward Island (PE) invaders. Crabs from PE were better competitors than those from NS and NB, but these differences were not significant. Interspecific competition experiments indicated that the feeding behaviour of recent invaders (NL) and genetically similar, but long-established invaders (NS), differed in the presence of juvenile lobsters. Our study documents striking behavioural differences among populations of green crab from a small geographic region, which may reflect a combination of both genetic differences and time since establishment. These differences may result in varying impacts on newly invaded habitats.

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Keywords Behaviour · Genetic variation ·
Competition · Foraging · Invasion time

Introduction

Recent estimates suggest that ballast water may transport more than 10,000 species per day globally (Carlton 1999), but only 5–20% of all species successfully establish in a new area (Lockwood et al.

2007). Successful invaders often exhibit dense population size in their native range, wide physiological tolerance, short generation time, and high genetic variability (Lockwood et al. 2007). Consequently, populations of an invader in a new region are unlikely to be genetically uniform, especially those species that span a wide range of environmental conditions in their native range. Once one or more populations of an invasive species establish in new areas, populations typically grow rapidly, often in response to reduced competition, predation, and parasitism pressures (Behrens Yamada et al. 2005).

Indigenous to Europe, the green crab (*Carcinus maenas*) inhabits the east coast of the Atlantic Ocean from southern Iceland and Scandinavia to northern Africa (Grosholz and Ruiz 1996; Audet et al. 2003). Over the past 200 years, populations of green crabs have become established worldwide in the western Atlantic, Australia, South America, Japan, and the northeastern Pacific (Cohen et al. 1995; Grosholz and Ruiz 1995). On the east coast of North America alone, genetic evidence suggests that extant populations represent multiple successful invasions (Roman 2006). Local and regional larval transport likely facilitated the first Canadian invasion in the 1950s that spread throughout the Bay of Fundy and Atlantic coast of southern Nova Scotia (NS) but appeared to stall near the Halifax area by the 1970s (Carlton and Cohen 2003). A second wave of invaders established in southeastern NS in the 1980s, subsequently invading coasts around the Gulf of St. Lawrence (northwestern NS, eastern New Brunswick (NB), Prince Edward Island (PE), and the Magdalen Islands of Quebec (QC)), and most recently Newfoundland (NL) (Klassen and Locke 2007; Blakeslee et al. 2010). The role of behaviour in invasion success has been under-represented in the literature (Holway and Suarez 1999), even though behaviour likely plays an important role in facilitating successful colonization, establishment, and dispersal. Furthermore, individual variation in behaviours may play a role in population level processes including species distribution (Duckworth and Badyaev 2007). Thus far, two studies have documented the behavior and interactions between a common native species (juvenile American lobster, *Homarus americanus*), and green crabs from northern NS and southern NB respectively (Rossong et al. 2006; Lynch and Rochette 2009). These studies found contrasting results in terms of green crab dominance, a

difference that may be related, among other factors, to genetic differences between green crab populations.

Newly arrived invasive species are often perceived as a genetic diversity bottleneck. Individuals within their new range are genetically similar to each other when populations remain small or establish very slowly (Suarez et al. 2008). Green crabs within Atlantic Canada show an opposite pattern and exhibit population diversity levels similar to their native ranges, suggesting multiple invasions and/or source populations (Roman 2006; Darling 2011). Genetic diversity alone does not necessarily indicate invasion success since populations with a range of diversity have successfully established (Darling 2011), instead, it may reflect variations in the potential for ecological impacts.

Genetic studies of green crab populations within Atlantic Canada identify spatial and temporal components associated with multiple introductions (Roman 2006). Bay of Fundy populations represented the first wave of invasions, comprised of 1–4 haplotypes thought to have originated from the southern UK (Roman 2006; Blakeslee et al. 2010) and that more closely resemble the eastern US population. The 2–3 distinct European haplotypes that comprise northern NS and PE populations, likely originated from populations at the northern extent of their European range and represent the second invasion of Atlantic Canada (Roman 2006). Mixed haplotypes from the first and second Canadian invasions comprise the NL and southern NS populations (Blakeslee et al. 2010).

In this study, we compare the competitive ability of green crabs from the Bay of Fundy (NB; first invasion), Prince Edward Island (PE; second invasion composed of different haplotypes), and Nova Scotia and Newfoundland (NS and NL, genetically mixed populations). The significance of these population differences on green crab ecology and the resulting relative impacts of local invasions on native ecosystems remain largely unexplored. We used a standard laboratory setting and a common food source to assess the competitive foraging behaviour of individuals from four Atlantic Canadian provinces. Given that genetic differences may influence competitive ability, aggression, and phenotypic plasticity, we expected that the outcome of these experiments would reflect genetic differences among populations and offer predictive insights into the potential ecological impacts of green crabs in these and other regions.

The question of foraging behavioural differences can also be relevant to genetically similar populations with different time of establishment in a given area. Unlike well-established populations of invaders, early invaders grow quickly in population size, potentially intensifying interactions with conspecifics and native species by quickly limiting preferred resources (Simberloff and Gibbons 2004; Pintor et al. 2009). We compared the competitive behaviour of green crabs from NL (early invaders) and genetically similar crabs from southern NS (long-established invaders) and their behaviour in the presence of native competitors, juvenile lobsters. For these experiments, we expected that NL green crabs would dominate foraging and feed more frequently than NS crabs.

Materials and methods

Field collections

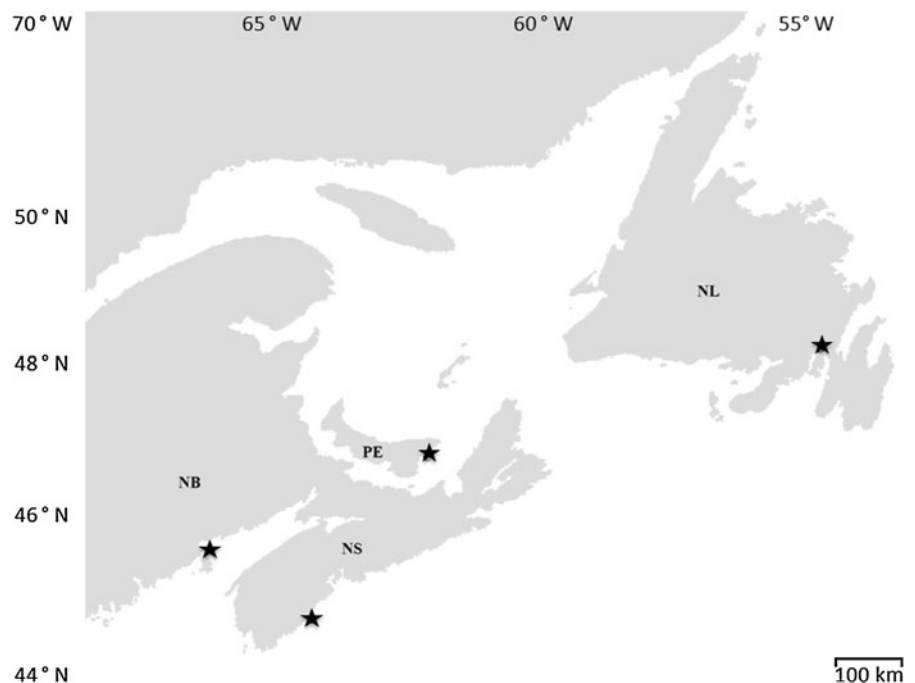
We collected green crabs ($n = 50$) using Fukui traps in Saint Andrews, NB ($45^{\circ} 04'34.57''$ N $67^{\circ} 03'09.55''$ W), Chance Harbour, NB ($45^{\circ}07'18.84''$ N $66^{\circ}21'04.28''$ W), Port Mouton, NS ($43^{\circ} 52'09.63''$ N $64^{\circ} 49'04.44''$ W), Souris, PE ($46^{\circ} 21'15.22''$ N $62^{\circ} 52'02.62''$ W) and North Harbour, NL ($47^{\circ} 09'20.90''$ N

$53^{\circ} 38'24.82''$ W) in July 2010 (Fig. 1). Green crab populations established in these communities by 1951 (both sites in NB), 1960, 1998, and 2007 respectively (Klassen and Locke 2007). All collection sites were in relatively uncontaminated areas distant from any cities and with fairly similar mixed mud and rock habitat and environmental conditions. Traps were baited with a standard amount of mackerel or herring and soaked for 1–2 h. The brief soaking time biased collection towards more aggressive crabs (Vasquez Archdale et al. 2003), and was consistent for all populations. We selected and transported only intact males (49–75 mm carapace width (CW)) to the Atlantic Veterinary College aquatic facility at the University of Prince Edward Island in Charlottetown, PE for use in experimental trials. Divers collected lobsters (24–49 mm carapace length (CL); $n = 30$, both sexes) in North Rustico, PE (an area without green crabs; $46^{\circ} 27' 29.84''$ N $63^{\circ} 18' 47.12''$ W) in August 2010 for transport to the same facility.

Housing and experimental tanks

Green crabs were separated by collection location and housed in opaque plastic storage containers ($108 \times 54 \times 46$ cm) within large round tanks (150 cm \times 86.5 cm; 2 plastic containers per tank). We covered

Fig. 1 Map of the Canadian Atlantic provinces and approximate location of the sites from where green crabs were collected



the bottom of each plastic container with a 2-cm layer of pea gravel, filled the container $\frac{3}{4}$ full with 30 ppt seawater, and then added an airstone and a mesh lid to prevent crab escape. To maintain isolation among populations prior to the experimental manipulations, we avoided mixing of water between storage containers. Within each large tank, a re-circulating system maintained the crab storage containers at 10.5°C. Prior to experimental trials, we fed green crabs a diet of mussels and changed water in the tanks regularly (every other day) to maintain quality. Green crab had a 1-week acclimation period in the tanks prior to use in the experiment and individual green crabs were starved for 48 h before the experiments to standardize hunger levels (Mascaro and Seed 2001; Rossong et al. 2011). Lobsters (both claws) were banded, placed individually in housing tanks (30 ppt, 10°C), and fed shrimp every second day during their 1-week acclimation period.

We filled a 1.5 m-diameter tank to a depth of 0.3 m with seawater similar in temperature and salinity to that described above, and covered the tank bottom with a thin layer of pea gravel. We then suspended one camera (Speco Technologies Weatherproof DSP VL-66 with infrared) over the middle of this tank ~100 cm from the substrate and secured a second camera on the side of the tank 50 cm above the sediment. Both cameras were connected to a 4 channel recorder (Samsung SHR-5042) located in a separate room.

Intraspecific competition experiment

The first set of experiments examined foraging competition for a limited resource between pairs of individual crabs from different populations (four provinces) known to exhibit genetic differences. We drilled a hole through the shell of a live mussel (*Mytilus edulis*) and fastened it with a cable tie anchored in the center of the tank, thereby ensuring that interactions took place in the camera's field of view, as in previous experiments (cf. Jensen et al. 2002; Rossong et al. 2006).

For each trial, we matched green crabs in 1 of 6 combinations ($n = 15$ trials per combination): NB versus NL, NB versus PE, NB versus NS, NL versus PE, NL versus NS, and NS versus PE. Green crabs in a given trial differed less than 5 mm in size (CW). Before each trial, green crabs were measured (± 1 mm), weighed (± 0.01 g), and labeled to facilitate identification during subsequent video analyses. For

each trial, we placed both green crabs in the tank for a 10-min acclimation period with the food source covered, followed by a 60-min trial period with the food exposed. We held all crabs used in experiments in holding tanks for 2 weeks after the experiment before euthanization to ensure they did not molt (molt cycle may affect behaviour; Tamm and Cobb 1978). In the PE versus NB experiments we only completed 11 of the 15 planned trials because of water quality issues detected within the PE crab tank. Once we detected the problem, we euthanized all PE green crabs and collected a new group of crabs for the remaining trials at a later date. We also excluded a few trials ($n = 3$) where the green crabs detached the mussel, making it difficult to determine interactions.

Experiment 2: feeding behaviour in the presence of juvenile lobster

The second set of experiments examined the feeding behaviour of two genetically similar green crab populations in the presence of a juvenile lobster. The set-up was identical to the previous experiment except that we paired unbanded lobsters with green crabs from a recently established population (NL; less than 5 years) and, a long-established population (NS; more than 45 years; $n = 25$ trials per combination). After the experiment, we labeled, measured, sexed, and held crabs and lobsters for 2 weeks prior to euthanizing.

Video and statistical analysis for competition experiments

Upon completion of trials, we analyzed video footage to determine which individual reached the mussel first, the time taken to find the food source, and the total time spent feeding. We also quantified the following behavioral observations: the number of approaches by the non-feeding crab on the feeding crab, the frequency by which one crab was able to displace the other crab from the resource, the duration of interactions, and the intensity of interactions based on a scale from 1 to 3 (1 indicated no physical contact; 2 minimal physical contact; 3 aggressive pinching/pushing by one or both crabs).

We assessed the amount of time feeding by each green crab using paired t tests, with a Bonferroni adjustment of significance levels ($\alpha = 0.05/n = 0.0083$ for $n = 6$ combinations; Minitab 16). We

assessed differences in body size using paired *t* tests on carapace width (CW; mm) and body weight (g wet weight). A binomial test was used to determine whether crabs in each treatment were equally likely to arrive first at the bait.

For the second experiment, we used two-sample *t* tests to evaluate genetically similar green crab behaviour in the presence of lobsters, with treatment groups of NL green crabs (from newly-established populations) and NS green crabs (from long-established populations). A regression of “time feeding” on “difference in body size” (crab CW–lobster CL) and a regression of “time to locate the mussel” on “difference in body size” were used to assess the influence of differences in body size on the response variables.

Results

Intraspecific competition

The pairing of crabs for each trial resulted in no significant differences in body size (CW and body weight) among paired crabs for all matchups (all *P* values > 0.150). NL crabs were first to the mussel in more trials than NS crabs (12 of 15) and NB crabs (10 of 13) but a binomial sign test revealed ratios were not significantly different from 1:1 at the Bonferroni-corrected significance level of 0.0083 (*P* = 0.035 and *P* = 0.093 respectively). PE crabs were significantly faster to the bait than NL crabs (14 of 15, *P* = 0.001), but not significantly faster than NS or NB crabs (10 of 15, *P* = 0.302; 6 of 11, *P* = 1.0 respectively). In the final match-ups, NB green crabs were faster to the bait than NS crabs in 10 of 14 trials but the ratio was not significant (*P* = 0.180).

Green crabs from NL spent significantly more time with the food source than green crabs from either NB (*P* < 0.001; Fig. 2a) or NS (*P* = 0.005; Fig. 2b) populations; however, there was no difference between NL and PE crabs (*P* = 0.629; Fig. 2c). PE crabs spent more time feeding than NS crabs (*P* = 0.009, Fig. 2d) and NB crabs (*P* = 0.064; Fig. 2e) although differences were not significant at the Bonferroni-corrected significance level of 0.0083. We detected no foraging dominance between NB and NS crabs (*P* = 0.556; Fig. 2f).

We then examined and compared the number of interactions and total interaction time between

treatments (See Table 1 for summary) and detected no significant differences (*P* = 0.076; *P* = 0.300, respectively); however, the longest interaction times occurred in the PE versus NB match-ups, followed closely by the match-ups with NL crabs. In all treatments, interaction intensity varied. In some cases, intensity increased as the trial continued whereas in other cases more passive encounters followed a few intense battles. In 10 of the 30 trials, the first crab to the mussel was never displaced from the resource, whereas the other crab took over for some portion of the time remaining in the trial. However, in most cases, ownership of the mussel reverted to the initial feeder.

Feeding behaviour of green crab in the presence of lobster

Lobsters spent most of the duration of the trial moving around the tank. They often approached the feeding crab but made no physical contact nor tried to take over the resource. In one trial only, the lobster initiated feeding when the green crab had abandoned the mussel.

During 25 trials, green crabs from NL took 480 ± 60 (mean \pm SD) seconds to locate the mussel and then fed on it for $2,100 \pm 120$ s. Green crabs from NS initially located the mussel in 660 ± 120 s and fed on it for an average of $1,560 \pm 180$ s. Although the time to locate the mussels did not differ significantly (*P* = 0.230), NL crabs spent significantly more time (34% longer) on the prey than NS crabs (*P* = 0.027; Fig. 3).

Regressions of “time feeding” on “difference in body size” were not significant for the NL or NS green crab/lobster trials (*P* = 0.071 and *P* = 0.933 respectively) and regressions of “time to locate the mussel” on “difference in body size” were not significant for the NL or NS green crab/lobster trials (*P* = 0.188 and *P* = 0.143 respectively), providing evidence that the difference in body size between paired organisms did not influence the responses.

Discussion

Competition experiments

In this study, NL green crabs dominated individuals from NB and NS populations in foraging experiments.

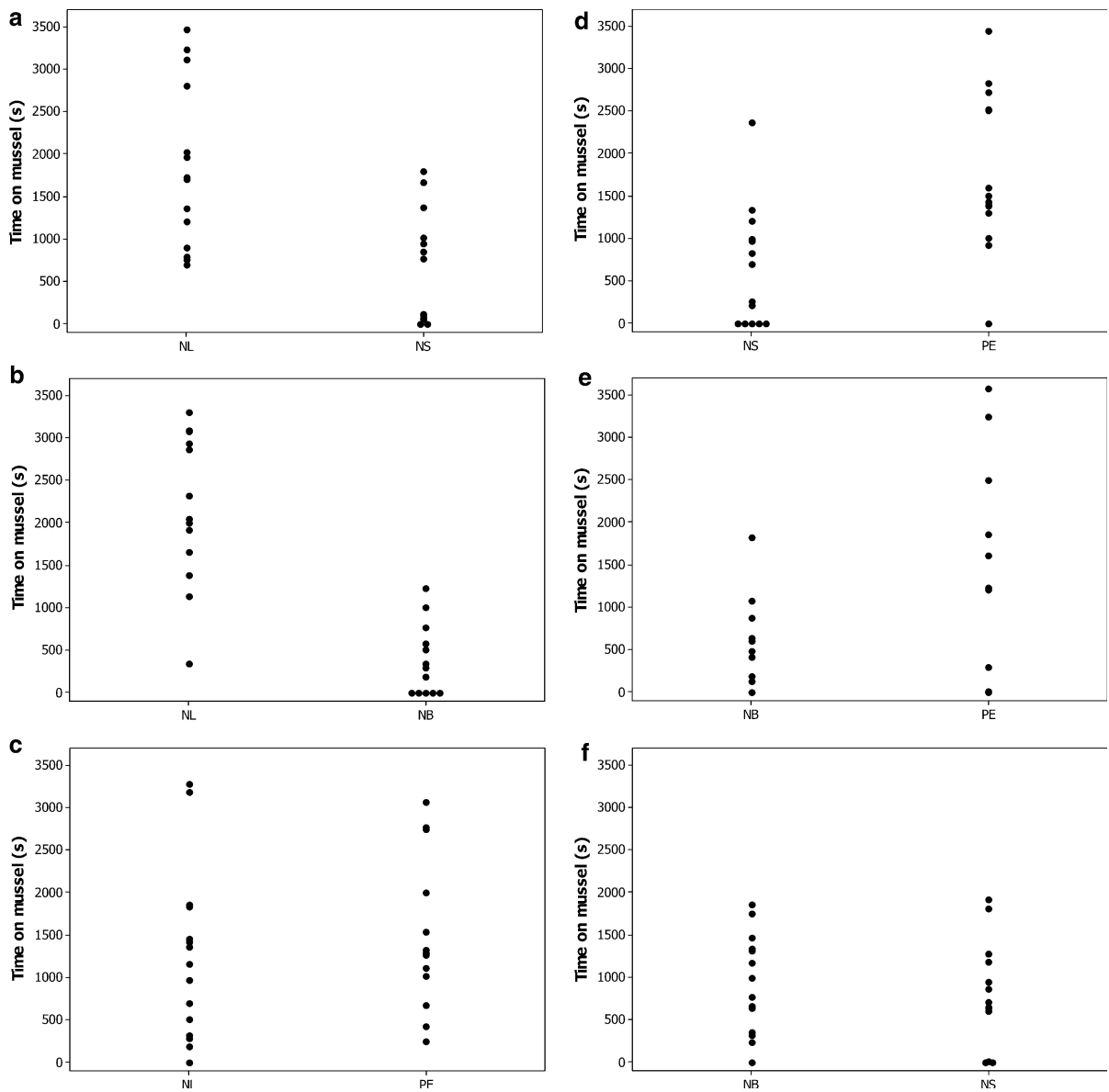


Fig. 2 Time spent feeding on the mussel by *green crabs* (each symbol represents a 1 h trial). **a** NL and NS ($n = 15$; $P = 0.0001$). **b** NL and NB ($n = 13$; $P = 0.005$). **c** NL and

PE ($n = 15$; $P = 0.629$). **d** NS and PE ($n = 15$; $P = 0.009$). **e** NB and PE ($n = 11$; $p = 0.064$). **f** NB and NS ($n = 14$; $P = 0.556$)

NL crabs were first to the mussel in the majority of trials and spent more time feeding on the mussel; however, no significant differences were observed in trials against green crabs from PE. PE crabs were the first to the mussel in all of their food trials (including NL) and spent more time feeding than NS and NB crabs. Although at this stage we cannot establish unambiguous cause-effects, these results clearly support our general expectations that; (a) green crab

populations in Atlantic Canada differ in competitive dominance, an aspect of their ecology that can be at least partly explained by their genetic differences; and (b) differences in competitive dominance between populations of similar genetic make-up may be related to the timing (recent vs. old) of their invasion. Acknowledging the many factors that may influence crab performance and the constraints imposed by a laboratory setting, we believe the behavior observed in

Table 1 A summary of the first to mussel, time to mussel, amount of time feeding, and interaction time for each match-up

GC 1	GC 2	First to mussel (majority of time)	Average time to mussel (s) (\pm SE)	GC1 average time on mussel (s) (\pm SE)	GC2 average time on mussel (s) (\pm SE)	Total interaction time (s) (mean \pm SE)	Average number of interactions (mean \pm SE)	<i>N</i>
NL	PE	PE*	359 \pm 67	1,229 \pm 259	1,447 \pm 219	314 \pm 68	9.06 \pm 1.72	15
NL	NB	NL	441 \pm 117	2,154 \pm 246*	374 \pm 115	307 \pm 71	7.91 \pm 1.34	13
NL	NS	NL	410 \pm 144	1,825 \pm 242*	589 \pm 167	363 \pm 96	7.21 \pm 1.43	15
NB	PE	PE	519 \pm 243	617 \pm 154	1,554 \pm 364	397 \pm 69	8.80 \pm 1.72	11
NB	NS	NB	803 \pm 208	914 \pm 156	754 \pm 170	166 \pm 40	4.07 \pm 0.54	14
PE	NS	PE	685 \pm 175	1,864 \pm 256*	635 \pm 175	222 \pm 49	5.93 \pm 0.89	15

* A significant result

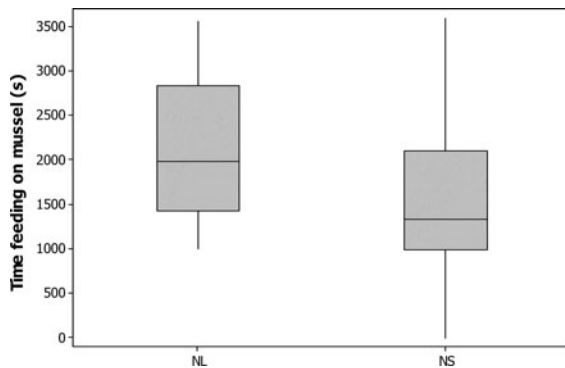


Fig. 3 Time spent feeding by green crab from NL and NS ($n = 25$ per treatment; $P = 0.027$) during a 1 h trial in the presence of juvenile lobsters. The horizontal line represents the median value

these trials is representative of the intensity of these crab interactions.

Genetic differences

Genetic evidence provides insight into the source of an invasion, transmission routes, and modes of introductions (Mikheyev and Mueller 2007; Darling 2011), but genetic differences may also influence behaviour. Two distinct source populations comprise eastern Canadian populations (Roman 2006; Darling 2011). One population (NB) shares a similar genetic make up with the majority of North American populations (Darling et al. 2008), whereas a second population (PE) comes from a completely different source. The lack of environmental barriers allows ready mixing of these populations, creating genetically distinct combinations of haplotypes similar to those in its native range (NS and NL; Roman 2006; Blakeslee et al. 2010). Most studies

on green crab impacts (e.g., Grosholz et al. 2000; Klassen and Locke 2007) thus far have focused on North American populations exhibiting low genetic diversity (Roman and Darling 2007; Darling et al. 2008). As a consequence, populations in this study may exhibit differing competitive abilities than previous studies on green crab behaviour in North America. For instance, interspecific hybridization in plants can produce more competitive invaders (Ellstrand and Schierenbeck 2000). If similar genetic mixing occurs between green crab populations, this could ultimately alter competitive ability and subsequent impacts on native organisms and habitats.

Two previous laboratory experiments on foraging competition between green crabs and juvenile lobsters (Rossong et al. 2006; Lynch and Rochette 2009) found sharply different levels of competitive dominance in green crabs. The only major difference between the two studies was the origin of the green crabs. Rossong et al. (2006) used green crabs from the Northumberland Strait, NS (genetically similar to PE populations). These crabs were significantly better competitors than lobsters, locating and dominating the food source in all trials. Moreover, in 6 of 11, 8 h trials of a shelter experiment, lobsters (28–57 mm CL) were actually consumed by green crabs (53–76 mm CW). In contrast, the study with green crabs from southern NB (population established by 1951) found that green crabs (33–70 mm CW) were more passive, and that lobster (16–48 mm CL) feeding and mortality remained unaffected by green crabs (Lynch and Rochette 2009). The results from our study are consistent with those two studies and provide an explanation for their contrasting results. In our PE and NB matchup, PE crabs spent more than twice as much time feeding in comparison to NB crabs (means of

1,554 and 617 s feeding, respectively). The average of the paired differences (937 s) was not significantly different from zero ($P = 0.064$), but the magnitude of the difference was substantial ($\sim 150\%$ relative to the mean time feeding for PE). Such a difference in competitive ability explains why one green crab population (PE) was able to dominate interspecific trials where a second population within the same region but with a different genetic make up (NB) did not.

As in our study, invasions by yellow crazy ants (*Anoplolepis gracilipes*) on a South Pacific island, and paper wasps (*Polistes dominulus*) in the USA represent multiple invasions with genetic variation among populations (Liebert et al. 2006; Abbott et al. 2007). Intraspecific competition experiments showed different levels of competitiveness between genetically distinct populations of ants (Abbott et al. 2007). The study also found that separate invasions led to two behaviourally and genetically distinct populations, where only one ant population became highly abundant. Our results on green crab competitive ability suggest the same phenomenon. In practical terms, it is impossible to predict the precise outcome of a green crab invasion into a new locale. However, our results suggest that an assessment of the genetic make up of the invading population should foretell the severity and intensity of impacts.

Time since establishment

Although genetic differences may explain differences in foraging abilities of green crab populations, other factors (such as time since establishment) likely play a role as well. Genetic evidence suggests that NL green crabs originated directly from southern NS (Blakeslee et al. 2010). However, despite their similar genetic makeup, we detected behavioural differences between these two populations in both intraspecific and interspecific competition experiments. In match-ups directly against each other, NL crabs spent over three times as much time feeding than NS crabs. In trials with a potential competitor (juvenile lobster), as in the intraspecific trials, individual crabs from NL spent significantly more time feeding on the mussel than NS crabs.

In the interspecific competition trials, the lobsters did not physically interact with the green crabs, and although we cannot completely rule out a potential effect of the lobster on green crab behaviour, we saw

no evidence of an effect in any of our video recordings. All green crabs were housed in the same settings, fed on a schedule of 48 h starvation prior to use in the experiment to regulate hunger levels, and acclimated for a 1-week period prior to experiments. Therefore other explanations for population differences are crab size differences, food preferences, and contrasting behaviours among populations. Smaller crabs may feed less than larger crabs, but we matched all crabs in intraspecific trials based on a size difference of 5 mm or less CW. Moreover, paired differences in body size were not significant within each matchup. In addition, differences in body size between paired crabs and lobsters did not influence the responses based on the non-significant regressions of the response variables on differences in body size. With respect to diet differences, green crabs from both southern NS (Elner 1981) and NL (Rossong unpublished data) show that bivalves, and mussels in particular, comprise the largest portion of both diets, so prey preference is unlikely a contributing factor to our results. Behavioural differences among populations are therefore the most plausible explanation and we hypothesize that these differences in foraging ability may be related to local invasion times.

During initial establishment at a new location, densities of green crabs increase rapidly, a phenomenon often associated with higher agonistic interactions in similar crab species (Clark et al. 2000; Reichmuth et al. 2011). Green crabs are generalist predators (Ropes 1968; Grosholz and Ruiz 1996; Klassen and Locke 2007), capable of depleting food resources in an area before moving on to new locations. In order to survive, green crabs must be strong competitors but as populations decline, competition for limited resources among conspecifics presumably decreases (Simberloff and Gibbons 2004). Therefore recent invaders need to be more active foragers in order to successfully become established.

Behaviour is often a good determinant of invasion success (Weis 2010). In the short term, behaviours associated with high competitive ability allow invaders to maintain high foraging and growth rates, thus increasing the likelihood of successful establishment. In the long term, invader populations may face a boom and bust cycle driven by limited resources or variation in potential dispersal (Williamson and Fitter 1996; Simberloff and Gibbons 2004; Pintor et al. 2009). For example, intraspecific competition in the invasive

crayfish (*Pacifastacus leniusculus*) is unusually high when resources are limited, and these heightened levels of aggression limit population growth (Pintor et al. 2008). Similarly, a study on funnel web spiders (*Agelenopsis aperta*) showed that when resources are depleted (which is often the case in newly invaded areas) spider populations became more competitive than similar populations with an abundant food source (Hendrick and Riechert 1989).

Invaders often prevail over native species in aggressiveness and boldness (Rehage and Sih 2004; Pintor et al. 2008). In newly invaded areas with dietary and spatial overlap with native species, green crabs, like other invasive organisms (e.g., crayfish; Pintor et al. 2008), may be more aggressive than in areas where competition is less intense. Aggressive individuals may be one of the drivers of range expansion of an invader. For example, in western bluebirds (*Sialia mexicana*), only aggressive males disperse and colonize new areas (Duckworth and Badyaev 2007) whereas non-aggressive individuals remain well within their natural distribution limits. Once the population has established itself in a new locale and outcompetes native species, aggression levels decrease again within several generations (Duckworth and Badyaev 2007). Although the evidence presented in this study is limited in terms of number of sites and populations, its scope is appropriate to the spatial scale of the region and what is known about the history of its invasion. Our study suggests decreased foraging intensity with increased time since invasion.

Although foraging success and aggression may be correlated (Reichmuth et al. 2011) it is clear that they are not necessarily equivalent. For example, in a study on juvenile crab foraging, green crabs were first to the bait in competition experiments (therefore considered more successful foragers) but were less aggressive than blue crabs (*Callinectes sapidus*; MacDonald et al. 2007). Further studies on the relationship between foraging ability and green crab intraspecific aggression are necessary in order to distinguish the two phenomena. It is, however, clear that aggression, high foraging rate, and superior competitive dominance all play a role in the success of invaders (Pintor and Sih 2010).

Conclusions

This study suggests that genetics and time since establishment of an invasive species both affect

behaviour of an invasive species. Early invaders may initially destroy new habitats but with time their impacts may lessen with changes in behaviour associated with lower population density and decreased competitive pressures. Green crabs from PE, and other locations along the Northumberland Strait are genetically different from the rest of Atlantic Canada as well as the eastern US and west coast of North America (Roman 2006). The behaviours of these crabs were similar to newly established populations from NL, suggesting that they may belong to a genetically more aggressive strain or that they have not been established long enough to lose their competitive dominance. Green crabs within Atlantic Canada and worldwide have negatively affected native organisms and habitats (Grosholz and Ruiz 1995; Cohen et al. 1995; Klassen and Locke 2007). Although previous studies examined behavior of green crabs, population-level differences in behaviour such as those assessed here were previously unexplored. The differences we document here for Atlantic Canada populations suggest that foraging competition, behavior, and overall impacts on a native habitat may differ depending on both genetics and invasion history.

Acknowledgments We thank Fisheries and Oceans Canada, M. Comeau, B. Comeau, R. Leblanc and G. Paulin for obtaining the juvenile lobsters and T. Wells, A. Nadeau, C. McCarthy, T. Pickering and L. Poirier for assistance with green crab collection and experiments. We also thank W. Petley and the personnel of the aquatic facility at the Atlantic Veterinarian College for their collaboration. Funding for this research was provided by NSERC Discovery Grants to PQ and PS, a contract from Fisheries and Oceans Canada as part of the Aquatic Invasive Species Research Program, NSERC PGS-D, NL RDC Ocean Industries Research Scholarship and a MUN graduate studies fellowship to MR. Comments from two anonymous reviewers improved the clarity of the manuscript.

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