Spatial overlap and biotic interactions between sub-adult American lobsters, *Homarus americanus*, and the invasive European green crab *Carcinus maenas*

by

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Dedication

To the late Robert Adrian, a brilliant scientist whose passion for understanding the natural world influenced many, particularly his grandchildren.

Abstract

I evaluate the spatial overlap between the invasive European green crab, *Carcinus maenas*, and sub-adult lobsters, *Homarus americanus*, in a lobster nursery area in Passamaquoddy Bay, New Brunswick. I also conduct two laboratory studies to investigate the biotic interactions between these two species; the first is a 62-day experiment to determine if green crabs (CW 33-70-mm) affect survival, growth, and behaviour of similar mass sub-adult lobsters (CL 15-48-mm), and the second is a 7-day experiment to determine if very large green crabs (CW 53-78-mm) affect the survival of sub-adult lobsters. While there was significant spatial overlap between these species in nature, green crabs did not affect survival, growth, activity, feeding, or sheltering behaviour of sub-adult lobsters. Rather, sub-adult lobsters regularly prey upon green crabs in the laboratory. My results suggest that green crabs represent no immediate threat to sub-adult lobsters. I discuss the discrepancy between my results and those of two recent studies, and outline areas of investigation that need be pursued to generate a more comprehensive picture of the ecological interaction between these species.

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1. General Introduction

1.1 Invasive Species

Biological invasions are considered to be one of the greatest threats to global biodiversity in the world today (Walker & Steffan 1997, Mack et al. 2000), second only to habitat destruction and fragmentation (Walker & Steffan 1997). Invasive species, defined by Kolar & Lodge (2001) as 'a nonindigenous species that spreads from the point of introduction and becomes abundant', are introduced to non-native habitats in numerous ways, which are almost entirely human-mediated (Ruiz et al. 1997). In terrestrial ecosystems, invasive species are primarily imported by humans as crop or livestock for agriculture, however introductions also occur via other routes including horticulture and the transport of farm products (Xu et al. 2006). In aquatic systems, dumping of ship ballast water is almost certainly the predominant cause of introduction of species to new habitats (Ruiz et al. 1997). Other causes of biological invasions in aquatic systems include transport of fouling communities on the bottoms of ships, release from aquaculture/fishery operations, the pet trade, and the connection of waterways through canals (Ruiz et al. 1997). Once introduced, invasive species can have numerous impacts on native organisms through a variety of mechanisms such as predatory, competitive and/or facilitative interactions.

1.1.1 Predation on native species

Upon introduction to a new habitat, invasive species must establish new trophic relationships in order to survive, reproduce and become established. This may result in the addition of a new predator for one or more native species, which can cause large declines in prey abundance. There are numerous examples of this in the literature from all over the world. For example, introduction of the planktivorous ctenophore, *Mnemiopsis leidyi*, had dramatic effects on community structure in the Black Sea (Shiganova 1998). The introduction of this ctenophore caused reductions in the abundance and species diversity of icthyoplankton and zooplankton, which it unselectively feeds upon (Shiganova 1998). These declines were reflected in reduced catches of planktivorous fish as well as reduced abundance of the larvae of fish with planktonic eggs, such as anchovy (Shiganova 1998). Another example comes from Guam where the accidental introduction of the brown treesnake, *Boiga irregularis*, from US recovery of war materials from New Guinea drastically changed that ecosystem (Fritts & Rodda 1998). The brown treesnake is a proficient predator, preying upon birds, bats, and lizards and its introduction to a previously predator-free environment has been blamed for extirpation of 3-12 bird species and 3-5 reptile species (reviewed in Fritts & Rodda 1998). This snake altered diversity and abundance of many animals on this island and completely rearranged the structure of Guam's food webs (Fritts & Rodda 1998).

1.1.2 Competition with native species

Introduction of new species forces invasive organisms into competition with native species for resources (Herbold & Moyle 1986), such as food and space (Crooks 2002). In natural systems, organisms have often specialized their diet and habitat requirements over evolutionary time to minimize competition for resources between species (Krebs 2001). Introduction of a new species, one that is not adapted to minimize resource-requirement overlap with other species in that system, can potentially put more pressure on those resources and reduce their availability to native species. For example, the invasive Argentine ant, *Linepithema humile*, competes for the same food resources as native ants in California (Human & Gordon 1996). In baiting experiments in the field, the invasive ant was able to displace native ants from food in 60% of encounters, which drastically reduced foraging success in this native ant species (Human & Gordon 1996). The introduction of this new ant species, and subsequent range expansions, corresponds with reductions in the range of the native ant species (Human & Gordon 1996). Another example of this comes from invasive geckos, *Hemidactylus frenatus*, in Hawaii. This species has a nearly identical diet with an endemic gecko *Lepidodactylus lugubris*, but the invasive gecko is a more proficient insectivore due to its larger size, faster running speed and reduced intra-specific interference during foraging (Petren & Case 1996). The introduction of *H. frenatus* caused significant declines in the abundance of *L. lugubris,* which are believed due to the competitive superiority of the invasive gecko (Petren & Case 1996). These cases demonstrate how invasive species can alter the distribution and survival of native species that are not well adapted to the presence of an invasive species.

Competition between invasive species and native species is not limited to food, but may also involve living spaces and habitat. This is well demonstrated on rocky intertidal shores in Chile by the invasive tunicate *Pyura praeputialis* (Castilla et al. 2004). This invasive tunicate requires rocky intertidal substrate on which to anchor and was shown to reduce survival of a native mussel (Castilla et al. 2004). The tunicates will encroach mussels by growing adjacent to and upon them, which reduces mussel survival and can cause them to drop from the substrate, freeing space for tunicate colonization (Castilla et al. 2004). Spatial competition potentially results in reduced survivorship in the poorer competitor.

1.1.3 Facilitation of native species

The effects of biological invasions are not always negative to all members of the community that is invaded. There is evidence that invasive species can facilitate native species by providing alternative prey items, reducing populations of predators and/or competitors and by modifying habitat (reviewed in Rodriguez 2006). Introduction of an invasive species can cause changes to native organism populations through predation and competition (described above) and these changes can alter abundances of native organisms and trophic relationships within the system. This can have positive effects on some members of the community, especially those who feed directly upon the invasive organism or have a predator or competitor whose population declines in response to the invasive. For example, the whelk *Rapana venosa* was introduced to Chesapeake Bay and first discovered there in 1998 (Harding 2003). This whelk is now suggested to make up a large part of the diet of native blue crabs, *Callinectes sapidus* (Harding 2003), potentially increasing their abundance through trophic subsidy. Invasive species can also facilitate native species by modifying habitat. For example, the invasive suspension-feeding polychaete, *Ficopomatus enigmaticus*, builds circular reefs up to 7-m in diameter (Schwindt et al. 2001). These reefs are composed of numerous calcareous tubes, which provide habitats for many marine organisms (Schwindt et al. 2001). The introduction of these worms to the Mar Chiquita lagoon, Argentina, modified the benthic environment by increasing the amount of shelter available to native crabs, *Cyrtograpsus angulatus*, whose population rapidly increased in response to this invasion (Schwindt et al. 2001).

1.2 *Carcinus maenas* as an invasive species

The European green crab, *Carcinus maenas*, is an invasive species occurring along the northeastern coast of North America. This crab invaded Eastern North America in the mid 1800's and was first observed between New Jersey and Massachusetts. This invasion was most likely caused by the dumping of ship ballast water containing green crab larvae, however transport in ship fouling communities has also been suggested to be the vector (Hidalgo et al. 2005). Since the original invasion, *C. maenas* has been continually expanding its range (Audet et al. 2003). By the early 1900's *C. maenas* was common in the Southern Gulf of Maine around the Cape Cod region and by 1950 it was found in very high abundances in the Northern Gulf of Maine near St. Andrews, New Brunswick. Today green crabs are commonly found throughout the Bay of Fundy and in many locations in coastal New Brunswick, Nova Scotia and Prince Edward Island (North American invasion of *C. maenas* reviewed in Audet et al. 2003). More recently, *C. maenas* has become abundant on the west coast of North America from southern California to Vancouver Island (Cohen et al. 1995, McDonald et al. 2001, Audet et al. 2003). The Pacific invasion is likely due to either larval transport in ship ballast water, or transport of crabs (or perhaps larvae) in seaweed used to pack commercial lobsters and/or baitworms from eastern North America (Behrens Yamada et al. 2005).

There is mounting evidence that green crab invasions have impacts on the areas they colonize, primarily through predatory and competitive relationships with native species. For example, *C. maenas* introduced in California have caused significant reductions in two bivalves (*Transennella confusa* & *T. tantilla*), one cumacean (*Cumella vulgaris*), and one amphipod (*Corophium* sp.) (Grosholz & Ruiz 1995). Shell remnants confirmed that predation by green crabs was the mechanism responsible for decreases in bivalve abundance; however, either predation or migration caused by green crabs is responsible for the decreases in cumacean and amphipod abundance (Grosholz & Ruiz 1995). Since the prey species most drastically affected by green crab predation are functionally important in these systems, Grosholz and Ruiz (1995) predicted that the community-level impacts of this invasion would be substantial. For example, they predicted that the observed removal of larger bivalves by green crabs would reduce available prey to other species that are dependent on these bivalves, such as Dungeness crabs, shorebirds, and surfperch. In addition, these bivalves filter the water column. Therefore, reductions in bivalve abundance may be reflected in plankton density as well as nutrient availability, which may further alter community-wide trophic relationships (Grosholz & Ruiz 1995). However, these indirect community-level effects remain to be investigated and quantified, though the direct population-level effects seem to persist in the long-term (>10 years) (Grosholz & Ruiz 1996). Invasive green crabs have also become the primary predator of venerid clams, *Katelysia scalarina*, in Australia (Walton et al. 2002). Increased predation pressure from *C. maenas* decreased the abundance of these economically important clams and is suggested to affect the proportion of adults available to the declining fishery (Walton et al. 2002). Another study, which used laboratory and field enclosure studies in the Pacific Northwest, found that *C. maenas* had the ability to displace similar-size Dungeness crabs, *Cancer magister*, from shelter and food resources (McDonald et al. 2001). These results suggest that the presence of green crabs might reduce recruitment to the Dungeness crab fishery by reducing survival of juveniles through displacement from shelters and reduced food availability (McDonald et al. 2001).

Surprisingly, relatively little is known about the predatory, competitive, or facilitative effects of introduced *C. maenas* on native species in the northwestern Atlantic. Green crabs are aggressive omnivores in this region and they regularly feed upon numerous organisms including bivalves, gastropods, crustaceans, and algae (Elner 1981). Despite knowledge of green crab diet in the northwestern Atlantic, the effects of this invasive predator on prey populations and community structure remain understudied. One recent study examines the population-level effects of introduced green crabs on 19 taxa in the northwestern Atlantic (Thompson 2007). In this study, field enclosure experiments revealed that the presence of green crabs caused significant declines in 8 taxa; green crabs directly preyed upon 4 species of gastropods and 2 species of polychaetes and caused emigration of 1 species of gastropod and 2 species of decapod (Thompson 2007). This study suggests that green crabs have the potential to change community composition and also change trophic relationships among native species. Other studies have shown that littorinid snails will modify their growth patterns (Brookes & Rochette 2007), feeding behaviours (Trussell et al. 2003), and predator-resistance behaviours (Edgell & Lynch, *in prep*) in the presence of invasive green crabs. These green crab-induced phenotypic changes in snails can have cascading effects through the community. For example, the introduction of green crabs causes snails to reduce feeding rates on intertidal algae, therefore algal survival is facilitated by the presence of green crabs (Trussell et al. 2003). This increased algal survival may enhance survival of other organisms by providing habitat, food, and/or buffering them from wave action, desiccation or thermal stress. Furthermore, green crabs have also been shown to induce thicker shells and stronger attachments in blue mussels (*Mytilus edulis*) transplanted to site where green crabs are in high density (Leonard et al. 1999) and green crabs are also known to drastically reduce density and abundance of soft-shell clams, *Mya arenaria*, in field enclosure experiments (Floyd & Williams, 2004).

Green crabs have the ability to compete with native species for food and space, which can have negative impacts on some members of the community (e.g. reduction of available prey to Dungeness crabs) and facilitative effects on others (e.g. release of algae from snail herbivory). As the European green crab continues to expand its range, the potential for negative impacts on coastal ecosystems is also expanding. It is therefore extremely important to understand how green crabs interact with native species to determine what changes they might cause to native communities, as well as ecologically and/or economically important species, such as the American lobster *Homarus americanus*.

2. Research Introduction

The European green crab, *Carcinus maenas*, invaded the eastern coast of North America in the late 1800s, and has been continually expanding its range since (Audet et al. 2003). Relatively little is known about the impact of green crabs on native species in Atlantic North America, but they have been shown to reduce the abundance of many epi-benthic and endo-benthic invertebrates in other areas where they have invaded (Glude 1955, Grosholz & Ruiz 1996, Grosholz et al. 2000). For example, on the west coast of North America, invasive green crabs have caused long-term (≈10 year) declines of many invertebrates including bivalves, cumaceans, and amphipods through predation and emigration (Grosholz and Ruiz 1995). Furthermore, green crabs have been shown to displace native decapods from shelter and food resources (McDonald et al. 2001) and they are known to feed upon benthic fish (Taylor 2005) and invertebrates (Grosholz & Ruiz 1996, Jensen et al. 2002), including juvenile decapod crustaceans (McDonald et al. 2001).

The majority of information available regarding the potential population-level impact of *C. maenas* in Atlantic North America comes from a recent caging experiment conducted in soft-bottom eelgrass beds in the Northumberland Straight, which involved 18 invertebrate taxa (Thompson 2007). In this study, *C. maenas* caused significant declines in the abundance of 4 species of gastropods and 2 species of polychaetes via predation, and 1 species of gastropod and 2 species of decapod via emigration (Thompson 2007. With its range expansion in eastern North America, *C. maenas* has likely become sympatric with many ecologically- and economically-important species, including the American lobster, *Homarus americanus*. Green crabs are known to inhabit both the rocky intertidal and shallow rocky subtidal zone to a depth of 5.5 m or greater (Crothers 1969, Aagaard et al. 1995, Lynch & Rochette 2007). Sub-adult lobsters are known to congregate in highly specific 'nursery areas' (Wahle & Steneck 1991), which are located in the shallow subtidal zone in areas comprised of cobble/gravel-based substrate (Hudon 1987, Wahle & Steneck 1991, 1992). The availability of nursery areas is suggested to be a demographic bottleneck to lobster recruitment because of the relative rarity of cobble habitat, which provides lobsters a better chance of avoiding predation (Wahle & Steneck, 1991). Therefore, increased competition or predation in these regions could significantly affect lobster abundance. Given these habitat requirements, spatial overlap between sub-adult lobsters and green crabs seems very likely, and the potential for interspecific interactions between these two species seems high. However, spatial overlap between native lobsters and invasive green crabs has never been quantified or documented *in situ*, despite the economic importance of the lobster fishery in eastern North America (Fisheries & Oceans, Canada, estimates landings were worth $684 million in Canada in 2005) and the potential threat green crabs pose to young lobsters.

American lobsters undergo a shift in shelter-seeking behavior during their ontogeny, which is probably related to vulnerability to predators (Wahle 1992). Juvenile lobsters (here referring to the combination of shelter-restricted, emergent, and vagile juveniles as described in Lawton & Lavalli (1995), carapace length [CL] ≈ 15-40mm) are particularly vulnerable to predation, primarily from fishes and crabs (Wahle & Steneck 1991). These lobsters spend most of their time sheltered under rocks, and are thought to only come out when food supply is low inside their shelters or when their perceived level of predation risk is low (Wahle 1992). Adolescent lobsters (CL ≈ 40-50mm) more frequently leave their shelters to forage (Lawton & Lavalli 1995), because, due to their size, they are less vulnerable to predators and they are probably not able to fulfill their nutritional requirements within their shelters (Wahle 1992). Adult lobsters (> 65 mm CL) are largely immune to predators; they spend much of their time unsheltered and they undergo long-distance migrations over open benthos (Cooper & Uzmann 1980, Lawton & Lavalli 1995). In this study we use the term "sub-adult" lobsters to refer to both juvenile and adolescent lobsters (total size range ≈15-50mm CL).

Little is known about intra- and inter-specific interactions involving sub-adult lobsters in nature (Spanier et al. 1998), but an understanding of these processes is important as sub-adult lobsters are believed to remain in nursery habitats until they reach sexual maturity, which can take 5 years or more (Cooper & Uzmann 1980). Recent short-term laboratory studies (ca. 1-6 hours) have suggested that green crabs may have the ability to outcompete sub-adult lobsters for food resources (Rossong et al. 2006, Williams et al. 2006), even when crabs are significantly smaller than lobsters (Rossong et al. 2006). Furthermore, in these lab experiments green crabs were observed to prey upon shelter-restricted sub-adult lobsters (Rossong et al., 2006), suggesting these crabs may also directly reduce survival of sub-adult lobsters in natural populations.

In my thesis I investigate the potential threat green crabs represent to lobster populations in areas where these species co-occur. There are three components to my study: (1) spatial overlap surveys to determine if, and to what extent, *C. maenas* and *H. americanus* overlap in a lobster nursery area in Passamaquoddy Bay, Bay of Fundy; (2) a 62-day laboratory experiment where sub-adult lobsters were held under resource-limited conditions (i) in isolation, (ii) with a conspecific, or (iii) with a green crab in order to determine whether the presence of green crabs affects lobster survival, mass increase, activity, feeding behaviour, or sheltering behaviour; (3) a 7-day laboratory experiment where sub-adult lobsters were housed with very large green crabs (> 50-mm carapace width) to determine if large crabs can affect survival of sub-adult lobsters. My study provides the first quantitative data on overlap between lobsters and green crabs in nature, and the first information about the effects of prolonged interaction (ca. two months) between sub-adult lobsters and green crabs. Such information constitutes a preliminary step in establishing whether management efforts are required to mitigate the impact of green crabs on lobster stocks, which support one of the most important fisheries on the Atlantic coast of North America.

3. Materials and Methods

After surveying eight locations in Passamaquoddy Bay, NB, using SCUBA diving, I identified lobster nursery areas at outer Birch Cove (45°08'66"N 67°01'86"W) and southern Minister's Island (45°05'40"N 67°02'04"W) (Fig. 1). These sites were both less than 7-m deep at low tide and comprised primarily of rocky cobble-based substrates in shallower areas and a combination of rocky cobble and gravel-mud substrates in deeper areas.

3.1 Field surveys: spatial overlap between *C. maenas* and *H. americanus*

In order to assess the extent of spatial overlap between *Carcinus maenas* and *Homarus americanus*, I established six transects parallel to the water line at outer Birch Cove. I set-up four 50-m transects (A, B, C, and D) in the subtidal zone and two 70-m transects in the intertidal zone (HI and LI). I deployed the deepest subtidal transect (A) 6.4-m below chart (zero) datum (average low low-tide), where it straddled the boundary between cobble-gravel based substrate and muddy-silt based substrate. I placed transects B and C in cobble-based substrate at depths of 2.4-m and 1.2-m below chart datum, respectively, and transect D at chart datum in similar substrate to transects B and C. I deployed intertidal transects 2.1-m (LI) and 2.3-m (HI) above chart datum among cobble-rock substrate that was densely covered in the intertidal alga *Ascophyllum nodosum*.

I surveyed transects monthly, near the beginning of each month, from August to November 2006. I surveyed subtidal transects using SCUBA by flipping all cobbles and movable rocks within 1-m of the seaward side of transects. Cobbles and rocks were carefully returned in their original position following inspection. This method has been shown to be equally effective as suction sampling protocols (which clear plots of all animals [Wahle & Incze 1997]), for locating lobsters above 10-mm carapace length (CL) (Wahle 1993). I recorded the position of each lobster along the transect (± 1-m) and classed them into one of three size classes based on a slightly-modified version of the classification scheme of Lawton and Lavalli (1995): juvenile lobsters (CL < 40-mm), adolescent lobsters (CL = 40-50-mm), or adult lobsters (CL > 50-mm). Due to the difficulty of catching these lobsters, gender determination and exact length measurements were not possible using my survey technique. However I categorized lobsters into size-classes by comparing lobster carapaces to a color coded (for different size classes) ruler which could be extended into burrows *in situ*. I caught all green crabs falling within the surveyed areas and measured carapace width to the nearest centimeter, and recorded their gender and position along the transect. I sampled intertidal transects using 1-m x 1-m quadrats that I deployed at every fourth meter along the 70-m transects. I placed quadrates on the seaward side of transects and rigorously searched all *A. nodosum* and cobbles for crabs and lobsters (though no intertidal lobsters were observed). Intertidal transects were all surveyed at low tide whereas subtidal transects were not. I used different methodology to assess lobster and crab density along intertidal and subtidal transects for logistic reasons. Intertidal areas are densely covered in *A. nodosum* making rigorous searching along the entire transect impossible during one low tide. In addition, subtidal transects could not always be surveyed at low tide due to logistic constraints imposed by diving (i.e. boat access, diver time, weather, etc.). However, I believe the data collected using these different techniques is comparable.

3.2 Experiment 1: effects of prolonged interaction between sub-adult lobsters and *C. maenas* in the laboratory

To determine if green crabs affect survival, mass change, sheltering behaviour, feeding behaviour or activity levels of sub-adult lobsters, I collected sub-adult lobsters (CL 16 - 48-mm) and adult green crabs (CW 33 - 70-mm) by SCUBA from southern Minister's Island. I transported these animals in coolers to holding facilities at the Huntsman Marine Science Centre, in St. Andrews, NB, Canada. I placed 50 lobsters (hereafter referred to as focal lobsters) into individual 56.7 L (61.44 cm x 31.43 cm x 30.96 cm) aquaria with approximately 3-cm of cobble/gravel substrate and one shelter (10-cm diameter x 20-cm length PVC pipe, cut lengthwise [adapted from Wahle, 1992]); the containers were supplied with filtered flow-through seawater throughout the experiment. I held 20 other lobsters (secondary lobsters) in four 710-L round tanks, which were fed with constant flow-through seawater and contained many shelters and cobbles (densities in these tanks were low, to prevent lobsters from harming one another). Crabs (≈ 50) were held in similar 710-L round tanks until needed. I maintained all aquaria under a 14-hour light photoperiod with water temperature between 11 and 14°C throughout the experimental period.

I allowed focal lobsters to acclimate and build burrows for 12 days, after which time I recorded their gender, carapace length (using digital calipers, ± 0.01-mm) and submerged mass (± 0.1-g). I randomly assigned each of the 50 focal lobsters to one of three treatment groups: (i) lobster-crab treatment: one green crab of similar submerged mass as the focal lobster was added to each of these aquaria (n = 20); (ii) two-lobster treatment: a second lobster of similar submerged mass was added to each of these aquaria (n = 15), (iii) solitary lobster treatment: no crab or lobster was added to these tanks (n = 15). I decided to have more replicates of the lobster-crab treatment group (20 replicates vs. 15 replicates for the solitary and two-lobster treatments), as it was the one in which I was most interested and I was anticipating lobster mortality. Initially, I observed some mortality in my two-lobster treatment group, so on day three I added one extra shelter to these tanks in an attempt to prevent further mortalities. This approach worked well and allowed us to retain this treatment group, however I still lost 2 replicates of this treatment due to death of focal lobsters (n=13 rather than 15). I held animals under these conditions for a total of 62 days, from September 28, 2006, until November 29, 2006. I fed animals 3 to 4-g rations of either hake (*Merluccius bilinearis*) or blue mussel (*Mytilus edulis*) flesh twice a week during the dark portion of the photoperiod, as lobsters and crabs are known to be more active during these times (Naylor 1958, Jury et al. 2005).

I filmed each tank once during the experiment (order determined at random) for one hour starting immediately before food was introduced (see also Williams 2006), using a dim red light to permit adequate conditions for video. I used these videos to quantify which animals fed, time spent feeding, time sheltering, and time active (i.e., out of shelter) for all 50 focal lobsters. Two videos were unfocussed and no data could be gathered from them; both videos were from solitary lobster tanks reducing the number of replicates for this treatment from 15 to 13 (only for the video data). In addition, to monitor the activity of each lobster throughout the 62-d experimental period, I performed bi-weekly 'spot-checks' of focal lobster activity (classified as sheltering vs. active), once during the daytime and once at night.

I monitored tanks daily for mortalities and/or moulting and any uneaten food was removed the day after feeding. I replaced all crabs (n = 36) and secondary lobsters (n = 8, though one focal lobster was responsible for 3 of these) that were killed by focal lobsters, immediately upon observation. I had collected replacement animals at the same time as experimental animals (see above). I observed a higher than expected mortality rate for crabs, which made 'size matching' increasingly difficult as the experiment progressed. In three cases very large crabs were placed with relatively small sub-adult lobsters. Interestingly, this did not affect survival of the focal lobster, but may have offered the crabs a better probability of survival. I ended the experiment after 62 days by measuring and weighing all animals using the same methods as I employed at the start of the experiment.

3.3. Experiment 2: effects of large *C. maenas* on survival of sub-adult lobsters

I designed a second lab experiment to determine whether very large green crabs (CW 53-78-mm) would kill sub-adult lobsters (much smaller than the crabs) under conditions where potential for interspecific interaction was heightened. In this experiment green crabs were on average 3.8 (± 0.6 SE; range = 0.5-13.3) times larger (blotted mass) than lobsters. I collected sub-adult lobsters of similar size as in the first experiment (CL 17 - 48-mm) via SCUBA from the Minister's Island lobster nursery area, and large green crabs using SCUBA from the Minister's Island site and by hand from the intertidal zone at Indian Point, St. Andrews, NB (45°04'14"N 67°02'36"W). Animals were transported to a wet-laboratory facility at University of New Brunswick Saint John where they were held in individual 3-L tanks, which were fed with recirculating seawater. After 1-week of starvation, lobsters were measured (CL) and weighed (blotted mass), their gender was recorded, and they were then transferred into 37.9-L (50.8 cm x 30.48 cm x 25.4 cm) experimental tanks. Experimental tanks contained cobble-gravel substrate and one PVC shelter (as described above), and were held at 12°C on a 14-hour (10 hour dark) photoperiod. Lobsters were allowed to acclimate and build burrows for one hour. After this acclimation period an individual crab, which had been previously measured and weighed, was placed into each experimental tank. I monitored mortality of lobsters and crabs daily over a 7-day period. Animals were not fed during the experiment. After 3 days, the shelter and 75% of the gravel were removed from tanks, to reduce sheltering opportunity and promote predation. This experiment ran in two 7-day blocks; block I and block II had 15 and 16 replicate tanks, respectively.

3.4 Analyses

Distribution of lobsters and green crabs

I used a Monte-Carlo randomization to determine if lobsters and crabs on my transects were more aggregated or segregated, relative to one another, than I would predict based on a random distribution of both species. I first determined the distance between each lobster (or crab) and the nearest member of the other species, on the same transect, using positional data recorded during the dive surveys. This gave a mean observed nearest heterospecific-neighbor distance for lobsters and crabs on a given transect. I then randomized the position of each crab and each lobster along the same transect, randomly allocating each individual to 1 of the 50 positions on the transect (every 1-m, animals could occupy the same position along the transects as in nature), and recalculated this nearest neighbor distance for all animals. I performed 10,000 iterations of this randomization procedure and compared my mean observed nearest heterospecific distance to the theoretical distribution of mean nearest-neighbor values obtained by randomization. I repeated this procedure separately for each survey period and transect where both lobsters and green crabs were observed.

Survival of focal lobsters in experiment 1

I used a Chi-Square contingency table analysis to determine if survival of focal lobsters was independent of treatment group (solitary lobster, two-lobster, lobster-crab). More than 20% of the expected values calculated in this test were less than 5, which violates an assumption of this Chi-square statistical test. Therefore, I performed a randomization test to validate results obtained with the Chi-square contingency analysis.

In this second test, I randomized the observed values of lobster survival (yes or no) among lobsters of the different treatment groups, and then estimated the Chi-square statistic of the randomized data; I performed 10,000 iterations of this randomization procedure, and then compared the Chi-square value I observed to those obtained during the 10,000 randomized iterations.

Mass increment of focal lobsters in experiment 1

I used a 2-way factorial analysis of covariance to determine if change in submerged mass of focal lobsters over the course of the experiment (submerged mass at end of the experiment – initial submerged mass) was affected by treatment group (solitary lobster, two-lobster, lobster-crab) or lobster gender. Initial carapace length was necessary as a covariate as overall change in submerged mass significantly varied with size of focal lobsters. Assumptions of normality and homoscedasticity were both met ($W = 0.987$, $p = 0.9314$; $F_{7,41} = 1.353$, $p = 0.251$).

Activity of focal lobsters over the course of the experiment 1

In order to determine if the activity (active or sheltered) of focal lobsters, as determined in my bi-weekly ‘spot-checks’, was affected by treatment group (solitary lobster, two-lobster, lobster-crab) or time of observation (day vs. night), I first used a Cochran-Mantel-Haenszel (CMH) test to justify pooling all activity scores obtained on different days (n=13) for a given focal lobster at day or night (I used time of observation as a stratification factor). I did not find lobster activity to be significantly affected by observation date in either of the three treatments groups (CMH test: solitary lobster treatment, $\chi^2 = 7.86$, df = 12, $p = 0.796$; lobster-lobster treatment, $\chi^2 = 9.25$, df = 12, p =

0.681; lobster-crab treatment, $\chi^2 = 20.86$, df = 12, p = 0.0525). In my lobster-crab treatment the activity of focal lobsters was nearly significant, however, inspection of the data revealed that two observation dates drove this result rather than a gradual increase or decrease of activity over the course of the experiment. I therefore decided to pool data across observation dates, and used a non-parametric two-factor analysis of variance (ANOVA) to determine if treatment group or time (day/night) affected the proportion of times focal lobsters were found active. I used a non-parametric analysis because the normality assumption was violated (W = 0.955, p = 0.0237) and the assumption of homoscedasticity was just upheld ($F_{5,72} = 1.964$, p = 0.0943).

Activity of focal lobster after being offered food

I used a Chi-Square contingency table analysis to determine if the number of focal lobsters that fed in the 1-hour period following addition of food to their aquarium (data gathered from video) was independent of treatment group (solitary lobster, two-lobster, lobster-crab). I then used the non-parametric Kruskal-Wallace test to determine if treatment group significantly affected (i) the proportion of time focal lobsters spent feeding (I excluded lobsters that did not feed from this analysis), and (ii) the proportion of time a focal lobster spent sheltering in the same videos. I used a non-parametric test for both of these analyses because the data violated the homoscedasticity assumption. Body size (submerged mass or carapace length) was not a significant covariate for either of these analyses.

Effect of body size on crab susceptibility to predation

I used logistic regression to determine whether the relative size of crabs and lobsters (crab submerged mass/lobster submerged mass) affected the probability of crab survival. Because several of the experimental lobsters killed multiple crabs, data points involved in this analysis were not all independent. To determine if this model violation affected the outcome of my analysis, I ran this analysis again using only the first crab paired with each lobster (independent data points).

Effects of large *C. maenas* on survival of sub-adult lobsters

I pooled data from the two blocks and used Fisher's exact test to determine if survival was independent of species.

4. Results

4.1 Spatial overlap

The spatial distribution of juvenile (15-40-mm CL), adolescent (40-50-mm CL) and adult (> 50-mm CL) lobsters overlapped with that of green crabs in each of the four months in which I conducted surveys at my outer Birch Cove site (Fig. 2). This overlap was evident for all size-classes of lobsters on transects B, C and D, which were at depths ranging from 2.4 m to chart datum (0-m), but was most pronounced between green crabs and juvenile lobsters on transect D (0-m). A single green crab was observed on transect A (6.4-m depth) during any of the four monthly surveys (September), and no lobsters were found on either intertidal transects throughout the survey period. During my SCUBA surveys, I commonly observed lobsters and crabs within less than 2-m of one another. The mean observed nearest neighbor distance for a given transect and month varied from approximately 0.5-m for the most-densely populated transects to 20-m for the less-densely populated transects, and these values were generally similar for lobsters and crabs (Table 1). The Monte-Carlo randomization revealed very little evidence of aggregation or segregation between lobsters and crabs (and vice versa) along transects in either of the four months surveyed; the two species appeared to be randomly distributed relative to one another (Table 1).

Green crab density was highest in the intertidal zone and generally decreased with depth; it was highest in August and September, and then decreased in October and again in November, probably because green crabs moved offshore during colder months (Atkinson & Parsons 1973) or perhaps buried themselves in the substrate at this time. In the shallower parts of the subtidal zone (transect D), green crabs were found in greater densities than lobsters (2 to 5 times more crabs in different months). The deeper I surveyed, the more lobsters I found relative to crabs; transect C had 0.8 to 2.67 times more crabs than lobsters in different months, transect B had 0.43 to 2 times more crabs, and transect A had 0.33 times more crabs than lobsters (only 1 crab found). Green crabs found in the intertidal zone were generally slightly smaller than those found in the subtidal zone (Fig. 3). In general, on my deeper surveys (transects B and A) I would find a small number of crabs, most of which were large (> 40-mm CW), and on shallow surveys (transect and C and D) I would find a much greater number of crabs, most of which were smaller (< 40-mm CW) (Fig. 3).

The spatial distribution of similar-sized lobsters was relatively consistent over the four months surveyed, but it did vary somewhat among transects (Fig. 2). Juvenile lobsters were found at their highest density near chart datum (transect D), and then declined in abundance in deeper areas (Fig. 2). Adolescent and adult lobsters were found at much lower densities, and generally somewhat deeper (transects C and B), than juveniles (Fig. 2). Based on these surveys, greatest spatial overlap occurred between green crabs and juvenile lobsters on the two shallowest subtidal transects, between 0 and 1.2 m below datum (Fig. 2). Within this area (transects D and C), the ratio of green crabs to sub-adult lobsters (juveniles + adolescents) was 3.10 in August, 1.92 in September, 2.67 in October and 0.75 in November.

4.2 Experiment 1

Mortality of focal lobsters during the 62-d lab experiment was not significantly affected by treatment group ($\chi^2 = 4.861$, df = 2, p = 0.088); 13.3% of focal lobsters were killed in the two-lobster group, but all those from the solitary-lobster group as well as the lobster-crab group survived. As assumptions of the above test were violated, I verified my results using a randomization procedure (10000 iterations), which indicated that the probability of obtaining the observed chi-square value, or something greater, under the null hypothesis of no effect of treatment group was 0.186; therefore I cannot conclude these results are not due to randomness. Most importantly, not a single lobster was killed by green crabs during this 62-d experiment.

The non-parametric two-factor analysis of bi-weekly spot-checks of lobster activity over the course of the 62-d experiment showed that activity of focal lobsters differed significantly among treatment groups ($H = 24.38$, $df = 1$, $p < 0.0001$), both during the day and at night (interaction between sampling time and treatment group was not significant: $H = 2.06$, $df = 2$, $p = 0.358$) (Fig. 4). It appeared that focal lobsters in the two-lobster group were more active than conspecifics in either the solitary-lobster or lobster-crab treatment groups (Fig. 4). Focal lobsters were also more active at night than at daytime in all treatments groups ($H = 7.56$, $df = 1$, $p = 0.0060$; Fig. 4).

The analysis of videos revealed that the number of lobsters that fed in the 1-h period following addition of food to the aquaria was independent of treatment group ($\chi^2 = 1.485$, $df = 2$, $p = 0.476$); 30.0% (6/20) of focal lobsters held with crabs fed, compared to 46.2 % (6/13) and 30.8% (4/13) for lobsters held alone or with conspecifics, respectively. When I considered only lobsters that did feed (Fig. 5), the proportion of time spent feeding was similarly independent of treatment group (Kruskal-Wallace $\chi^2 = 1.000$, $df = 2$, $p = 0.607$). The proportion of time focal lobsters spent sheltering during this 1-h period was also not significantly affected by treatment group (Kruskal-Wallace $\chi^2 = 2.708$, df = 2, p = 0.258) (Fig. 5).

Change in lobster submerged mass significantly, and positively, co-varied with the initial carapace length of the lobsters ($F_{1,35} = 4.353$, p = 0.0443) (Fig. 6). However, treatment group did not have a significant effect on change in submerged mass over the experimental period ($F_{2,35} = 0.838$, p = 0.441), and there were no significant interactions between the covariate and any of the main effects ($P > 0.6$ in all cases). Similarly, neither gender nor the interaction between gender and treatment were significant (p = 0.220 & 0.897, respectively).

A total of 36 crabs were killed in the 62-d experiment by 11 different lobsters; 9 focal lobsters did not kill their crab aquarium-mate. Size ratio (crab submerged mass/lobster submerged mass) had a significant effect on the probability of crabs surviving (Loglikelihood $\chi^2 = 12.56$, df = 1, p = 0.0004); the larger the crab was relative to the lobster, the greater its probability of survival (Fig. 7). As multiple crabs were killed by single lobsters, this analysis violated the data independence assumption. When I repeated this analysis but only considered the first crab held with each lobster I obtained similar results: size ratio had a significant effect on the probability of crabs surviving (Loglikelihood $\chi^2 = 5.28$, df = 1, p = 0.0215). I then repeated the whole-dataset analysis using lobster submerged mass and again using crab submerged mass as independent variables (instead of size ratio) to determine if either of these affected crab survival on their own. Given the sizes of lobsters and crabs paired in this experiment, lobster submerged mass did have a significant effect on the probability of crab survival

(Loglikelihood χ^2 = 14.04, df = 1, p = 0.0002), but crab submerged mass did not (Loglikelihood χ^2 = 0.982, df = 1, p = 0.322).

4.3 Experiment 2

A total of 4 crabs and 1 lobster were killed during the 7-day experiment (87.1% crab survival, 96.8% lobster survival). Although more crabs were killed than lobsters, survival was statistically independent of species (Fisher's Exact Test, p = 0.354). The one lobster that was killed was one of the smallest lobsters used in either lab experiment (CL = 18.8-mm, blotted mass = 5.5 g), weighing only 0.11 times the crab that killed it. The four large crabs (CW = 56-67-mm, blotted mass = 48-68 g) were killed by four of the largest lobsters (CL = 44-48-mm, blotted mass = 72-90 g), and weighed between 0.51-0.92 times the lobster that killed them. Removal of shelters and 75% of the substrate did not seem to enhance interaction between green crabs and lobsters, as I suspected it would have. Only one lobster was killed during this experiment, and although this mortality occurred after the shelter had been removed, it is unclear whether the death was due to enhanced interaction due to shelter removal or simply the fact that this lobster was extremely small and housed with a crab ten times it's mass.

5. Discussion

The spatial distributions of both sub-adult and adult *H. americanus* overlap significantly with that of *C. maenas* at my main study site, particularly in the shallower parts of the subtidal zone (between chart datum and 2.4-m) where the substrate is composed of cobble and gravel. The strongest overlap occurred between juvenile lobsters (< 40-mm CL) and adult green crabs (> 20-mm CW). I observed, but did not quantify, similar patterns of lobster and green crab distribution at my southern Minister's Island collection site in Passamaquoddy Bay, and Williams et al. (2006) similarly suggest that overlap between these species occurs in Nova Scotian waters, based on fishermans' catches as well as trapping surveys. Though my study has only quantified overlap between these crustaceans at one site, I believe these patterns would likely be similar wherever these two species are sympatric. To my knowledge this is the first time spatial overlap has been quantified between *H. americanus* and *C. maenas*, which is a necessary first step in assessing whether invading green crabs have the potential to cause declines in lobster abundances as they have for other benthic invertebrate populations (Grosholz & Ruiz 1996, Grosholz et al. 2000, Thompson 2007).

Juvenile and adolescent lobsters were most abundant on transects from chart datum to 1.2-m below. In this area I found between 0.068 and 0.093 lobsters/m^2, and 0.123 to 0.345 green crabs/m^2; on average (across months), green crabs were 1.86-3.72 times more abundant than lobsters on the three transects in this area. My nearest neighbor analysis showed that lobsters were between 0.56-m and 20.00-m (mean = 5.17-m) away from the nearest green crab along the same transect at any given time; the great range in nearest neighbor values is largely owed to variation in the number of crabs and lobsters found on a particular transect and time. This analysis also revealed very little evidence of aggregation or segregation between lobsters and crabs (or vice versa). The nearest neighbor data suggests that lobsters and crabs almost certainly encounter each other regularly in areas of strongest overlap, as on high-density transects these animals occur very near each other. Nearest-neighbor values in the range of one to several meters were not only common, they almost certainly underestimate real nearest neighbor values, because only animals within a 1-m wide corridor were surveyed.

In these shallow subtidal areas with high abundance of lobsters and crabs, these species undoubtedly utilize similar shelter and food resources. Green crabs are extremely mobile, sometimes moving upwards of 300-m during one tidal cycle (Dare & Edwards 1981). Conversely, sub-adult lobsters are thought to remain in shelters within nursery habitats (Wahle 1992). Given the mobility of crabs and the overlapping habitat requirements, random encounters between these species in nature seem inevitable. Slightly deeper, at 2.4-m, density of green crabs and lobsters decreased, and lobsters were as abundant as crabs (1.08:1 lobsters to crab). My deepest transect (6.4 m) was on the boundary between the cobble-gravel habitat and the mud-silt habitat, and was effectively the border of the nursery area. Predictably, lobsters and green crabs were found in much lower densities on this transect; I only found 1 green crab and 3 adult lobsters during the four monthly surveys of the deepest transect.

As these species overlap in lobster nursery areas, the potential for competition seems high. At the densities of lobsters and crabs I observed, it is likely that food items in the nursery area would be first encountered and consumed by a green crab, because they are at higher densities and are often roaming over open benthos during the day and at night (Lynch & Rochette 2007) compared to sub-adult lobsters, which are associated with shelters during these life stages (Wahle 1992, Lawton and Lavalli 1995). If food is a limiting resource in lobster nursery areas, then green crabs may reduce lobster access to food simply by encountering and consuming it first, regardless of relative competitive abilities of green crabs and lobsters. Therefore, green crabs may have indirect negative effects on lobster growth and perhaps survival, as there is considerable dietary overlap between green crabs and juvenile lobsters [see Lawton and Lavalli (1995) for review of sub-adult lobster diet and Elner (1981) for description of crab diet].

I observed no predation by adult green crabs on sub-adult lobsters in my first lab experiment, where lobsters were held for 62 days with crabs of roughly similar body mass. Furthermore, I observed only a single lobster mortality during the second lab experiment, where lobsters were held for 7 days with crabs much heavier then themselves; the single mortality I observed was of an extremely small lobster (5.5 g), which was consumed by a crab that was over ten times its mass. In this second experiment, a sub-adult lobster was held in a 37.9 L tank with a very large starved crab for 7 days and on day 4 all refugia and most substrate was removed to promote predation (by limiting natural defenses such as avoidance, escape, and sheltering behaviour). These results suggest that there is little threat to sub-adult lobsters from green crabs, as my set-up promoted interaction. Based on these results, I have next to no evidence that green crabs would prey upon lobsters of this size range in nature. This is particularly true considering my laboratory experiments likely enhanced, and probably very much so, opportunities for green crabs to prey upon lobsters, first by having the two species in such close proximity to one another, and secondly by limiting the lobster's ability to escape attacks by fleeing the area. If adult green crabs prey on sub-adult lobsters in nature, I would have expected to see numerous predation events under my artificial lab conditions; this was not the case. My results are contrary to recent literature where sub-adult lobsters were consumed by green crabs in over 50% of trials (Rossong et al. 2006). However, my results are consistent with a stomach content identification study of wild-caught green crabs in Nova Scotia, where no lobster remains were found in over 300 crab stomachs; although lobsters were present at sites where crabs were collected (Elner 1981).

Predation by conspecifics appears to be more of a threat to sub-adult lobsters than is predation by green crabs (13.3% of focal lobsters were killed when housed with a conspecific, compared to zero mortality caused by crabs in the same experiment, even though the two-lobster aquaria contained 2 shelters). Reduced survival in the two-lobster treatment was expected, as there are many studies documenting agonistic interactions between lobsters (Karavanich & Atema 1993, Cromarty et al. 1999), and lobsters are likely more spaced in nature than they were in my laboratory set-up. Although many studies have documented violent agonistic interactions between lobsters in lab settings, it is unclear how important these interactions are in nature, as field studies on agonistic interaction between juveniles have not yet been conducted (Rutishauser et al. 2004).

Lobsters possess well-developed chemosensory capabilities, and they have been shown to increase use of shelter and also forgo foraging opportunities in the presence of predator chemical cues (Wahle 1992); there are studies suggesting that sub-adult lobsters are susceptible to predation and competitive interactions with invasive crabs such as *Hemigrapsus sanguineus* (Demeo & Riley 2006) and *Carcinus maenas* (Rossong et al. 2006, Williams et al. 2006). However, I found no evidence that green crabs affect the behavior of sub-adult lobsters, even though food was often (although not always) completely consumed in the 12-16 hour feeding period. In my study green crabs had no impact on the propensity of sub-adult lobsters to approach food, consume food, or utilize shelters. My mass-increment data corroborate my behavioural observations; I found no difference in submerged mass change between lobsters held with or without crabs over the duration of my longer lab experiment. If crabs had out-competed lobsters for food resources, or caused them to increase their use of shelter due to perceived threat, then I would have expected to observe smaller mass increments in lobsters housed with crabs than in solitary conspecifics. This was not the case; in fact, 5 of the 6 largest mass increments were for lobsters housed with green crabs (the 6th was for a lobster housed with a conspecific), perhaps because these often consumed green crabs. Taken together, my behavioral and mass increment data strongly suggest that sub-adult lobsters did not perceive green crabs as a predation threat, and it does not seem that their access to nearby food or shelter was compromised by the presence of green crabs.

Interestingly, in my study both juvenile and adolescent lobsters regularly fed upon adult green crabs: 36 green crabs were killed by lobsters, and were either fully (only carapace debris remained) or partially (carapace debris and some flesh remaining) consumed. This apparent predator-prey relationship was most noticeable in trials where the lobster was larger than the crab. As the size ratio of crabs to lobsters increased, the probability of crab survival increased. However, this relation appeared driven more by the size of the lobster than that of the crab, as crab survival was negatively correlated with lobster size, but was independent of crab size. That larger lobsters were more likely to kill green crabs suggests they have a higher tendency to attack, and/or are more successful when they do, as compared to smaller conspecifics. It is difficult to elucidate which of these factors drives the relationship between lobster size and crab survival because, to my knowledge, no studies examining predation efficacy or aggression of sub-adult lobsters exist. My experiment indicates that lobsters pose a significant threat to green crabs which, though unsupported by other studies on lobster-green crab interaction (Rossong et al. 2006, Williams et al. 2006), could be predicted based on the tendency for lobsters to feed upon other decapods (Cooper & Uzmann 1980, Lawton & Lavalli 1995), including brachyuran crabs (Gendron et al. 2001). In addition, other decapods often dominate green crabs during agonistic interactions in both the field and the laboratory (Lohrer & Whitlatch 2002, DeRivera et al. 2005). For example, Blue crabs (Callinectes sapidus) are suggested to limit the distribution of green crabs as Blue crabs readily prey on *C. maenas* in both field and laboratory experiments (DeRivera et al. 2005). Furthermore, the invasive Asian shore crab, *Hemigrapsus sanguineus*, also preys upon juvenile and adult *C. maenas* and have been suggested to potentially cause declines in green crab abundance (Lohrer & Whitlatch 2002). Given the density of green crabs in the nursery area I surveyed and the evidence suggesting green crabs are often dominated by other decapods, green crabs could provide an abundant and very high-quality prey item to lobsters, as other species of brachyuran crabs are among the most nutrient-rich and preferred prey of lobsters (Gendron et al. 2001).

In previous studies, green crabs were more often in control of food, able to displace lobsters from food, and although they did not out-compete lobster for shelter, they often preyed upon the lobsters during shelter trials (Rossong et al. 2006, Williams et al. 2006). Although I am unsure why my results differ so markedly from previously published work, there are a number of potential explanations for these differences. For example, the geographic origin of the animals used, in particular whether experimental animals co-existed with the other species where they were collected in nature, might explain some of the observed differences. In previous studies, allopatric animals were used, whereas the animals used in my study had been sympatric for at least 55 years (Audet et al. 2003). This co-existence between heterospecific crustaceans may be important on both evolutionary and ecological timescales. First, on an evolutionary level, natural selection over the past 55 years of sympatry between *H. americanus* and *C. maenas* in Passamaquoddy Bay, NB, may have selected for lobsters that are behaviourally adapted to surviving amongst green crabs. However, such local adaptations to a non-ubiquitous invasive seem unlikely considering the short time-period involved and the highly-dispersed larvae of lobster (Lawton & Lavalli 1995); larval supply to nursery areas where green crabs occur could probably be provided from sites without green crabs. Interaction over an ecological timescale, and in particular previous experience with green crabs during a lobster's lifespan is probably more important. Lobsters have the ability to recognize individuals (Karavanich & Atema 1998) and change their sensitivity to certain prey types when repeatedly exposed to them (Derby & Atema 1981). Sub-adult lobsters can also detect chemical cues from predators and are known to decrease their susceptibility to predation in the presence of predators by increasing shelter use (Wahle 1992) and reducing foraging time and food consumption (Spanier et al. 1998). Lobsters exposed to green crabs in nature may learn to recognize green crabs as a predator and modify their behaviour to reduce susceptibility. This process is known to occur in other malacostracan crustaceans; crayfish exposed to goldfish predator cues will learn to recognize them and decrease their vulnerability to predation by reducing feeding and locomotion behaviours (Acquistapace et al. 2003). Lobsters naïve to green crabs may be unprepared to be housed with green crabs, which are omnivorous (Elner 1981), and aggressive towards other crustaceans (McDonald et al. 2001, Jensen et al. 2002, Rossong et al. 2006). In addition, green crabs naïve to lobsters may not perceive lobsters as a predation threat and may be more willing to attack a lobster.

In addition to geographic origin, methodological differences and/or differences in experimental conditions may also have caused the marked discrepancies between my study and previously published work on lobster-green crab interaction. For example, water temperature differed between my study and earlier ones, and is known to drastically affect the behaviour of both lobsters and green crabs (Naylor 1963, Atkinson & Parsons 1973, Crossin et al. 1998). Whereas lower temperatures generally result in overall reductions in activity in both species (Naylor 1963, Atkinson & Parsons 1973, Crossin et al. 1998), "threshold temperatures" different between them. In lobsters, little molting, growth, locomotion or feeding are thought to occur at or below 10 °C (Aitken & Waddy 1986, McLeese & Wilder 1958; as cited in Crossin et al. 1998), however, in green crabs similar reductions in activity are generally not seen until temperatures dip below 7 °C (Ropes, 1972). In my study water temperature was always above 11.5 °C, whereas studies by Williams and colleagues (2006) as well as Rossong and colleagues (2006) were conducted at 10 °C. Therefore, in these earlier studies (but not in mine) the activity of lobsters may have been affected more strongly by water temperature than that of green crabs. Furthermore, in my experience, lobsters will not feed within hours, and at times days, of being added to a new experimental aquarium, whereas crabs will often feed directly after handling. I posit that the acclimation time used in these earlier studies (15 minutes) was insufficient to promote lobster feeding, and may have markedly affected results obtained. Lastly, sub-adult lobsters are central placed foragers (Wahle 1992, Lawton & Lavalli 1995), and will normally bring back food to their borrows to consume it. However, in the earlier studies mentioned above, the bait was anchored, preventing lobsters from bringing it back to their burrow, which may have reduced their willingness to feed. In regards to this latter point, it is also noteworthy that neither of these earlier studies had a control to show that lobsters would in fact feed under their experimental conditions, even in the absence of a green crab. I suggest these ecologically-relevant (temperature) and non-relevant (acclimation/stress, anchoring of food) experimental differences could have contributed to differences between our results and those of earlier studies.

5.1 Conclusion

Historically, invasive species have almost always been thought of as a problem, and today they are considered one of the greatest threats to biodiversity and community structure in the world (Mack et al. 2000). Perhaps not surprisingly, the majority of studies on invasive species focus on their negative impacts on native organisms, usually via competition and predation (Mack et al. 2000, Rodriguez 2006). However, there is considerable evidence that many invasives actually facilitate natives in a variety of ways including habitat modification, trophic subsidy, and competition and predation release (reviewed in Rodriguez 2006). My study demonstrates that invasive green crabs may not always have negative impacts on native organisms, as they may provide additional high-quality prey items to sub-adult lobsters; this new prey might enhance lobster survival, as other species of brachyuran crabs are among the most nutrient-rich and preferred prey of lobsters (Gendron et al. 2001). While my results contradict some recent literature, I believe that results of these earlier studies should be interpreted with caution, as they were based on allopatric populations of lobsters and crabs and are potentially methodologically flawed. My results strongly suggest that green crabs pose little direct threat to sub-adult lobsters in the long term. If there is any predation on lobsters by green crabs in nature, it is probably upon newly settled lobster post-larvae, which are extremely vulnerable to predation and likely occur in the same habitats as green crabs (Lawton and Lavalli 1995). Presumably, indirect effects of green crabs may reduce availability of prey items to lobsters, but this has not been documented. Future research should be directed at the effects of green crabs on newly settled post-larval lobsters through predation or exploitation of food and/or shelter resources. Also, the results of laboratory studies can often misrepresent what actually goes on in nature, and I therefore recommend broader-scale *in situ* studies of the interactions between these species to determine if these results are upheld in the field.

6. General Conclusions

My results indicate that while spatial overlap does occur between sub-adult lobsters, adult lobsters, and adult green crabs in nature, the presence of green crabs in a laboratory setting has little to no effect on the mass change, survival or behaviour of sub-adult lobsters. While these results contradict some recent literature, I believe that previous studies are potentially biased methodologically as well as in their use of allopatric lobsters and crabs, and that my results suggest that green crabs pose little direct threat to sub-adult lobsters in the long term. However, the results of laboratory studies can often misrepresent what actually happens in nature. Therefore, I recommend broader-scale *in situ* studies of the interactions between these species to determine if my results are upheld in the field.

6.1 Effects of *C. maenas* at colonization

There is likely some limited threat to sub-adult lobsters from green crabs, though perhaps mainly when the green crabs first colonize a new area. At the time of invasion, sub-adult lobsters would not have habituated (through learning a new threat/food item) or adapted (through selection) to the presence of a new aggressive decapod. Therefore sub-adult lobsters may be somewhat vulnerable to green crab predation in the early stages of an invasion. This added predation pressure upon colonization may be able to reduce lobster growth and/or survival in the short-term, however there seems to be very little ‘post-invasion’ threat to sub-adult lobsters from green crabs.

6.2 Effects of *C. maenas* on post-larval lobsters

If there is significant 'post-invasion' predation on lobsters by green crabs in nature, it would likely be upon newly settled lobster post-larvae (< 15-mm), which are extremely vulnerable to predation (reviewed in Lawton and Lavalli 1995). Lobster larvae are pelagic for 6-8 weeks until they settle (Ennis 1995), and the substrate-type where they settle affects their survivorship and hence, the number reaching adulthood (Ennis 1995). Lobster larvae preferentially settle on substrate with crevices and/or cover and will postpone settlement if suitable habitat is not available (Ennis 1995). Survival of post-larval lobsters is enhanced when lobsters settle amongst complex substrate because their vulnerability to predation is reduced (reviewed in Ennis 1995). Post-settlement lobsters are consumed by a number of predators, the majority of which are crabs and fishes (Lawton & Lavalli 1995). In settlement areas where green crabs are present, they are probably a major predator of post-settlement lobsters as these crabs are known to prey upon newly settled benthic decapods (McDonald et al. 2001). It is extremely important to understand what effects green crabs might have upon newly settled lobsters, from both an ecological and a fisheries point of view. Ecologically, lobsters are among the major benthic predators in Atlantic Canada (Lawton & Lavalli 1995). Reduced survival of lobsters in this region could release their prey species (primarily bivalves, decapods, echinoderms and polychaetes [Lawton & Lavalli 1995]) from predation, subsequently increasing their abundances and causing a cascade of indirect community-level effects. These types of community effects are illustrated well by sea otters and urchins on the west coast of Vancouver Island. When sea otters (predominant urchin predator) were removed from coastal BC via the fur trade industry, sea urchins were released from otter predation (Breen et al. 1982). This caused drastic increases in urchin populations, which in turn increased the grazing pressure on kelps and seaweeds. The overall result was a shift from a 'kelp-forest' ecosystem home to numerous fishes and invertebrates to an 'urchin-barrens' ecosystem where there were many urchins, no seaweeds and very few fishes (Estes & Duggins 1995). From a fisheries point of view, predation of green crabs on newly settled lobsters is also important. It is possible that reduced survival in post-settlement life stages are reflected in the amount of lobsters recruiting to the fishery. However, this is uncertain as it has historically proven very difficult to identify the factors directly affecting recruitment to the American lobster fishery (Incze et al. 2003). Since this is the most economically important fishery in Canada, it is extremely important to understand how the green crab invasion might be affecting this industry, which is valued annually at $684 million in landings in Canada alone (Fisheries and Oceans Canada, Statistical Services 2005). There is a need for both laboratory and field studies to investigate the predatory threat that green crabs pose to post-settlement lobsters.

6.3 Indirect effects of *C. maenas* on *H. americanus*

It is very likely that indirect effects of green crabs may reduce availability of prey items to lobsters, although this has not been documented. In the lobster nursery area I surveyed, green crabs were 1.8 to 3 times more abundant than lobsters in the areas of strongest overlap between the two species. At these densities food items in a lobster nursery area would probably be first encountered by a green crab and not by a lobster, because green crabs are at higher densities and are more often roaming over open benthos during the day and at night (Lynch & Rochette 2007) compared to sub-adult lobsters, which are associated with shelters during these life stages (Wahle 1992, Lawton and

Lavalli 1995). If food is a limiting resource in lobster nursery areas, then the capacity for green crabs to consume food before lobsters would reduce the available food to lobsters, regardless of the relative competitive abilities of these species. The exploitation of lobster food items by green crabs could significantly affect both survival and growth of sub-adult lobsters, hence reducing the amount of lobsters surviving to reproduction or to the fishery. Further studies are needed to address food availability in lobster nursery areas, as well as the relative proportion consumed by lobsters vs. crabs, to determine the exploitative effects of green crabs on sub-adult lobsters. This is particularly important in the smallest benthic lobsters, as they are probably not capable of utilizing green crabs as a food source, as my data suggest the larger juvenile and adolescent lobsters are.

6.4 *C. maenas* as a trophic subsidy to *H. americanus*

Our results indicate that green crabs may provide an alternative prey item to sub-adult and probably also adult lobsters, which might enhance lobster growth and/or survival, as other species of brachyuran crabs are among the most nutrient-rich and preferred prey of lobsters (Gendron et al. 2001). This trophic subsidy seemed to be most apparent among the larger juveniles and adolescent lobsters, and less apparent amongst the smallest lobsters I studied. Although it may enhance the survival of some sub-adult lobsters by providing additional abundant prey, the benefit of this trophic subsidy likely comes with a cost: the other negative community-level effects inferred by green crab invasions, such as their abilities to potentially reduce lobster's natural prey and potentially increase mortality in post-settlers.

6.5 Concluding Remarks

It is currently not possible to predict the overall effect of invasive European green crabs on lobster populations, due to the several potential positive and negative outcomes of this interaction. The trophic subsidy provided to lobsters from consuming green crabs is potentially negligible on a large scale, as there does not seem to be much evidence that food is limiting in lobster populations. Therefore, I feel that the potential threat that green crabs pose to post-larval lobsters along with the indirect effects of the presence of green crabs may outweigh any trophic subsidy, especially in lobster nurseries, which are thought to be a bottleneck in lobster populations (Wahle and Steneck 1991). Future research on the (i) effects of green crabs on post-larval lobsters, (ii) indirect effects of green crabs on lobsters via exploitation of common resources, and (3) food availability in lobster habitat is necessary to reach a more complete understanding of the outcome of ecological interactions between these species.

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Table 1. Summary of Monte-Carlo randomization used to determine if lobsters and crabs were distributed randomly relative to each other along subtidal transects in the four months these were surveyed; transects where I did not find both lobsters and crabs were excluded from this analysis. The number of lobsters and crabs found on each transect/month is indicated in parenthesis after the transect label (# lobsters, # crabs). Values reported are mean observed and theoretical nearest neighbor distances (NN), that is the mean distance separating different lobsters (or crabs) on a given transect/month from the nearest member of the other species. Mean theoretical distances with 95% confidence interval were derived from the Monte Carlo randomization.

		Homarus americanus			***Carcinus maenas***		
Month	Transect	Observed mean NN Distance (m)	Theoretical NN Distance and 95% C.I. (m)	Times Theoretical > Observed (/10,000)†	Observed mean NN Distance (m)	Theoretical NN Distance and 95% C.I. (m)	Times Theoretical > Observed (/10,000) †
August	B (14, 3)	4.14	7.52, 3.6 - 16.4	9280	2.00	1.73, 0.3 - 4.3	2696
August	C (9, 11)	2.00	2.22, 0.9 - 4.8	4880	3.00	2.69, 1.2 - 5.7	2883
August	D (18, 30)	0.56	0.79, 0.4 - 1.4	7874	0.97	1.36, 0.8 - 2.4	8557
September	A (3, 1)	20.00	16.64, 4.7 - 33.3	2866	20.00	16.6, 4.7 - 33.7	2192
September	B (5, 3)	3.80	7.48, 2.4 - 17.8	8650	4.00	4.78, 1.0 – 13.0	2799
September	C (15, 4)	3.27	5.83, 2.8 - 12.5	9188	1.25	1.62, 0.3 – 4.0	4888
September	D (15, 21)	1.27	1.16, 0.5 - 2.1	2962	1.38	1.62, 0.9 - 3.0	5367
October	B (1, 2)	1.00	10.47, 0.0 - 33.0	8881	11.50	16.59, 3.0 - 36.5	6764
October	C (3, 4)	7.67	5.85,1.3 - 15.3	2154	12.00	7.53, 1.7 - 19.7	1318
October	D (9, 12)	2.33	2.04, 0.8 - 4.3	2677	3.33	2.70, 1.3 - 5.6	2192
November	B (6, 4)	13.17	5.83, 2.0 - 13.8	287**	2.00	4.04, 1.0 - 10.5	8253
November	D (6, 7)	2.89	3.99, 1.7 - 8.8	6999	1.17	2.03, 0.7 - 4.7	7952
Mean		5.17	5.82, 3.9 - 8.4	6791	5.24	5.27, 3.4 - 7.7	4806

** Indicates statistically significant deviation from random distribution at alpha = 0.05

† For number of times theoretical < observed subtract this column from 10,000

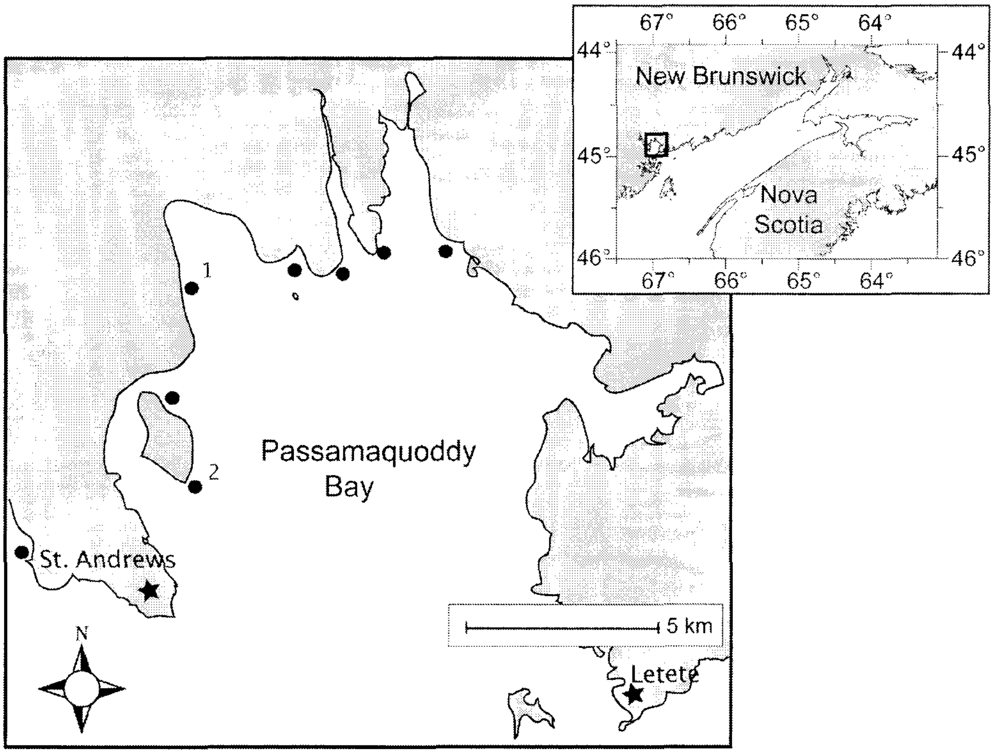

Figure 1. Map of Passamaquoddy Bay showing locations (black dots) where I searched for lobster nursery areas using SCUBA diving. Site labeled 1 is the Birch Cove nursery area (main site used in this study), and site labeled 2 is the southern Minister's Island nursery area.

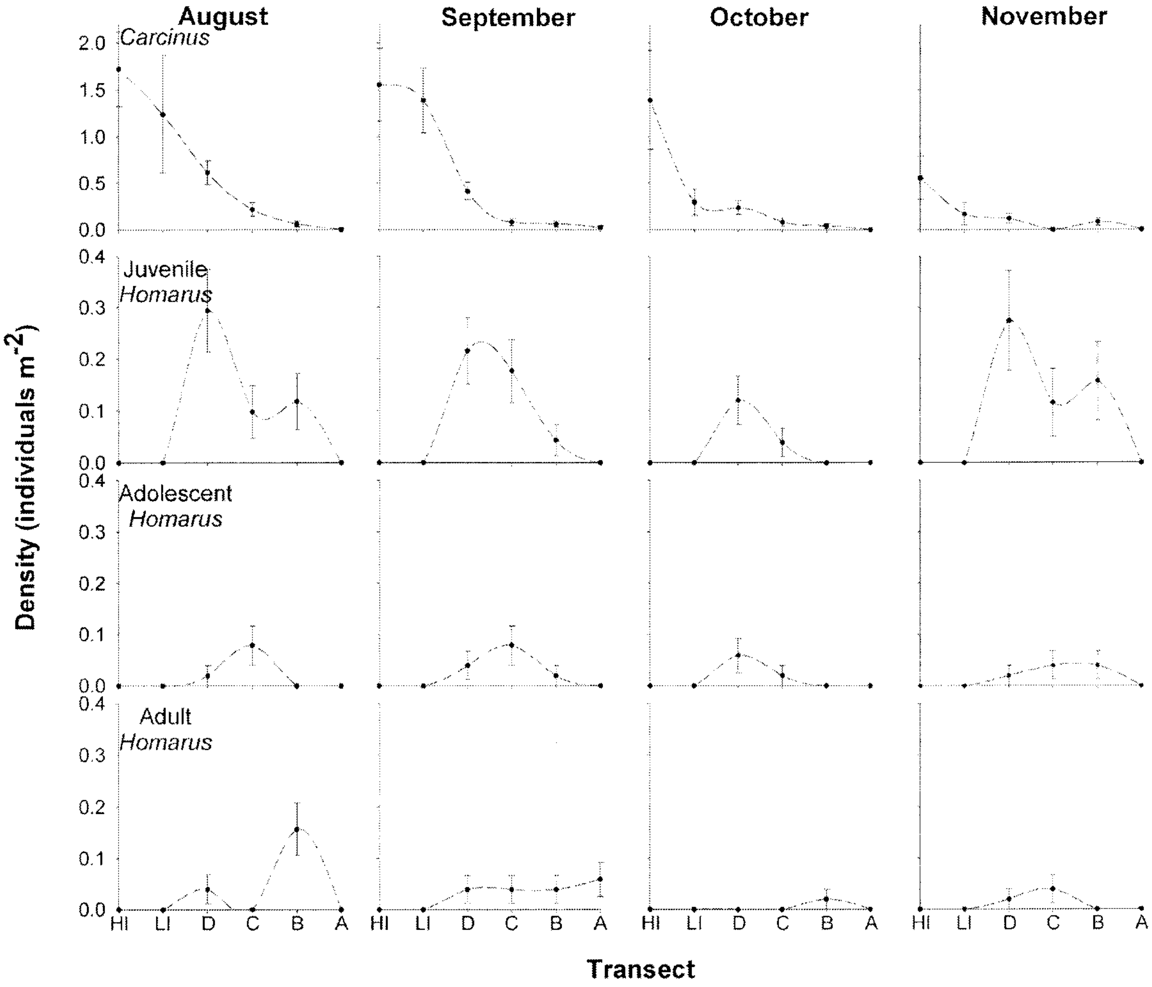

Figure 2. Mean densities (± SE) *Carcinus maenas* and *Homarus americanus* densities at Birch Cove, NB, during August-November, 2006, intertidal and subtidal surveys. Transect A: 6.4m below chart datum; B: 2.4m below datum; C: 1.2m below datum; D: at chart datum; LI: lower intertidal, 2.1m above datum; HI: higher intertidal, 2.3m above datum. Note: density scale differs between *C. maenas* and *H. americanus*.

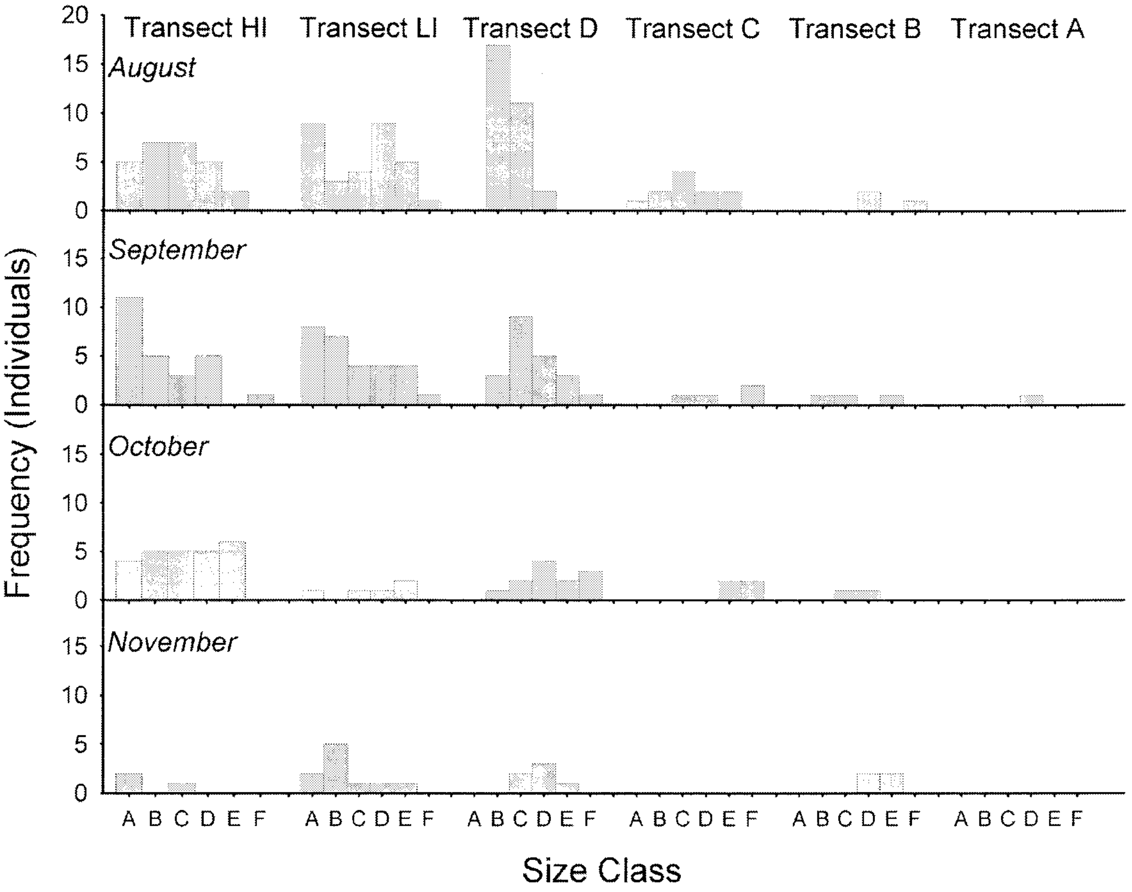

Figure 3. Size-frequency distribution of *Carcinus maenas* crabs found at Birch Cove, NB, during August-November, 2006, intertidal and subtidal surveys. Size classes are binned in 10-mm groups (A: <20-mm, B: 20 to 29.9-mm, C: 30-39.9-mm, D: 40-49.9-mm, E: 50-59.9-mm, F: >60-mm). Transect HI: higher intertidal, 2.3m above chart datum; LI: lower intertidal, 2.1m above datum; D: at chart datum; C: 1.2m below datum; B: 2.4m below datum; A: 6.4m below datum.

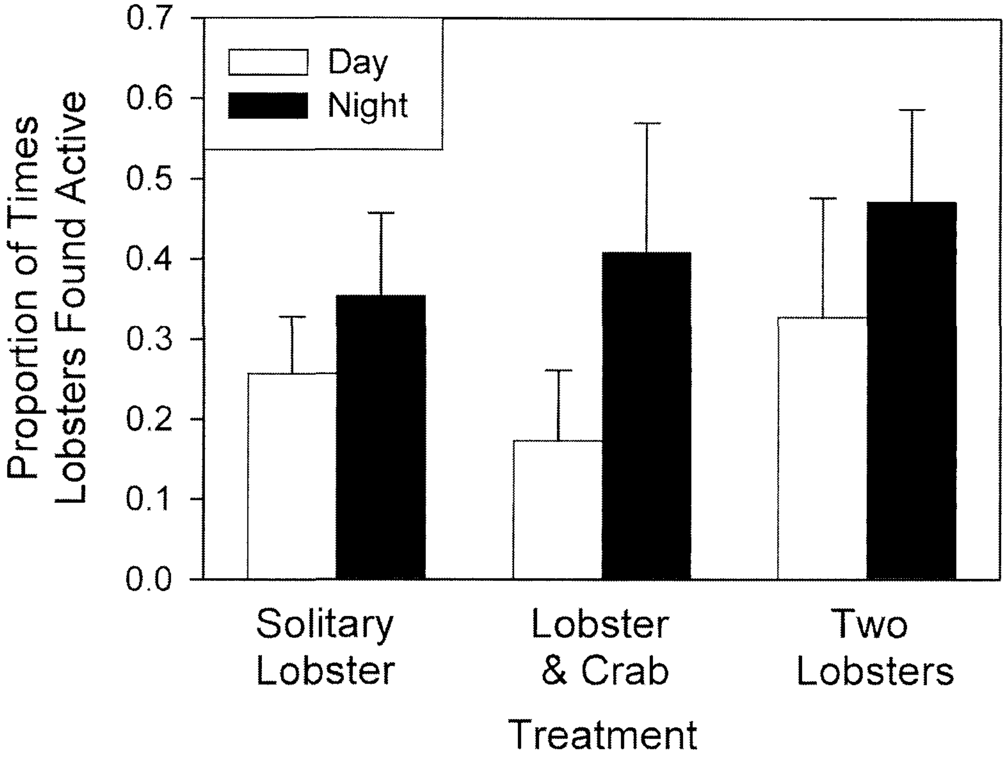

Figure 4. Proportion of lobsters (+ SD) found active during once daily and once nightly spot-checks of lobsters activity in three treatment groups. Lobsters were considered active when they were outside of shelters and actively moving.

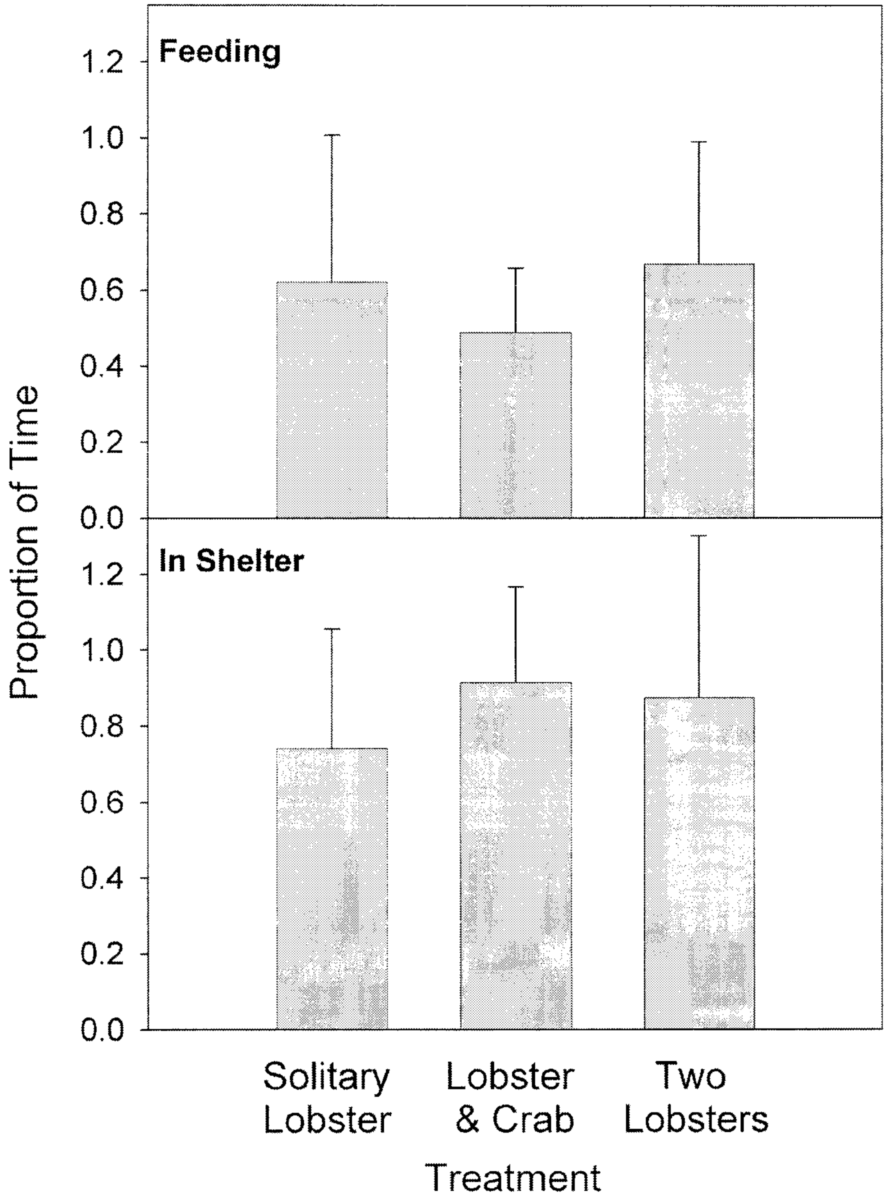

Figure 5. Mean proportion of time (+ SD) focal lobsters spent feeding and sheltering during the hour following addition of food to the aquarium in each of the three treatment groups. Note: feeding graph only depicts lobsters that fed.

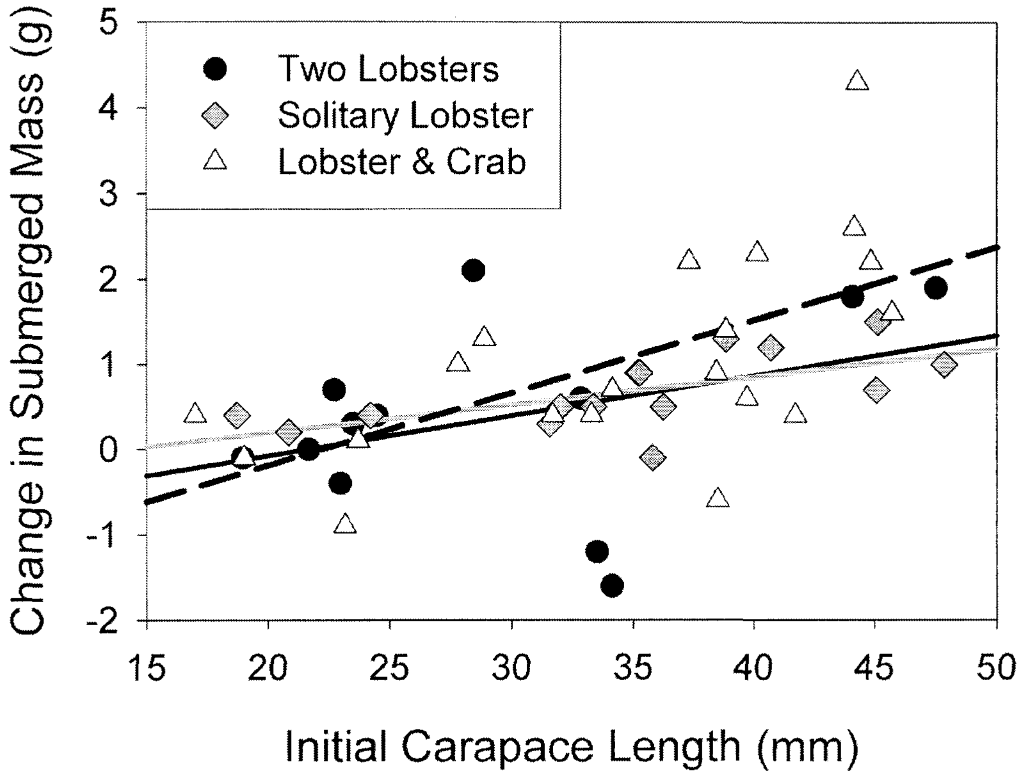

Figure 6. Change in submerged mass of focal lobsters from the three different treatment groups over the course of the 62-day lab experiment (final mass – initial mass), as a function of initial carapace length.

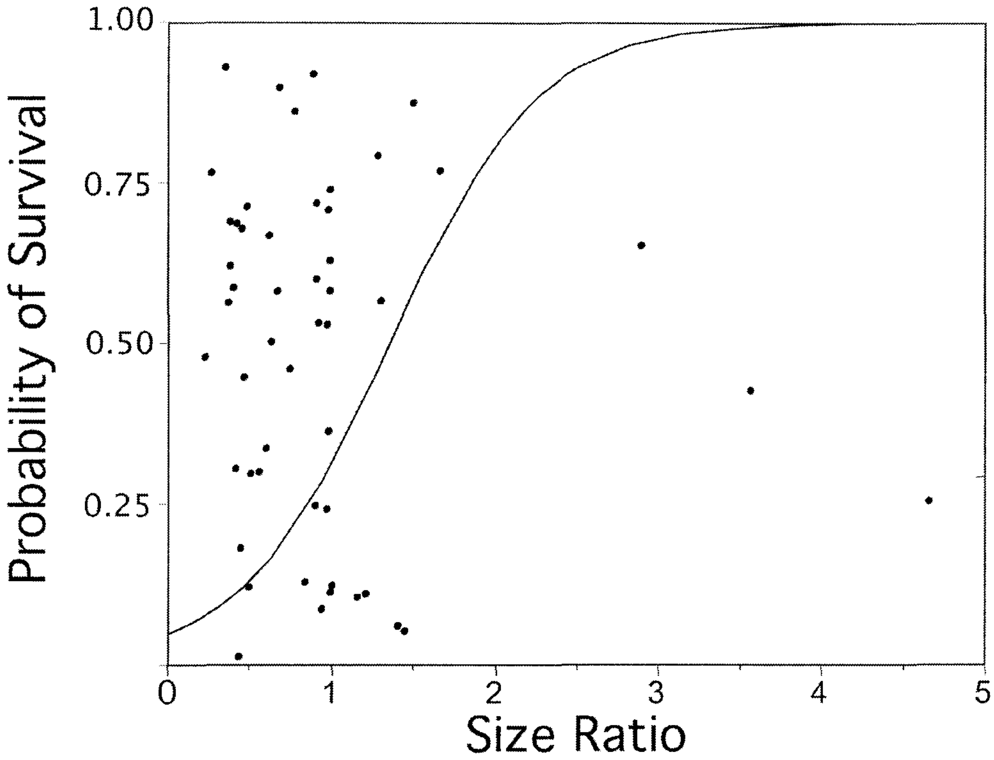

Figure 7. Logistic regression of crab survival as a function of size ratio (crab submerged mass/lobster submerged mass). ($r^2 = 0.2031$).

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Lynch, B. R., and R. Rochette. 2007. Circatidal rhythm of free-roaming sub-tidal green crabs, *Carcinus maenas*, revealed by radio-acoustic positional telemetry. Crustaceana 80:345-355.

Koch, N., B. Lynch, and R. Rochette. In press. Tradeoff between mating and predation risk in the marine snail, *Littorina plena*. Invertebrate Biology.

Conference Presentations:

Lynch, B. R. and R. Rochette. 2007. Spatial overlap and laboratory interactions between sub-adult American lobsters, *Homarus americanus*, and the invasive European green crab *Carcinus maenas*. Oral presentation at the 1st general meeting of the Canadian Society for Ecology and Evolution. Toronto.

Lynch, B. R. and R. Rochette. 2007. Spatial overlap and interspecific interactions between sub-adult American lobsters, *Homarus americanus*, and the invasive European green crab *Carcinus maenas*. Oral presentation at the 46th annual meeting of the Canadian Society of Zoologists. Montreal.