PREDATOR EFFECTS OF THE INVASIVE GREEN CRAB (*CARCINUS MAENAS*) AND THE NATIVE ROCK CRAB (*CANCER IRRORATUS*) ON SOFT-SEDIMENT MACROFAUNA

by

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Submitted in partial fulfillment of the requirements
for the degree of Master of Science

at

Dalhousie University
Halifax, Nova Scotia
December 2012

DALHOUSIE UNIVERSITY

DEPARTMENT OF BIOLOGY

The undersigned hereby certify that they have read and recommend to the Faculty of Graduate Studies for acceptance a thesis entitled "Predator Effects of the Invasive Green Crab (*Carcinus maenas*) and the Native Rock Crab (*Cancer irroratus*) on Soft-Sediment Macrofauna" by Anne V. Cheverie in partial fulfillment of the requirements for the degree of Master of Science.

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DALHOUSIE UNIVERSITY

DATE: December 7, 2012

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TITLE: Predator Effects of the Invasive Green Crab (*Carcinus maenas*) and the Native Rock Crab (*Cancer irroratus*) on Soft-Sediment Macrofauna

DEPARTMENT OR SCHOOL: Department of Biology

DEGREE: MSc CONVOCATION: May YEAR: 2013

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ABSTRACT

When multiple predators foraging together have different individual consumption rates than predators foraging in isolation, they exhibit non-independent multiple predator effects on prey. I examined multiple predator effects in a system consisting of invasive green crabs (*Carcinus maenas* L.), native rock crabs (*Cancer irroratus* Say) and benthic macrofauna prey. First, I examined multiple predator effects when green crabs and rock crabs forage on soft-shell clams (*Mya arenaria* L.) in different habitat types (sand, sand with artificial seagrass) and assessed the behavioural mechanisms responsible for the observed predation effects. Independent multiple predator effects on prey were detected for most conspecific and heterospecific pairs in both habitat types. In general, crab foraging behaviours were not affected by the presence of another predator. Interactions between predators did not influence foraging behaviours because encounters were infrequent, short in duration and predominantly non-aggressive. A non-independent multiple predator effect on prey (marginally significant) was observed when green crabs foraged with rock crabs in artificial seagrass. This effect, however, could not be explained by the observed crab behaviours. Second, I investigated multiple predator effects when green crabs and rock crabs forage on a soft-sediment macrofauna community. Because crabs did not have significant predation effects on the community throughout the experiment, I did not evaluate multiple predator effects on prey. It is possible that crab predation was not important in regulating the macrofauna community, in which case multiple predator effects were non-existent. Predation may have been suppressed due to a combination of factors, including interactions between predators, harsh environmental conditions or a sub-optimal prey field. Alternatively, my ability to detect significant predation effects may have been hindered because of prey movement in and out of cages or low statistical power. Overall, results from this thesis demonstrate that multiple predator effects on prey may differ with habitat and highlights the importance of conducting behavioural observations to better understand interactions between predators and the resulting consequences for prey. Multiple predator effects on a soft-sediment community should be re-evaluated to assess the importance of these crab species in regulating benthic macrofauna under natural conditions.

LIST OF ABBREVIATIONS AND SYMBOLS USED

ANOSIM	Analysis of Similarities
BEST	Bio-Env + STepwise
C_{ab}	Predicted proportion of prey consumed when predator *a* and predator *b* are foraging together
CC	Cage control
CF	Consumption in the field
cm	Centimeter
CW	Carapace width
d	Day
df_1	Numerator degrees of freedom
df_2	Denominator degrees of freedom
Fig.	Figure
g	Grams
G	Green crab
GP	Grid point
H	Habitat
hr	Hour
km	Kilometer
L	Liter
m	Meter
MDS	Multidimensional scaling
min	Minute
mL	Milliliter
mm	Millimeter
MS_1	Numerator mean squares
MS_2	Denominator mean squares
n	Number of observations
N	North
NC	Natural control
NFLD	Newfoundland

NS	Nova Scotia
NW	North west
Obs	Observed
P_a	Observed proportion of prey consumed by predator *a* when foraging alone
P_b	Observed proportion of prey consumed by predator *b* when foraging alone
p	P-value
P	Predator treatment
pers. comm.	Personal communication
pers. obs.	Personal observation
ppt	Parts per thousand
Pred	Predicted
PRIMER	Plymouth Routines in Multivariate Ecological Research
PVC	Polyvinyl chloride
R	Rock crab
RA	Reduced abundance in field experiment
RB	Reduced biomass in field experiment
REML	Restricted maximum likelihood
RG	Rock crab with a green crab
RM ANOVA	Repeated-measures analysis of variance
s	Second
S	Sampling round
SC	Stomach contents
SD	Standard deviation
SE	Southeast
SN	Sand
SG	Seagrass
SE	Standard error of the mean
SIMPER	Similarity percentages
SIMPROF	Similarity profile
SL	Shell length
T	Treatment

Unpubl.	Unpublished
WS	Weather station
α	Statistical significance level
ρ_s	Spearman's coefficient
$\bar{\delta}$	Average dissimilarity between groups
$\bar{\delta}_i$	Average contribution from the *i*th species to average dissimilarity ($\bar{\delta}$)
µm	Micrometer
°C	Degrees Celsius

ACKNOWLEDGEMENTS

First of all, I would like to thank my supervisors, Melisa Wong and Claudio DiBacco, for their encouragement, patience and guidance. Thank you Melisa for always making yourself available and being ever helpful. Claudio, I am appreciative of your insights and constant reassurance. I am also grateful to my committee members, Bob Scheibling and Anna Metaxas, for their support, dedication and feedback. Thanks must also be extended to the Scheibling lab for the use of their facilities and assistance in animal collection. I would like to thank NSERC and the Lett Fund for supporting my studies. Fisheries and Oceans grants to Drs. Claudio DiBacco and Melisa Wong made this research possible.

I am greatly indebted to the numerous individuals who assisted with my research. First and foremost, I would like to thank Steph Mogensen for always being available to help, no matter how ridiculous the request, and keeping things in perspective. I am grateful for the help of Jen MacArthur, whose enthusiasm and dedication greatly contributed to the success of my lab experiment. Finally, I would like to thank Kristin Dinning, Beth Fraser, Michelle Kenny, Laura Hartman, Monica Bravo, Gwen Chapman, Anders Dorbeck, Jessie Short and Donald Renouf. The talents, hard work and encouragement of these individuals were instrumental in the completion of this thesis.

I am deeply appreciative of the support from my family. Thanks to my mom for being encouraging, no matter the circumstances, and for always being there for me. To Becky and Ted, thank you for always brightening my day and coaxing me from my apartment. Thank you to Mike and Don for your input along the way.

Finally, I must thank my husband Lorne. Completing my thesis is not just my success, but also his. I would not have made it without his love, but perhaps more importantly, his delicious cooking. I love you.

To all my family and friends, thank you for your encouragement, prayers and love.

Praise the good Lord, I'm finished!

CHAPTER 1

Introduction

Predation is a key factor regulating prey populations and communities (e.g., Connell, 1975; Sih et al., 1985). Prey populations are often exposed to multiple predator species simultaneously. Predator species foraging together have independent effects on prey when their combined consumption is simply the sum of predation rates by each predator in isolation (Sih et al., 1998). Alternatively, multiple predator species have non-independent effects on prey when combined prey consumption is higher or lower than the sum of predation rates of isolated predators, resulting in risk enhancement or risk reduction for prey, respectively (Sih et al., 1998). Risk reduction can occur due to interactions among predators, modified predator foraging behaviours or changes in prey behaviours that reduce its vulnerability to predation (Crowder et al., 1997; Griffen and Byers, 2006a; Griffen and Williamson, 2008; Wong et al., 2010). In contrast, changes in prey behaviours or habitat use that increase its vulnerability to predation can result in risk enhancement (Soluk, 1993; Losey and Denno, 1998; Swisher et al., 1998). Multiple conspecific predators can also generate non-independent effects on prey (Vance-Chalcraft et al., 2004; Vance-Chalcraft and Soluk, 2005; Wong et al., 2010; Wong et al., 2012), in which case predators alter their predation rates in response to changes in predator density. Consequently, multiple predator species are said to have emergent non-independent effects on prey when the magnitude of non-independence differs between conspecific and heterospecific predators, indicating that changes in predation rates are due to predator species identity and not simply a consequence of predator density (Sih et al., 1998; Vance-Chalcraft et al., 2004).

Multiple predator effects on prey have been widely studied since the late 1980s and have been assessed in terrestrial, marine and freshwater systems (see reviews in Sih et al., 1998; Schmitz, 2007). It has become apparent that multiple predator effects on prey are quite complex, as they can change with a number of factors, including predator density (Griffen and Williamson, 2008), the relative sizes of predators (Griffen and Byers 2006b), prey density (Soluk, 1993; Losey and Denno, 1998; Griffen, 2006), prey species

(Soluk and Collins, 1988; Hughes and Grabowski, 2006) and the available size range of prey (Wong et al., 2010). Several factors which modify multiple predator effects on prey require further investigation. First, environmental heterogeneity, such as habitat type, can alter multiple predator effects on prey; however, it is typically not included in multiple predator studies (but see Swisher et al., 1998; Finke and Denno, 2002; Siddon and Witman, 2004; Warfe and Barmuta, 2004; Griffen and Byers, 2006a; Hughes and Grabowski, 2006; Grabowski et al., 2008; Wong et al., 2010). Habitat type can alter the prevalence of interactions among predators or modify interactions between predators and their prey, both of which can impact predation rates (Swisher et al., 1998; Finke and Denno, 2002; Warfe and Barmuta, 2004; Griffen and Byers, 2006a; Grabowski et al., 2008). Second, although predator and prey behaviours are important mechanisms determining multiple predator effects on prey (Sih et al., 1998; Crumrine and Crowley, 2003), most multiple predator studies do not conduct detailed behavioural observations (but see but see Peckarsky, 1991; Wissinger and McGrady, 1993; Crumrine and Crowley, 2003; Griffen and Byers, 2006a; Griffen and Williamson, 2008;Wong et al., 2010; Wong et al., 2012). Finally, multiple predator effects on a prey species may be altered by the presence of alternative prey species or may indirectly affect non-prey species by modifying trophic pathways (Peckarsky and McIntosh, 1998; Cardinale et al., 2003; Siddon and Witman, 2004). Despite this, most studies investigate multiple predator effects on a single prey species and do not assess the consequences of multiple predator effects on non-prey species (but see van Buskirk, 1988; Martin et al., 1989; Hurd and Eisenburg, 1990; Morin, 1995; Nyström et al., 2001; Cardinale et al., 2003; Ross et al., 2004; Siddon and Witman, 2004; Griffen and Byers, 2009). Consequently, I incorporated these three factors into studies examining multiple predator effects on prey. Specifically, I investigated a) the influence of habitat type on multiple predator effects and the underlying behavioural mechanisms, and b) multiple predator effects on an entire community.

I examined multiple predator effects on prey in a marine system, consisting of invasive European green crabs (*Carcinus maenas* L.), native Atlantic rock crabs (*Cancer irroratus* Say) and soft-sediment macrofaunal prey. Native to Europe, the green crab was

first detected in eastern Canada in 1951 in Passamaquoddy Bay, New Brunswick and has subsequently spread to all of the Atlantic Provinces (MacPhail, 1953; Audet et al., 2003; Cohen and Carlton, 2003 and references therein; Blakeslee et al., 2010). In eastern Canada, green crabs overlap in distribution with rock crabs (Breen and Metaxas, 2009; Gregory and Quijón, 2011, J. Tremblay, unpubl. data, A. Cheverie, pers. obs.). These crab species interact and may be important competitors, as they occupy the same habitat types, have overlapping diets and consume one another (Crothers, 1968; Ropes, 1968; Scarratt and Lowe, 1972; Elner, 1981; Hudon and Lamarche, 1989). Green crabs can significantly reduce soft-sediment macrofauna populations and rock crabs are likely also important predators in this habitat (e.g., Grosholz et al., 2000; Floyd and Williams, 2004; Quijón and Snelgrove, 2005a). Few studies have examined the combined predation effects of green crabs and rock crabs. Results to date indicate that depending on the experimental conditions, these crab species may forage independently or exhibit risk reduction for prey (Bélair and Miron, 2009a; Gregory and Quijón, 2011). Risk reduction for prey can result from changes in foraging behaviours, aggressive interactions and intraguild predation (Siddon and Witman, 2004; Griffen, 2006; Griffen and Byers, 2006a; 2006b; Griffen and Williamson, 2008; Wong et al., 2010). Consequently, green crabs and rock crabs may influence the foraging success of the other species, potentially resulting in non-independent multiple predator effects on prey. It is important to assess multiple predator effects on prey in this system to a) predict the collective impact of green crab and rock crab predation on soft-sediment macrofauna, b) assess the influence of the green crab invasion on the foraging ability of a native competitor, and c) increase our understanding of multiple predator effects on marine soft-sediment macrobenthos, which has rarely been explored (but see Martin et al., 1989; Ross et al., 2004; Hughes and Grabowski, 2006; Wong et al., 2010).

I examine multiple predator effects of green crabs and rock crabs on soft-sediment macrofauna in a laboratory and manipulative field experiment. Chapter 2 investigates multiple predator effects on prey in different habitat types and the underlying behavioural mechanisms in a laboratory experiment. Specifically, I examine green crab and rock crab predation on soft-shell clams (*Mya arenaria* L.) in sand and sand with artificial seagrass,

and conduct detailed observations of predator foraging behaviours and interactions between crabs. Chapter 3 investigates multiple predator effects on an entire community in a manipulative field experiment. Here, I explore green crab and rock crab predation effects on a soft-sediment macrofauna community. I present a summary and conclusions in Chapter 4.

CHAPTER 2

Influence of Habitat Type on Multiple Predator Effects of Invasive and Native Crabs on a Bivalve Prey

2.1 Abstract

Non-independent multiple predator effects occur when predators foraging together have different individual consumption rates than predators foraging alone. While multiple predator effects have been well studied, there has been little emphasis on how environmental heterogeneity and behaviours affect overall consumption rates. I examined the influence of habitat type on multiple predator effects when invasive European green crabs (*Carcinus maenas*) and native rock crabs (*Cancer irroratus*) prey on soft-shell clams (*Mya arenaria*), and used behavioural data to assess the mechanisms responsible for the observed effects. In the laboratory, predators (single crabs, conspecific pairs and heterospecific pairs) of similar sizes were offered juvenile clams in sand or in sand with artificial seagrass. Independent multiple predator effects on prey were detected for most paired predators in both habitat types. Generally, foraging behaviours of crabs with a conspecific or heterospecific were similar to isolated crabs. Because encounters between crabs were infrequent and short in duration, predator interactions did not reduce time spent foraging. Consequently, the presence of conspecific and heterospecific crabs may not reduce predation risk for soft-shell clam populations in eastern Canada. A non-independent multiple predator effect on prey (marginally significant) was detected for heterospecific crabs in artificial seagrass, indicating that multiple predator effects of these crab species may be habitat-specific. This result could not be explained by the observed foraging behaviours. Although green crabs had higher predation rates than rock crabs, both species were important predators of juvenile clams, even in artificial seagrass where searching efficiency was likely reduced. This study suggests it is important to incorporate environmental heterogeneity into multiple predator studies and that behavioural data are valuable to better understand interactions between predators and their outcomes for prey.

2.2 Introduction

Under natural conditions, prey are often subjected to multiple predators species. Multiple predators have independent effects on their prey when their combined effect is the sum of consumption rates by each predator in isolation (Soluk and Collins, 1988; Sih et al., 1998). Non-independent multiple predator effects occur when predators foraging together have either lower or higher individual consumption rates compared to when they forage alone, resulting in reduced or enhanced predation risk for prey, respectively (Sih et al., 1998). Risk reduction has been attributed to interactions between predators, reduced predator foraging in the presence of another predator and changes in prey behaviour which reduce its vulnerability to predation (e.g., Soluk and Collins, 1988; Crowder et al., 1997; Crumrine and Crowley, 2003; Griffen and Byers, 2006a; Griffen and Williamson, 2008; Wong et al., 2010). In contrast, facilitation among predators and altered prey behaviour or habitat use that results in increased susceptibility to predation are suggested as mechanisms for risk enhancement (Soluk, 1993; Losey and Denno, 1998; Swisher et al., 1998). Thus, the behavioural responses of both predators and prey are important mechanisms determining multiple predator effects (Sih et al., 1998; Crumrine and Crowley, 2003). Despite this, the majority of multiple predator studies do not incorporate detailed behavioural observations, hindering the ability to identify the important underlying mechanisms (but see Peckarsky, 1991; Wissinger and McGrady, 1993; Crumrine and Crowley, 2003; Griffen and Byers, 2006a; Griffen and Williamson, 2008; Wong et al., 2010; Wong et al., 2012).

Although predators and their prey often coexist in heterogeneous environments, studies usually do not examine multiple predator effects on prey in different habitats (but see Swisher et al., 1998; Finke and Denno, 2002; Siddon and Witman, 2004; Warfe and Barmuta, 2004; Griffen and Byers, 2006a; Hughes and Grabowski, 2006; Grabowski et al., 2008; Wong et al., 2010). Yet, results to date indicate that habitat type and its structural components often influence multiple predator effects on prey (e.g., Hughes and Grabowski, 2006; Wong et al., 2010). Habitat type and habitat complexity (i.e., number of distinct structural components, McCoy and Bell, 1991) can affect the prevalence of interactions among predators and consequently their combined predation effect (Finke and Denno, 2002; Grabowski et al., 2008). For example, Griffen and Byers (2006a) observed that intraguild predation and associated behaviours (i.e., prey switching by top

predator, reduced foraging by intermediate predator) resulted in greater risk reduction for prey in a habitat where intermediate predators were more vulnerable to top predators relative to a habitat which offered more protection. Additionally, habitat type or complexity can influence interactions between predators and their prey, which can also alter multiple predator effects on prey (Swisher et al., 1998; Warfe and Barmuta, 2004). For instance, Swisher et al. (1998) observed risk enhancement for prey at a low vegetation density and independent multiple predator effects on prey at higher densities because the prey's behavioural response to one predator increased its visibility to the other predator in the least dense habitat. Consequently, it is essential to predict predation impacts on prey populations by understanding how interactions among predators and between predators and their prey alter predation rates in different habitats. Yet, few multiple predator studies have examined the influence of habitat and behaviour on combined prey consumption (but see Griffen and Byers, 2006a; Wong et al., 2010). Here, I investigated multiple predator effects on prey by an invasive and native predator in different habitat types and the underlying behavioural mechanisms.

The European green crab (*Carcinus maenas* L.) is a successful invasive species, which has expanded its native range in Europe to include both coasts of North America, South Africa, Australia, Japan and Argentina (Carlton and Cohen, 2003 and references therein; Hidalgo et al., 2005). In eastern Canada, green crabs first appeared in New Brunswick in 1951 and reached Nova Scotia (NS) by 1953 (MacPhail, 1953). More recently, they have spread into Prince Edward Island (1997), Quebec's Magdalen Islands (2004) and Newfoundland (NFLD) (c.2002) (Audet et al., 2003; Paille et al., 2006; Blakeslee et al., 2010). In parts of this range, green crabs overlap spatially and temporally with native Atlantic rock crabs (*Cancer irroratus* Say) in shallow waters (Breen and Metaxas, 2009; Gregory and Quijón, 2011; J. Tremblay, unpubl. data; A. Cheverie, pers. obs.). Overlap has been observed between juveniles and early adults (< 30 mm in carapace width (CW)) of these species and also among adults (Breen and Metaxas, 2009; Chris McCarthy, unpubl. data; J. Tremblay, unpubl. data). Based on trapping data, these crab species coincide in many habitat types, including mud, sand and gravel (J. Tremblay, unpubl. data). Green crabs and rock crabs likely interact, as they have broad diets with overlapping prey and are known to consume one another (Ropes,

1968; Scarratt and Lowe, 1972; Elner, 1981; Drummond-Davis et al., 1982). The consequences of interactions for these species are not well known, but may be context dependent (i.e., location, time of year). For example, in NFLD, rock crabs appear to be negatively influenced by the green crab invasion because their abundance often increases when green crabs are removed through trapping (DFO, 2011). However, in the Bras d'Or Lakes (NS), there appears to be no relationship between the abundance of juvenile and early adult green crabs and rock crabs (Breen and Metaxas, 2009).

Interactions between green crabs and rock crabs may also have important repercussions for prey populations. Multiple predator studies often document risk reduction for prey when decapod species forage together due to aggressive interactions, intraguild predation or changes in foraging behaviours (Siddon and Witman, 2004; Griffen and Williamson, 2008; Griffen and Byers, 2006a; 2006b; Griffen, 2006; Wong et al., 2010). Consequently, interactions between green crabs and rock crabs may be important in regulating their predation rates, but few studies have investigated their combined predation effects on prey. Bélair and Miron (2009b) found that green crab and rock crab predation rates on blue mussels (*Mytilus edulis*) were similar whether they foraged alone or with a heterospecific under most experimental conditions. Similarly, Matheson and Gagnon (2012a) observed that chemical cues from live green crabs did not influence the number of mussels captured by rock crabs. In contrast, Gregory and Quijón (2011) observed reduced polychaete and mollusc density when green crabs and rock crabs foraged together at a low density, but no predation effects at a higher density due to interactions among these predators. These studies suggest that whether interactions among green crabs and rock crabs alter predation rates depends on the experimental conditions. Consequently, multiple predator studies are required to predict the predation effects of these crab species in a particular system.

I conducted a laboratory experiment to examine multiple predator effects and the associated behavioural mechanisms when green crabs and rock crabs forage on soft-shell clams (*Mya arenaria* L.) in different habitat types. Clam predation was investigated in sand or sand with artificial seagrass blades, mimicking *Zostera marina* L., habitats where both crab species are known to occur (e.g., Heck et al., 1989; Hudon and Lamarche,

1989). Soft-shell clams are consumed by rock crabs and a significant prey item for green crabs (e.g., Ropes, 1968; Elner, 1981; Floyd and Williams, 2004; Miron et al., 2005). In eastern Canada, green crabs are considered a threat and rock crabs constitute a potential threat to the soft-shell clam industry (Floyd and Williams, 2004; Miron et al., 2005). It is therefore important to examine how interactions among these crab species influence predation rates and consequently their collective impact on clam populations. Further, this study investigates whether the presence of the invasive green crab affects the foraging ability of native rock crabs, a species which is also fished commercially in eastern Canada (DFO, 2008). Specifically, my objectives were to determine (1) if independent or non-independent multiple predator effects on prey occur when green crabs and rock crabs consume soft-shell clams in sand and seagrass habitats, (2) if multiple predator effects on prey differ between habitat types, and (3) how predator behaviours contribute to the observed predation results.

2.3 Materials and Methods

2.3.1 Experimental Materials

The influence of habitat type on green crab and rock crab predation of soft-shell clams was examined in a laboratory experiment from 10 September to 1 November 2011 at Dalhousie University (Halifax, NS, Canada). The experiment was conducted in 12 glass aquaria (0.6 x 0.3 x 0.3 m, length x width x height) with flow-through seawater (~1L min^{-1}). Tanks were covered with black nylon netting (1.91 cm^2 mesh size) to prevent crabs from escaping. Between trials, water temperature and salinity ranged from 7.9 to 16.1ºC and 31.0 to 32.4 ppt. The laboratory received artificial light for 14:10 hr light / dark cycles. Light levels within all experimental tanks were measured at the sediment surface (~13 cm depth) during each replicate using the Milwaukee® SM700 portable lux meter with waterproof probe. Light in tanks containing artificial seagrass ranged from 20-146 lux, while tanks with only sand ranged from 54-286 lux.

Juvenile soft-shell clams were hand-dug in East Chezzetcook, NS in July and September 2011. Clams used in the experiment were 10-20 mm in shell length (SL), measured as the greatest anterior to posterior shell dimension. Clams within this size

range are easily consumed by both rock crabs and green crabs (e.g., Cohen et al.,1995; Floyd and Williams, 2004; Miron et al., 2005). Prior to use in trials, clams were held a maximum of three months in glass aquaria, and fed Shellfish Diet® 1800 (Reed Mariculture Inc.) for 30 mins daily at a concentration of ~1.0 x 10^4 cells mL^{-1} of water.

SCUBA diving and trapping were used to collect crabs from June to August 2011 at several field sites near Halifax, NS. Only male crabs were used in the experiment to prevent potential sex biases, and all crabs had undamaged chelae and a minimum of six intact walking legs. Both crab species were 50-69 mm in CW, measured as the distance between the notches anterior to the most distal marginal teeth. Based on trapping data, these crab species overlap spatially and temporally within this size-range in coastal habitats of eastern Canada (C. McCarthy, unpubl. data; J. Tremblay, unpubl. data). Individuals of each species were kept in separate holding tanks (0.92 x 0.62 x 0.40 m, length x width x height) covered with chicken wire for a maximum for five months prior to use in trials. Shelter for crabs was provided by black plastic sheet covering 50% of the holding tanks and plastic pipes placed within the tanks. Crabs were fed frozen fish in the holding tanks, which were replaced every 3-5 days to ensure continual access to food.

Sediment used in the experiment was collected from Martinique Beach, Musquodoboit Harbour, NS in February 2009. Sediment was homogenized by removing large material (e.g., cobble, shells, plant material) with a 4-mm sieve and was subsequently rinsed with fresh water for sterilization. Sediment particle size was determined by drying ~138 g sediment for ~24 hrs at 60ºC, weighing the dried sample, separating the sample into the gravel (> 2 mm) and sand (0.063 - 2mm) fractions by wet sieving, and then drying each fraction ~24 hrs at 60ºC and weighing (Bale and Kenny, 2005). The % of sand or gravel content was calculated as (fraction mass/initial mass) x 100 and % loss was attributed to silt and clay. Percent sand content was 95.80 ± 0.16 % (mean ± SE, n=3), percent gravel was 0.24 ± 0.06 %, and percent silt and clay was 3.96 ± 0.22 %. The percent sand content of the sediment used in our experiment was similar to that where soft-shell clams occur naturally (Blundon and Kennedy, 1982a; LeBlanc and Miron, 2006). To ensure that clam burial was not inhibited, all experimental tanks were filled with 10 cm of sand (Blundon and Kennedy, 1982a; Zaklan and Ydenberg, 1997).

Sand was flushed with seawater for at least two weeks prior to the experiment to allow natural biofilm growth.

Habitats used in the experiment were sand and sand with artificial seagrass. Artificial seagrass was constructed of green ribbon (4.75mm width) attached to corrugated plastic which was buried at the bottom of the tanks. Shoot density was approximately 700 shoots m^{-2}, falling within the range of naturally occurring densities in NS during the summer and early fall (Robertson and Mann, 1984; M. Wong, unpubl. data). Shoots were distributed in a systematic fashion to ensure that shoot density remained consistent throughout the tank. Each shoot consisted of two blades with lengths of 10 - 50cm from the sediment surface, mimicking natural lengths in the summer and early fall (Schneider and Mann, 1991; M. Wong, unpubl. data). The dimensions, rigidity and buoyancy of artificial blades were a close approximation to natural seagrass blades. The root-rhizome system was not included in this design. Although these belowground components may hinder predator foraging on bivalves (Blundon and Kennedy, 1982a; Peterson, 1982; M. Wong, unpubl. data), I expected the blades to regulate multiple predator effects on clams. Relative to the sand habitat, blades should provide refuge for crabs, modifying their interactions and the resultant multiple predator effects.

2.3.2 Experimental Design

The experimental design was a complete unreplicated block with habitat (2 levels: sand and artificial seagrass) and predator treatment (5 levels: single green crab, green crab conspecific pair, single rock crab, rock crab conspecific pair, and the heterospecific pair) as fixed factors, and temporal block (8 levels of 36 hrs each) as a random factor. Blocking was utilized to account for variability in experimental conditions, such as different water temperatures between trials, which likely influenced green crab and rock crab predation rates (Wallace, 1973; Elner, 1980; Barbeau and Scheibling, 1994; Bélair and Miron, 2009a; Matheson and Gagnon, 2012a). One replicate of each habitat and predator treatment combination was randomly assigned to an experimental tank in each time block, for a total of 8 replicates for most treatment combinations. The exceptions were for the single rock crab and heterospecific pair in sand, which had 7 replicates due

to an escape and lack of feeding. Trials began at 20:30 and lasted for 36 hrs. Each trial consisted of two nights as green crabs and cancrid crabs, including rock crabs, are predominantly characterized as nocturnal (reviewed in Novak, 2004).

In experimental tanks, crabs were offered 160 juvenile soft-shell clams (~890 individuals m^{-1}), falling within the range of naturally occurring juvenile densities in clam beds of eastern Canada (Emerson and Grant, 1991; Floyd and Williams, 2004, A. Cheverie, pers. obs.). Based on a preliminary feeding experiment, this prey density was chosen so prey availability was not reduced by more than 60 % during the 36 hr trials. Clams were randomly distributed on the surface of experimental tanks 24 hrs before each trial began to allow for burial. Clams that were not buried 2 hrs before a trial began were replaced by new clams buried into the sand. During each temporal block, one control tank (without predators) for each habitat type was established to assess natural clam mortality. Due to low clam mortality in both habitats (10 clams died in both sand and artificial seagrass controls), controls were not included in statistical analyses. Prior to each trial, hard-shelled crabs observed foraging were isolated within the holding tanks in plastic containers with holes and starved for 48 hrs to standardize hunger levels. To allow for acclimation, these plastic containers were transferred to experimental tanks 30 mins before each trial began. Because the relative size of paired crabs can influence interactions (e.g., Jachowski, 1974), crabs of similar CW (0.6 ± 0.1 mm, mean difference ± SE) were used in conspecific and heterospecific pairs. Each crab was used only once.

2.3.3 Crab Predation Data

Following each trial, sand in experimental tanks was picked through by hand to remove shell fragments and intact clams. The number of remaining clams was used to calculate the total number of clams consumed. The proportion of clams consumed was calculated as the number of clams consumed / the number of clams originally available (i.e., 160).

2.3.4 Crab Behavioural Data

To determine the behavioural mechanisms responsible for the observed multiple predator effects, personal observations of all predator treatment and habitat combinations

were performed for multiple 30 min intervals throughout each trial. Observations were conducted from 21:00-24:00, 1:00-4:00, 6:30-9:30, 11:00-14:00 and 16:00-19:00 for a total of seven observation periods across the 36 hr trial (3.5 hrs total). To prevent observer effects, observations were conducted behind a black plastic blind suspended in front of the tanks (during the day) or using a headlamp with red light (at night), as crustaceans are insensitive to these wavelengths (reviewed in Cronin, 1986). For conspecific pairs, one individual was randomly selected as the focal crab for observations and identified with a dot of Wite-Out (BIC Corporation) on the top of the carapace approximately 1 cm posterior to eye stalks. The Wite-Out did not appear to influence crab behaviour or survivorship. For heterospecific crabs, observations were conducted twice during each observation period, in order to examine each crab species separately, generating 3.5 hrs of observation time for each species during a trial.

Crab behaviours were categorized as foraging (searching for and handling prey) and non-foraging (walking, climbing, grooming, buried, inactive on surface, and interactions between predators) (see results section for further description of behaviours). The duration of behaviours were quantified throughout each observation period. The proportion of time spent (i) searching, (ii) handling and (iii) foraging were calculated as the total duration of behaviour / total observation time. Encounter rates with prey were calculated as the total number of encounters / search time. Handling time per prey was calculated as the total time a crab manipulated one clam (Wong and Barbeau, 2005; Wong et al., 2010). The proportion of time engaged in interactions was quantified and encounter rate between predators was calculated as total number of encounters / observation time (Wong et al., 2010; Wong et al., 2012).

2.3.5 Statistical Analyses

2.3.5.1 Analysis of Crab Predation Data

The total proportions of clams consumed were analyzed with a linear mixed-effects model, with predator treatment (5 levels) and habitat type (2 levels) as fixed factors and temporal block (8 levels) as a random factor.

To test for multiple predator effects on prey of conspecific and heterospecific pairs of crabs in different habitats, I compared the observed proportion of clams consumed to the predicted proportion consumed if predators foraged independently, calculated using the multiplicative risk model (Soluk and Collins, 1988; Wilbur and Fauth, 1990; Soluk, 1993; Sih et al., 1998):

$$C_{ab} = P_a + P_b - P_a P_b$$

where C_{ab} is the predicted proportion of prey consumed when predator *a* and predator *b* are foraging together, P_a is the observed proportion of prey consumed by predator *a* when foraging alone, and P_b is the observed proportion of prey consumed by predator *b* when foraging alone. The $P_a P_b$ term incorporates prey depletion into the model, by assuming that the same prey item cannot be consumed by both predators (Sih et al., 1998). Predicted proportion consumed was calculated for conspecific and heterospecific pairs in each habitat type using appropriate single predator treatments within each temporal block. For example, predicted proportion consumed by heterospecific pairs in sand during the first temporal block was calculated by inserting the proportion of clams consumed by a single rock crab in sand and a single green crab in sand from this temporal block into the multiplicative risk model. Consequently, predicted values were independent of the observed proportion consumed by paired crabs because predation data from different crabs were utilized to generate each value. To test for differences between observed and predicted values, separate linear mixed-effects models were conducted for each paired predator treatment and habitat combination, with predation (observed or predicted) as a fixed factor and temporal block as a random factor. A significant difference between observed and predicted values indicated the presence of a non-independent multiple predator effect on prey.

2.3.5.2 Analysis of Crab Behavioural Data

Because crab foraging occurred predominantly at night (see 'Results'), behavioural data were only analyzed for the night observation periods (21:00-24:00, 1:00-4:00), for a total of 2 hrs of observation time per trial for focal crabs in each predator treatment and habitat combination. Behavioural data were analysed with linear mixed-effects models, with predator treatment and habitat type as fixed factors and

temporal block as a random factor. To avoid non-independence in data of predator behaviour in heterospecific pairs, all foraging behaviours (proportion of time searching, proportion of time handling, encounter rates with prey, handling time per prey) were analysed with two linear mixed-effects models. The first model (full model) included all predator treatments; however, only data from rock crabs were included for heterospecific pairs. To further examine the contribution of green crabs to the observed multiple predator effects on prey, I ran a second analysis (green crabs only model) for each foraging behaviour which included only predator treatments with focal green crabs (single, conspecific and heterospecific green crabs). Both data are presented together in all figures. Interactions between predators (encounter rates between predators, proportion of time interacting) were analysed using the full linear mixed effects model, pooling data collected from rock crabs and green crabs in the heterospecific pairs, as these behaviours do not depend on the predator species being observed.

Statistical analyses were run in R 2.14.1 (R Development Core Team, 2011). All linear mixed-effects models were conducted using lme() from the package nlme (Pinheiro et al., 2012). Restricted maximum likelihood estimates (REML) were used as this estimation procedure produces variance components that are less biased than maximum likelihood estimates (Patterson and Thompson, 1971; Harville, 1977). Assumptions for within-group errors and random effects were assessed graphically with normality Q-Q plots of residuals, plots of residuals versus fitted values and plots of residuals against temporal blocks (Draper and Smith, 1998; Pinheiro and Bates, 2000). Violations of the assumptions were corrected using logit transformations on proportion data (Warton and Hui, 2011), $\log_{10}$ or square root transformations. To be certain that main effects were not inappropriately interpreted in the presence of a potential interaction, I investigated all interactions with $p \leq 0.1$ (as in Hamilton et al., 2006). Main effects and post-hoc comparisons were evaluated at a significance level of $p=0.05$. When significant main effects or interactions were detected, post-hoc comparisons were conducted using Tukey's tests with the Kramer modification for unequal sample sizes (Day and Quinn, 1989; Quinn and Keough, 2002). Post-hoc testing was conducted with glht() from the multcomp package, with comparisons averaged over the interaction term (Hothorn et al., 2008, R. Heiberger, pers. comm.).

2.4 Results

2.4.1 Crab Predation of Soft-Shell Clams

2.4.1.1 Total Proportion Consumed

The proportion of clams consumed by crabs was significantly affected by habitat type, and was higher in sand than in artificial seagrass (Table 2.1, Fig. 2.1). This trend was particularly evident for single green crabs and heterospecific pairs. The total proportion of clams eaten also differed significantly with predator treatment (Table 2.1, Fig. 2.1). For both crab species, conspecific pairs consumed a greater proportion of clams compared to single crabs of the same species (Tukey tests, $p<0.05$). When crabs foraged alone, green crabs consumed more clams than rock crabs (Tukey test, $p<0.05$). Daily consumption rates ranged from 25.3 – 71.3 clams d^{-1} in sand and 28.7 – 46.7 clams d^{-1} in artificial seagrass for isolated green crabs, and from 10.0 – 46.7 clams d^{-1} in sand and 8.7 – 45.3 clams d^{-1} in artificial seagrass for single rock crabs. For paired predator treatments, both conspecific green crabs and heterospecific crabs consumed a greater proportion of clams than conspecific rock crabs (Tukey tests, $p<0.05$).

2.4.1.2 Multiple Predator Effects on Prey

For paired predator treatments in sand habitat, there were no significant differences between the observed and predicted proportion of clams consumed, indicating independent multiple predator effects on prey (Table 2.2, Fig. 2.1). In artificial seagrass, independent multiple predator effects on prey were also observed for conspecific pairs

Table 2.1 Results from linear mixed-effects model examining total proportion of soft-shell clams consumed in different predator treatments and habitat types. P-values in bold indicate significant results. Post-hoc comparisons are ordered from lowest to highest treatment level means; those sharing a common underline do not differ significantly. df_1 = numerator; df_2 = denominator; P = predator treatment; H = habitat; R = rock crab; G = green crab; SG = artificial seagrass; SN = sand.

Source of variation	df_1, df_2	F-value	P-value	Post-hoc comparisons
P	4, 61	21.07	**<0.0001**	R R+R G R+G G+G
H	1, 61	6.67	**0.012**	SG SN
P x H	4, 61	1.26	0.294	

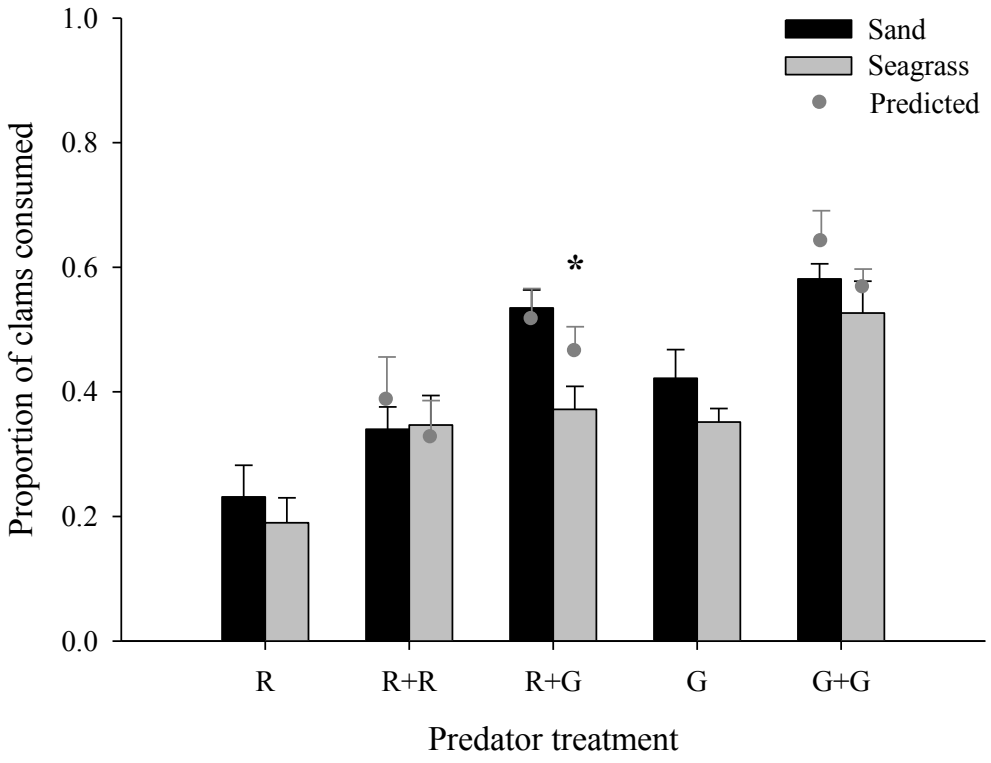


Figure 2.1 Observed (bars) and predicted (circles) proportions of soft-shell clams consumed (mean + SE, n = 7 or 8) by single and paired rock crabs (R) and green crabs (G) in sand and artificial seagrass. Predicted values were calculated using the multiplicative risk model. * Indicates marginal significant difference between observed and predicted values.

Table 2.2 Results from linear mixed-effects models comparing the observed total proportion of soft-shell clams consumed by rock crabs and green crabs in sand and artificial seagrass to predicted values generated by the multiplicative risk model. Data from conspecific rock crabs in sand were logit transformed. Data for conspecific green crabs in both habitats and heterospecific crabs in sand could not be transformed to meet assumption of homogeneity of variance. Marginally significant values are italicised. df_1 = numerator; df_2 = denominator; R = rock crab; G = green crab; Obs = observed proportion consumed; Pred = predicted proportion consumed.

Predator treatment	Habitat	Source of variation	df_1, df_2	F-value	P-value	Post-hoc comparisons
R+R	Sand	Predation	1, 6	0.37	0.564	
R+R	Seagrass	Predation	1, 7	0.04	0.855	
R+G	Sand	Predation	1, 5	0.04	0.859	
R+G	Seagrass	Predation	1, 7	5.42	*0.053*	Obs Pred
G+G	Sand	Predation	1, 7	1.56	0.252	
G+G	Seagrass	Predation	1, 7	0.74	0.418	

(Table 2.2, Fig. 2.1). However, the difference between observed and predicted values for heterospecific pairs was marginally significant (Table 2.2, Fig. 2.1) with crabs consuming a lower proportion of clams than predicted, suggesting a non-independent multiple predator effect on prey for this treatment. This difference was not significant because of relatively low statistical power (51%). An effect size of 0.14 proportion consumed (or 22.48 clams) would have been detectable with 80% power. Although I did not obtain statistical significance, the difference between observed and predicted proportion consumed for heterospecific crabs in artificial seagrass is biologically meaningful. In this habitat type, clam consumption by single green crabs (0.35 ± 0.02 proportion consumed, mean ± SE, n=8) was similar to that of heterospecific crabs (0.37 ± 0.04 proportion consumed, mean ± SE, n=8), which strongly suggests that the presence of a heterospecific reduced crab predation rates.

2.4.2 Crab Behaviour

2.4.2.1 Description of Behaviours

Both rock crabs and green crabs searched for prey while moving or at rest by probing the substrate with the tips of their walking legs or by digging through the sediment (Sponaugle and Lawton, 1990; Wong and Barbeau, 2003; Wong et al., 2012). An encounter with prey occurred when a crab captured a clam, either by extracting the clam from the sediment or picking up the clam from the sediment surface using its chelae. Handling behaviour began when a clam was encountered and ended when it was either rejected or consumed and the shell was discarded (Wong and Barbeau, 2003). Handling time per prey was the duration that a single clam was manipulated. Crabs opened clams by crushing or pulling the valves apart with their chelae and extracted the flesh using their chelae or mouthparts. Both crab species were observed consuming flesh from shell fragments that had been discarded on the sediment surface. This behaviour was included in overall handling time, but not in handling time per prey. Some crabs would simply hold an intact or partially eaten clam but made no attempt to manipulate or consume it. This holding behaviour was exhibited by 24% of observed crabs, the majority of which were rock crabs, and was not included in the analyses of handling behaviour. Crabs spent a greater proportion of time foraging during the night observation

periods (21:00-24:00, 1:00-4:00) than during the day (6:30-9:30, 11:00-14:00, 16:00-19:00) in each predator treatment and habitat (Fig. 2.2a, b).

Interactions between crabs were categorized as: fighting, non-aggressive, threatening and other. During fights, crabs were observed grasping, pushing, rubbing, poking, fending and embracing (Jachowski, 1974; Smallegange et al., 2006). Non-aggressive encounters occurred when a crab changed its direction of travel to avoid the other crab (Smallegange et al., 2006) or when crabs touched but did not exhibit fighting behaviours (Wong et al., 2010). Threatening interactions consisted of a crab threatening another crab by opening their chelae and placing their cheliped(s) close to 180º to their body (Smallegange et al., 2006), but no fighting was observed. If one crab approached the other aggressively and there was no resulting physical contact, it was categorized as an 'other' interaction. Predator encounters began once a crab advanced within one CW of the other crab (Brown et al., 2005) and ended when a crab moved further than one CW away or when crabs resumed other behaviours.

2.4.2.2 Predator Foraging Behaviours

The proportion of time that crabs spent searching for prey was significantly affected by predator treatment, but not habitat type (full model, Table 2.3, Fig. 2.3). Isolated green crabs and green crabs with a conspecific spent a greater proportion of time searching than rock crabs alone, with a conspecific, or with a green crab (Tukey's tests, $p<0.05$). Single rock crabs and rock crabs with a conspecific or green crab, however, spent similar proportions of time searching for prey (Tukey's tests, $p>0.05$). For the analysis of predator treatments with only green crabs, neither predator treatment nor habitat had a significant effect on the proportion of time green crabs searched for prey (green crabs only model, Table 2.3, Fig. 2.3), indicating that green crab search time was not influenced by the presence of a conspecific or heterospecific crab.

The proportion of time crabs spent handling prey was significantly affected by habitat type (full model, Table 2.3, Fig. 2.3), and was greater in sand than in artificial seagrass, as more clams were consumed in sand. Predator treatment also significantly influenced the proportion of time spent handling prey (full model, Table 2.3, Fig. 2.3).

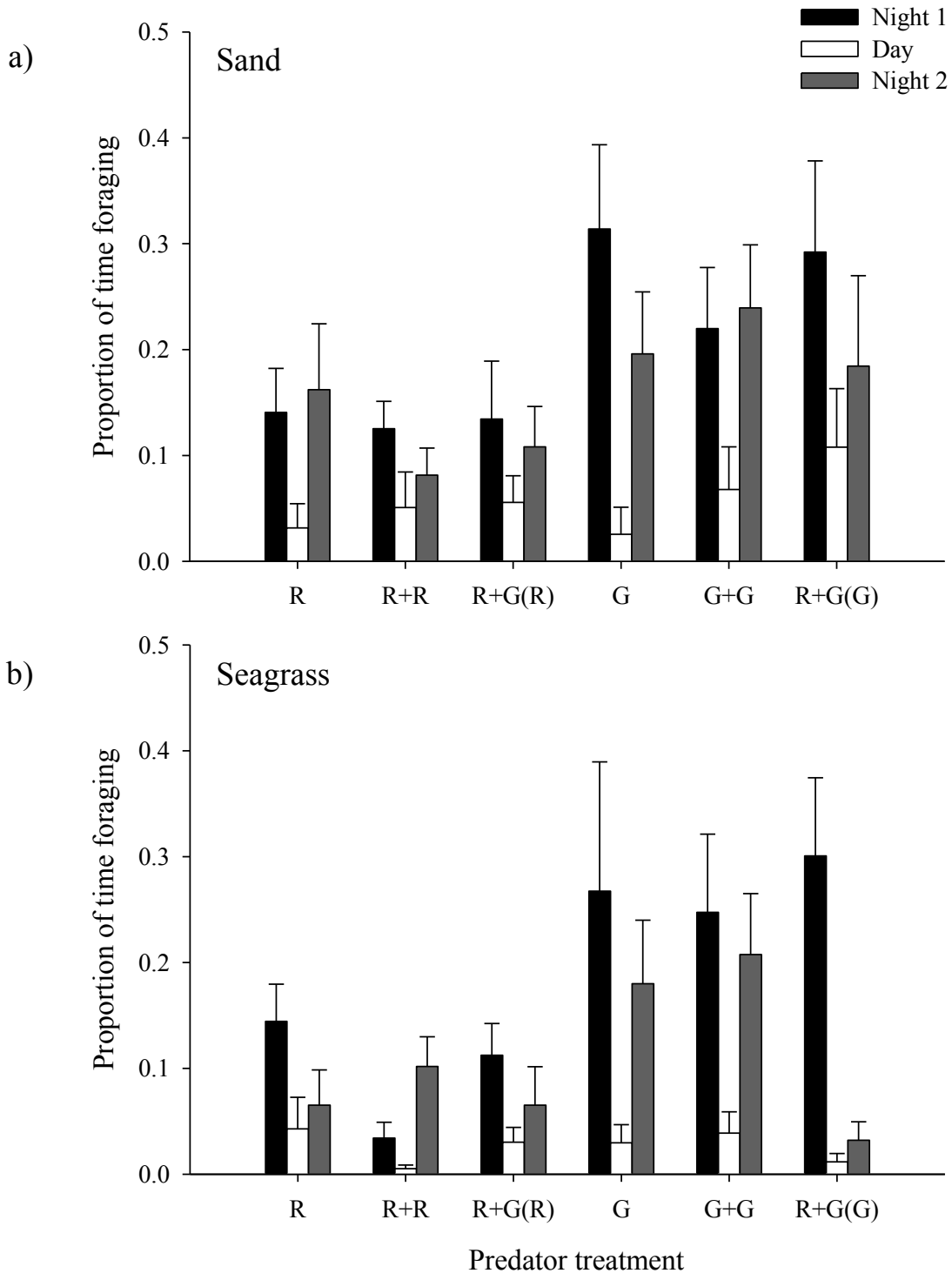


Figure 2.2 Proportion of time single and paired rock crabs (R) and green crabs (G) foraged during day and night observation periods (mean + SE, n = 7 or 8) in a) sand and b) artificial seagrass. For paired predator treatments, data are presented for one crab, with brackets identifying the focal species in the heterospecific treatment.

Table 2.3 Results from linear mixed-effects models examining foraging behaviours of rock crabs and green crabs in sand and artificial seagrass. For each behaviour, both the full model and green crabs only model (G model) are presented (see text). Logit transformations were applied to proportion of time spent searching for the full model, and to the proportion of time spent handling prey for both models. Prey encounters in both models and handling time per prey in the full model were transformed with square root(x+0.5) and square root(x), respectively. Handling time per prey for the green crabs only model was $\log_{10}(x)$ transformed. For prey encounters (full model) and handling time per prey (full model), data did not meet the assumption of homogeneity of variance. P-values in bold indicate significant results and marginally significant differences are italicised. Post-hoc comparisons are ordered from lowest to highest treatment level means; those sharing a common underline do not differ significantly. df_1 = numerator; df_2 = denominator; P = predator treatment; H = habitat; R = rock crab; G = green crab; SG = artificial seagrass; SN = sand.

	Model	Source of variation	df_1, df_2	F-value	P-value	Post-hoc comparisons
Proportion of time searching	Full	P	4, 61	11.07	**<0.0001**	R R+G R+R G+G G
		H	1, 61	0.14	0.706	
		P x H	4, 61	0.68	0.610	
	G only	P	2, 33	0.42	0.659	
		H	1, 33	0.03	0.869	
		P x H	2, 33	0.16	0.852	
Proportion of time handling prey	Full	P	4, 61	4.27	**0.004**	R+R R+G R G+G G
		H	1, 61	4.71	**0.034**	SG SN
		P x H	4, 61	0.33	0.859	
	G only	P	2, 33	0.42	0.661	
		H	1, 33	0.70	0.407	
		P x H	2, 33	0.12	0.890	
Prey encounters / search hr	Full	P	4, 58	5.08	**0.001**	G+G G R+R R+G R
		H	1, 58	3.95	*0.052*	SG SN
		P x H	4, 58	0.76	0.560	
	G only	P	2, 30	0.19	0.826	
		H	1, 30	4.62	**0.040**	SG SN
		P x H	2, 30	0.14	0.872	

	Model	Source of variation	df_1, df_2	F-value	P-value	Post-hoc comparisons
Handling time per prey	Full	P	4, 260	5.26	**0.0004**	R+R R+G G G+G R
		H	1, 260	0.08	0.779	
		P x H	4, 260	2.27	**0.063**	SN:R+R G G+G R R+G SG:R+R R+G G+G G R
						R: SN SG R+R: SG SN R+G: SG SN G: SN SG G+G: SG SN
	G only	P	2, 214	0.44	0.646	
		H	1, 214	0.54	0.464	
		P x H	2, 214	1.20	0.302	

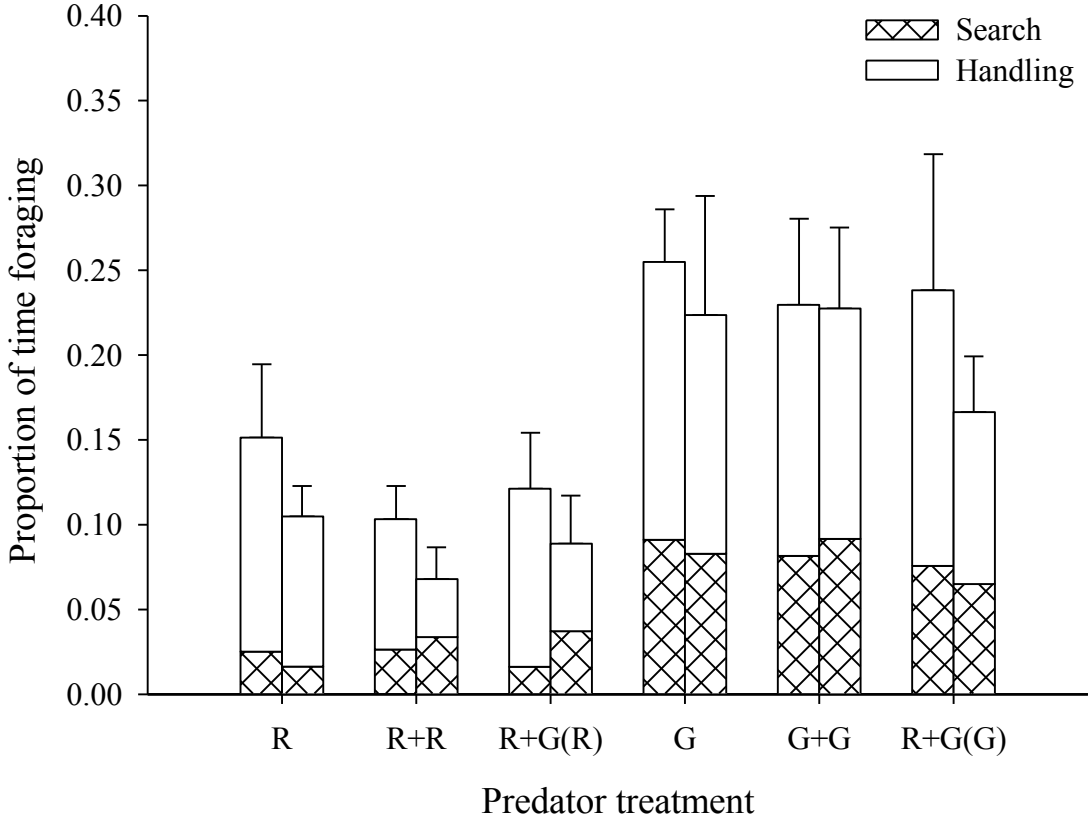


Figure 2.3 Proportion of time rock crabs (R) and green crabs (G) were observed foraging in single and paired predator treatments in sand and artificial seagrass (mean + SE, n = 7 or 8). For paired predator treatments, data are presented for one crab, with brackets identifying the focal species in the heterospecific treatment. For each predator treatment, the left bar depicts sand habitat and the right bar shows artificial seagrass habitat.

Single green crabs and green crabs with a conspecific spent a higher proportion of time handling prey than rock crabs with a conspecific (Tukey's tests, $p<0.05$). The proportion of time spent handling prey did not differ when rock crabs foraged alone, with a conspecific, or with a green crab (Tukey's tests, $p>0.05$). When predator treatments with only green crabs were analyzed, the proportion of time spent handling prey was not significantly affected by habitat or predator treatment (green crabs only model, Table 2.3, Fig. 2.3). Similar to rock crabs, green crabs did not alter their proportion of time spent handling prey when foraging with a conspecific or rock crab.

Encounter rate with prey was affected by habitat (full model, Table 2.3, Fig. 2.4), and was higher in sand than in artificial seagrass. However, this effect was only marginally significant and data transformation could not fulfill the assumption of homogeneity of variance, inflating the probability of a type 1 error (Underwood, 1997). Encounter rate with prey differed significantly with predator treatment (full model, Table 2.3, Fig. 2.4). Single rock crabs had higher encounter rates with prey than rock crabs with a conspecific, single green crabs and green crabs with a conspecific (Tukey's tests, $p<0.05$), indicating that single rock crabs were more efficient at searching. When green crabs were analysed separately, encounter rates with prey were significantly different with habitat (green crabs only model, Table 2.3, Fig. 2.4), with higher rates observed in sand. This provides support for the marginal habitat effect detected for the full model and indicates that green crabs contributed to this effect. Green crabs foraging alone, with a conspecific or a heterospecific had similar prey encounter rates.

A significant interaction between predator treatment and habitat was detected for handling time per prey (full model, Table 2.3, Fig. 2.5), although data could not be transformed to achieve homogeneity of variance, increasing the probability of a type 1 error (Underwood, 1997). In sand, handling time per prey did not differ across predator treatments (Tukey's tests, $p>0.05$). However, in artificial seagrass, rock crabs with a conspecific had lower handling times per prey than isolated rock crabs and isolated green crabs (Tukey's tests, $p<0.05$). For each predator treatment, handling time per prey was similar in both habitat types (Tukey's tests, $p>0.05$). For the green crabs only model, handling time per prey was not significantly affected by either habitat type or predator

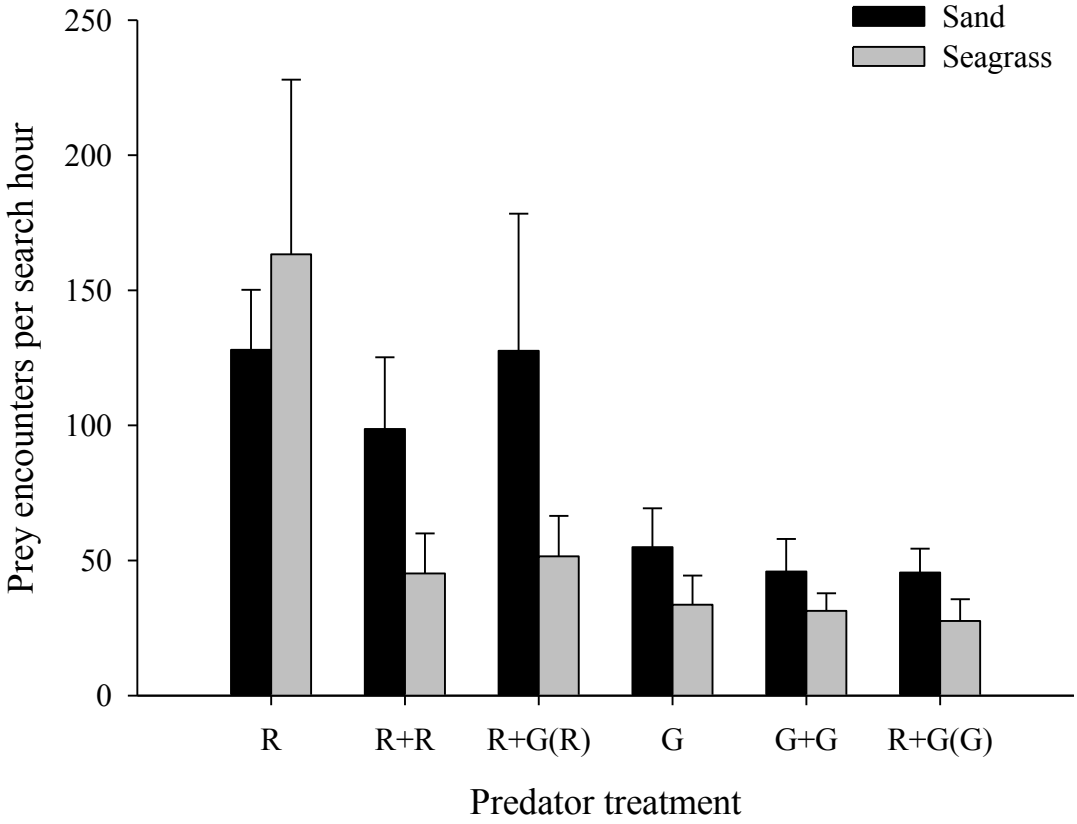


Figure 2.4 Number of encounters between rock crabs (R) or green crabs (G) with prey per search hour in single and paired predator treatments in sand and artificial seagrass (mean + SE, n = 5, 7 or 8). For paired predator treatments, data are presented for one crab, with brackets identifying the focal species in the heterospecific treatment. For each predator treatment, the left bar depicts sand habitat and the right bar shows artificial seagrass habitat.

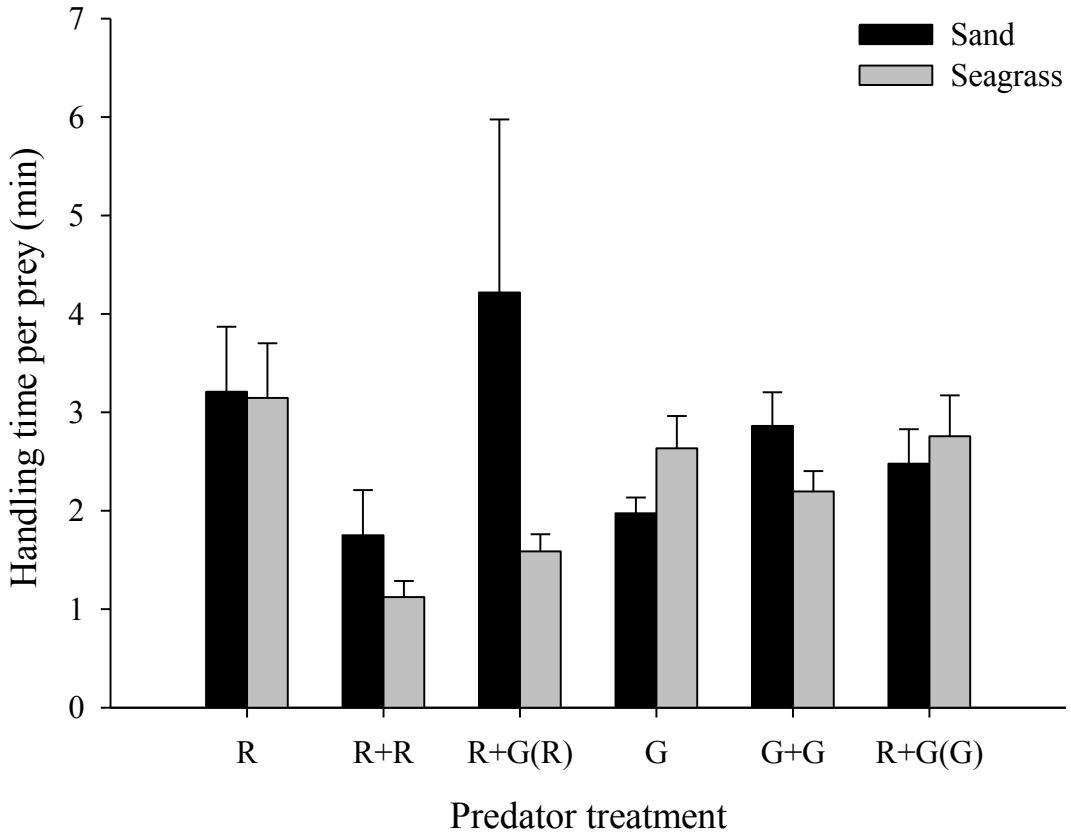


Figure 2.5 Handling time per prey for rock crabs (R) and green crabs (G) in single and paired predator treatments in sand and artificial seagrass (mean + SE, n =6 to 59). For paired predator treatments, data are presented for one crab, with brackets identifying the focal species in the heterospecific treatment. For each predator treatment, the left bar depicts sand habitat and the right bar shows artificial seagrass habitat.

treatment (Table 2.3, Fig. 2.5).

2.4.2.3 Encounters between Predators

Predator encounter rates were higher in sand than in artificial seagrass; however, this difference was only marginally significant (Table 2.4, Fig. 2.6a) due to high variability for conspecific green crabs in sand. Encounter rates between predators did not differ significantly with predator treatment (Table 2.4, Fig. 2.6a), but the nature of encounters appeared to be influenced by predator species identity. The majority of encounters between conspecific rock crabs (68 ± 7 and 71 ± 7 % of total encounters (mean ± SE, n = 8 and 6) in sand and artificial seagrass, respectively) and heterospecific crabs (83 ± 7 and 79 ± 7 %, n = 6 and 8 in sand and artificial seagrass) were non-aggressive, regardless of habitat type. In contrast, most encounters between green crab conspecifics in sand involved fighting (68 ± 5 %, n = 8), while in artificial seagrass, fighting (47 ± 8 %, n = 8) and non-aggressive encounters (48 ± 8 %, n = 8) were observed equally.

Interactions between predators were further examined to determine if the duration of encounters differed between conspecific and heterospecific crabs. The proportion of time that crabs were engaged in interactions did not differ significantly with either habitat or predator treatment (Table 2.4, Fig. 2.6b). Similar to encounter rate data, non-aggressive encounters constituted the majority of interaction time for conspecific rock

Table 2.4 Results from linear mixed-effects models examining interactions between conspecific and heterospecific rock crabs and green crabs in sand and artificial seagrass. Data collected from both crab species were pooled for heterospecific pairs. Encounter rate between predators was $\log_{10}(x+1)$ transformed. Marginally significant differences are italicised. df_1 = numerator; df_2 = denominator; P = predator treatment; H = habitat; SG = artificial seagrass; SN = sand.

Analysis	Source of variation	df_1, df_2	F-value	P-value	Post-hoc comparisons
Predator encounter rate / observation hr	P	2, 34	1.57	0.223	
	H	1, 34	3.69	*0.063*	SG SN
	P x H	2, 34	0.37	0.693	
Proportion of time engaged in interactions	P	2, 34	0.37	0.694	
	H	1, 34	0.92	0.345	
	P x H	2, 34	1.27	0.294	

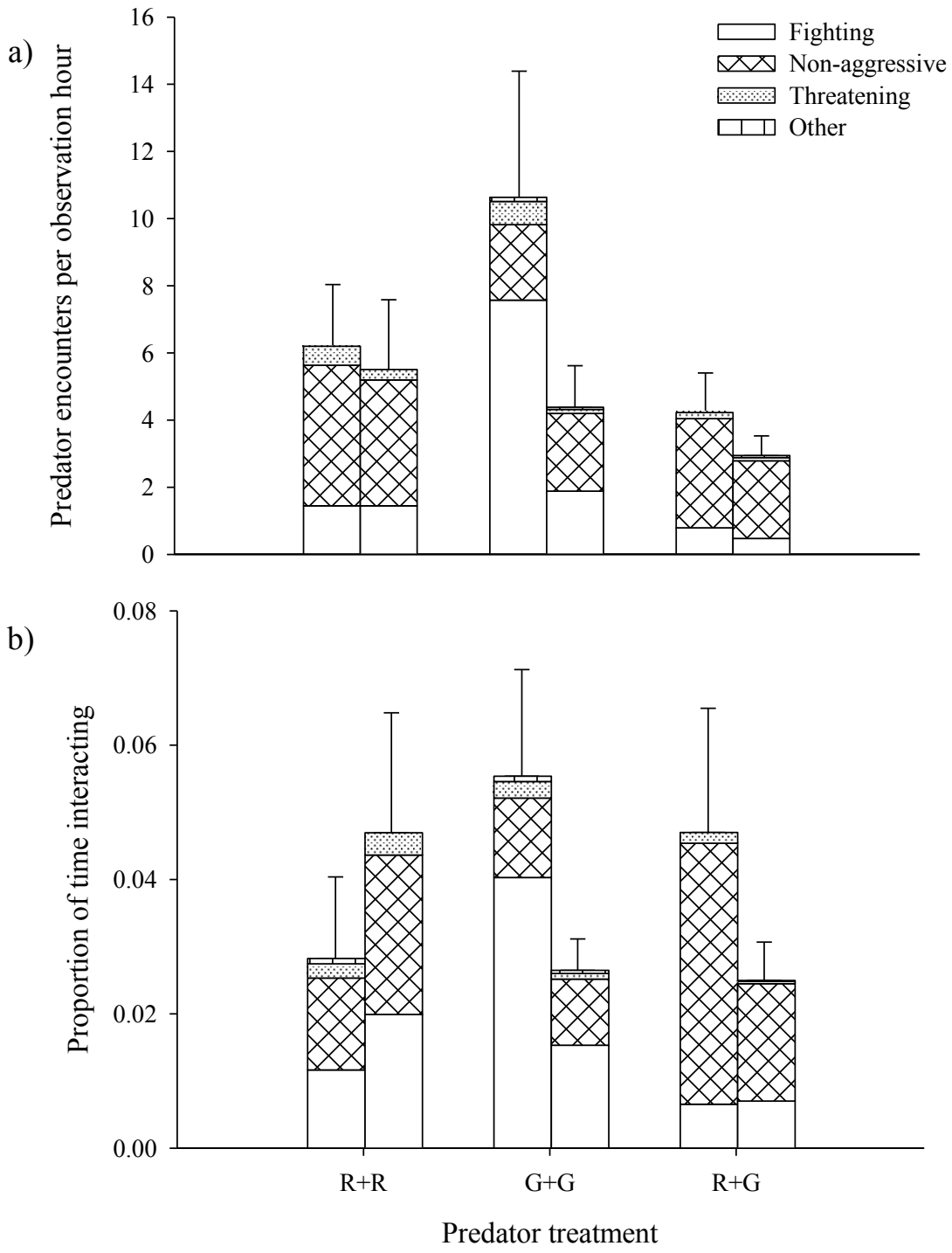


Figure 2.6 a) Number of encounters between predators per observation hour and b) proportion of time crabs were interacting when rock crabs (R) and green crabs (G) were paired (mean + SE, n = 7 or 8). For conspecific pairs, data is presented for one crab. For heterospecific crabs, data were pooled from both species. For each predator treatment, the left bar depicts sand habitat and the right bar shows artificial seagrass habitat.

crabs (64 ± 11 and 59 ± 10 % of total interaction time (mean ± SE, n = 8 and 6) in sand and artificial seagrass, respectively) and heterospecific crabs (78 ± 9, 70 ± 9 %, n = 6 and 8 in sand and artificial seagrass) in both habitats. However, fighting encounters dominated the interaction time of conspecific green crabs (65 ± 9, 59 ± 9 %, n = 8 in sand and artificial seagrass), irrespective of habitat type.

2.5 Discussion

Overall, I found independent multiple predator effects on prey for most paired predator treatments in both habitat types. The only exception was marginally significant risk reduction for prey when heterospecific pairs foraged together in artificial seagrass. The independent multiple predator effects on prey can be explained by observed predator behaviours. Predator foraging behaviours did not change whether crabs were alone or with a conspecific or heterospecific (except for conspecific rock crabs, see below), indicating that the presence of another predator did not hinder the focal crab's ability to search for prey, or limit the time spent handling juvenile clams. These results suggest that conspecific green crabs and heterospecific crabs foraged independently in both habitat types. Although rock crabs with a conspecific spent similar proportions of time searching for prey as isolated rock crabs, they had lower prey encounter rates, suggesting that the presence of a conspecific reduced searching efficiency. This may be attributable to vigilance, which has been observed in other studies when crabs forage together (Wong et al., 2010; Matheson and Gagnon, 2012b). Additionally, in artificial seagrass, rock crabs with a conspecific exhibited reduced handling times per prey compared to isolated rock crabs, suggesting that rock crabs with a conspecific consumed less flesh per clam. However, considering that rock crabs foraging alone or with a conspecific spent a similar proportion of time handling prey, rock crabs with a conspecific may have augmented their flesh intake by consuming meat from shell remains from previous feeding events. While conspecific rock crabs exhibited some behavioural changes relative to isolated crabs, the magnitude of these changes was not strong enough to produce non-independent multiple predator effects on prey.

Numerous studies have documented reduced predation rates due to aggressive interactions among crabs (e.g., Mansour and Lipcius, 1991; Clark et al., 1999; Smallegange et al., 2006; Griffen and Williamson, 2008; Wong et al., 2010); however, my study suggests that intra- and interspecific interactions among green crabs and rock crabs may not be important in regulating their consumption of soft-shell clams, providing further support for the observed independent multiple predator effects on prey. Encounter rates between predators were only marginally different in sand and artificial seagrass, but the proportion of time crabs engaged in encounters was comparable between habitats. Other studies suggest that the strength of interactions between crabs differs with habitat, allowing crabs to consume more prey in habitats where contact among crabs is reduced (e.g., Grabowski and Powers, 2004; Griffen and Byers, 2006a; Grabowski et al., 2008), but artificial seagrass blade density (~700 shoots m^{-2}) in my experiment may have been too low to reduce interactions between crabs relative to sand. Encounter rates between predators and time engaged in interactions did not differ with predator treatment, but encounters involving fighting were more common among conspecific green crabs than conspecific rock crabs or heterospecific pairs in both habitat types. Consequently, green crabs were more aggressive with a conspecific than a heterospecific, which has been previously documented (unpubl. data in Griffen, 2006; Griffen and Williamson, 2008), and seem to be more aggressive than rock crabs. However, regardless of differences in aggression between paired predator treatments, encounters between predators were short in duration (~2.23 mins per observation hr) and infrequent (~5 per observation hr). This suggests that encounters between predators did not reduce the time available for foraging, and consequently foraging success, irrespective of habitat type or predator species.

Independent multiple predator effects on prey for most paired predator treatments in both habitat types likely occurred because soft-shell clams were easily detected and consumed. Although soft-shell clams can obtain a partial refuge from crab predation with burial depth, juvenile clams are located near the sediment surface, where crabs are more efficient foragers (Blundon and Kennedy, 1982a; Boulding, 1984; Zaklan and Ydenberg, 1997). Additionally, the physical structure of soft-shell clams does not inhibit predation, as they have relatively thin, weak shells with gaping valves (Blundon and

Kennedy, 1982b; Boulding, 1984; Pickering and Quijón, 2011). As clams were never limiting, the presence of another crab predator likely had no effect on foraging success.

A non-independent multiple predator effect on prey was detected for heterospecific crabs in artificial seagrass (marginally significant). Risk reduction in systems with decapod predators is common and is typically attributed to aggressive interactions, prey switching from shared prey to the other predator, decreased crab density due to intraguild predation and/or changes in predator behaviours, such as reduced foraging in the presence of another predator (Siddon and Witman, 2004; Griffen, 2006; Griffen and Byers, 2006a; 2006b; Grabowski et al., 2008; Griffen and Williamson, 2008; Wong et al., 2010). However, in my study, heterospecific crabs in artificial seagrass did not change their foraging behaviours relative to isolated crabs, nor did they exhibit increased encounters or aggression between predators compared to other paired predator treatments. This suggests that these mechanisms for risk reduction were not important in regulating crab predation rates in my study. Other multiple predator studies have also documented lower predation rates in more structurally complex habitats (Swisher et al., 1998; Warfe and Barmuta, 2004). Swisher et al. (1998) observed risk enhancement for prey at low vegetation density and independent effects at higher densities, which they attributed to conflicting prey defenses (i.e., prey response to one predator increased its vulnerability to the other predator) which only occurred in the low vegetation density. In contrast, Warfe and Barmuta (2004) detected risk reduction for prey when predators foraged among macrophytes with a complex shape and independent effects with simpler macrophyte shapes because the predator avoidance strategy of the intermediate predator reduced its ability to capture prey only in the complex shape. However, these behavioural mechanisms were not present in my study. Thus, other multiple predator studies investigating the influence of habitat or utilizing decapod predators do not provide support for the non-independent effect observed in my study. Mechanisms responsible for this non-independent effect may be more complex than could be assessed in my experiment. One possible explanation is that rock crab foraging success may have declined due to the combined influence of reduced searching efficiency in artificial seagrass and the substantial removal of clams by green crabs, resulting in a non-independent effect on prey in artificial seagrass but not sand.

The multiple predator effects on prey observed in this experiment are consistent with other studies. Independent effects have been detected when conspecific green crabs forage on blue mussels (*Mytilus edulis*) (Wong et al., 2012) and conspecific rock crabs forage on sea scallops (*Placopecten magellanicus*) (d'Entremont, 2005). Similarly, Bélair & Miron (2009a, 2009b) found that green crabs and rock crabs foraging alone, with a conspecific or with a heterospecific had similar behavioural time budgets and per capita predation rates on mussels under most experimental regimes. However, non-independent multiple predator effects on prey have also been documented when green crabs forage with conspecifics (risk enhancement, risk reduction) or *Hemigrapsus sanguineus* (risk reduction) (Griffen and Byers, 2006a; 2006b; Griffen, 2006; Griffen and Williamson, 2008; Wong et al., 2012). Similarly, Gregory & Quijón (2011) observed a reduced predatory impact on infauna when green crabs and rock crabs foraged together at a high predator density compared to a low density. Multiple predator effects when crab predators forage together can be affected by relative crab size (Griffen and Byers, 2006b), predator density (Griffen and Williamson, 2008), prey size range (Wong et al., 2010), prey density (Griffen, 2006), habitat type (Griffen and Byers, 2006a; Wong et al., 2010) and habitat complexity (Grabowski et al., 2008). In addition to these studies, my results also suggest that multiple predator effects of crab predators are context dependent. Consequently, under different experimental conditions, green crabs and rock crabs may not forage independently with conspecifics and heterospecifics and habitat could play a more significant role in regulating multiple predator effects on prey.

Green crab and rock crab predation on soft-shell clams was significantly lower in artificial seagrass than in sand, but this did not translate into changes in predator behaviours causing non-independent multiple predator effects on prey. Crabs spent a similar proportion of time searching for prey in both habitats, but prey encounter rates were lower in artificial seagrass, particularly for green crabs, indicating that searching efficiency was reduced in this habitat. This is not a surprising result given that crab foraging success tends to be lower in structurally complex habitats (Sponaugle and Lawton, 1990; Grabowski, 2004; Hughes and Grabowski, 2006). It appeared that crab mobility was impeded in artificial seagrass because they often became tangled in the blades. Consequently, crabs in artificial seagrass may have had a lower search velocity

than those on sand, potentially reducing prey encounters. Because artificial seagrass blades were also present below the sediment surface, blades may have impaired crab detection and extraction of prey. Increased infaunal bivalve survivorship is often observed in seagrass relative to unvegetated soft-sediments and has been attributed to the root-rhizome system, which provides a refuge for prey by impeding predator digging (Reise, 1978; Blundon and Kennedy, 1982a; Peterson, 1982; Orth et al., 1984). However, blades may have served a similar function in this experiment. The ability of crabs to search for prey by probing the sediment with the ends of their walking legs and/or digging (Sponaugle and Lawton, 1990; Wong and Barbeau, 2003; Wong et al., 2012) was likely impeded by blades. However, the inclusion of a root-rhizome system would likely further hinder crab detection and retrieval of prey and potentially modify multiple predator effects on prey. For instance, crabs may spend more time searching to compensate for reduced searching efficiency, which could increase encounters between crabs and result in non-independent effects on prey. Alternatively, crabs may increase handling time per prey due to difficulty in extracting clams, which could reduce interactions between crabs and generate independent effects on prey.

In conclusion, I examined multiple predator effects on prey and the underlying behavioural mechanisms for green crabs and rock crabs foraging on commercially valuable soft-shell clams in different habitat types. Consistent with previous studies, both green crabs and rock crabs were significant predators of soft-shell clams and may have important effects on the clam fishery in eastern Canada (MacPhail et al., 1955; Floyd and Williams, 2004; Miron et al., 2005). In this study, crabs exhibited independent multiple predator effects on soft-shell clams for most paired predator treatments in both habitat types, indicating that the presence of conspecifics or heterospecifics will likely not reduce green crab and rock crab predation rates on clam flats. Although conspecific and heterospecific crabs did interact, encounters between predators appeared to have no effect on foraging time as juvenile clams were readily available and easily captured and consumed. Marginally significant risk reduction for prey was observed when heterospecific crabs foraged in artificial seagrass, indicating that the presence of structural complexity can modify multiple predator effects on prey when these crab species forage together. Further research is required to determine the cause of this non-

independent effect and to assess whether green crabs affect the foraging success of native rock crabs, their populations, and subsequently the commercial industry. This study demonstrates that multiple predator effects on prey may not be consistent across habitats and that behavioural observations are instrumental in explaining the observed multiple predator effects on prey.

CHAPTER 3

Influence of Invasive and Native Crab Predators on Soft-Sediment Community Structure

3.1 Abstract

I conducted a field experiment examining predation by invasive European green crabs (*Carcinus maenas*) and native rock crabs (*Cancer irroratus*) on a soft-sediment macrofauna community in Caribou Harbour, NS. Treatments consisted of an open plot or cages containing no crabs, single green crab, single rock crab, green crab conspecific pair, rock crab conspecific pair and heterospecific pair. Macrofauna was sampled after 3 and 6.5 weeks. Based on ANOSIM and SIMPROF tests, green crab and rock crab predation did not affect macrofauna community structure. It was not possible to determine with certainty whether a) crabs were not important in structuring the macrofauna community or b) predation effects were masked by other factors. Crabs predation was likely suppressed by the combined influence of interactions among crabs, harsh environmental conditions or a sub-optimal prey field. Alternatively, prey movement in and out of cages or low statistical power may have hindered the detection of significant predation effects. I did, however, observe an unexpected spatial gradient in community abundance across the study site, which persisted throughout the experiment. Because green crabs are recent successful invaders in this region, it is important to assess their impacts on a competing crab species and on their prey populations.

3.2 Introduction

Predation is an important structuring mechanism for prey populations and communities (e.g., Connell, 1975; Sih et al.,1985). Prey populations are often subjected to multiple predator species. Predator species foraging together can have independent effects on their prey (e.g., Wilbur and Fauth, 1990; Sokol-Hessner and Schmitz, 2002), meaning their combined consumption is the sum of prey consumed by each predator in isolation (Sih et al., 1998). However, numerous laboratory and field studies have documented non-independent multiple predator effects on prey (see reviews in Sih et al., 1998; Schmitz, 2007). These occur when the combined consumption of different

predator species foraging together is higher (risk enhancement for prey) or lower (risk reduction for prey) than the sum of prey consumed by predators foraging alone (Sih et al., 1998). Risk reduction can occur when changes to predator behaviours reduce foraging success, such as reduced activity in the presence of another predator, or increased interactions between predators (e.g., Crumrine and Crowley, 2003; Griffen and Williamson, 2008; Wong et al., 2010). Risk enhancement can result when the prey's defense mechanisms against one predator (e.g., behaviour, habitat use) increases its risk of being preyed upon by the other predator (e.g., Soluk, 1993; Losey and Denno, 1998; Sih et al., 1998). Predators foraging with conspecifics can also have non-independent effects on prey (Vance-Chalcraft et al., 2004; Vance-Chalcraft and Soluk, 2005; Wong et al., 2010; Wong et al., 2012). An emergent multiple predator species effect on prey only occurs when the magnitude of non-independence differs between conspecific and heterospecific predators, indicating that predator species identity, and not simply predator density, is responsible for the non-independent effect on prey (Sih et al., 1998; Vance-Chalcraft et al., 2004).

Although predators likely interact simultaneously with many different prey species in natural communities, studies usually examine multiple predator effects on only a single prey species (but see van Buskirk, 1988; Martin et al., 1989; Hurd and Eisenburg, 1990; Wilbur and Fauth, 1990; Morin, 1995; Nyström et al., 2001; Schmitz and Sokol-Hessner, 2002; Cardinale et al., 2003; Ross et al., 2004; Siddon and Witman, 2004; Hughes and Grabowski, 2006; Prasad and Synder, 2006; Griffen and Byers, 2009). However, studies have shown that the combined predation impact of multiple predator species foraging on multiple prey species may not be predictable based on results from subsets of the system (i.e., one predator species with multiple prey species, multiple predator species with one prey species) (Wilbur and Fauth, 1990; Prasad and Synder, 2006). Multiple predator species may alter their predation rates when faced with alternative prey species or indirectly affect non-prey species by modifying trophic pathways (Peckarsky and McIntosh, 1998; Cardinale et al., 2003; Siddon and Witman, 2004). For example, Cardinale et al. (2003) observed a trophic cascade where multiple predator species had risk enhancing effects on prey, resulting in increased yield of the prey's food source. Consequently, in order to determine the role of multiple predators in

structuring natural communities, it is important to monitor changes in species' populations which may be either directly or indirectly influenced by predation. Additionally, emergent multiple predator species effects on prey can only be identified by separating the influence of predator species richness and predator density (Sih et al., 1998), but the appropriate predator treatments to do so have not been included in studies examining multiple predator effects on prey in multi-predator multi-prey systems. Here, I investigated multiple predator effects of an invasive and a native epibenthic predator on a marine soft-sediment community using the full complement of predator treatments required to test for emergent effects on prey.

The invasive European green crab (*Carcinus maenas* L.) was first detected in the eastern United States in 1817 and expanded northward into Nova Scotia (NS) by 1953 (Say, 1817; MacPhail, 1953; Roman, 2006). A secondary introduction, likely originating from northern Europe, occurred during the 1980s and allowed green crabs to expand into northern NS and the Gulf of St. Lawrence (Audet et al., 2003; Roman, 2006). In the Gulf of St. Lawrence, green crabs overlap in distribution with native rock crabs (*Cancer irroratus* Say), a commercially harvested species in the region (DFO, 2008; Gregory and Quijón, 2011; A. Cheverie, pers. obs.). These species utilize the same habitat types, have broad, overlapping diets and sometimes consume one another (Crothers, 1968; Ropes, 1968; Scarratt and Lowe, 1972; Elner, 1981; Hudon and Lamarche, 1989), indicating that they interact and are potentially important competitors for the same prey species. Crabs foraging with conspecifics or heterospecifics can have independent effects on prey (Griffen and Byers, 2006b; Griffen and Williamson, 2008; Wong et al., 2010; Wong et al., 2012; Chapter 2). However, sometimes conspecific or heterospecific crabs can exhibit risk reduction for prey due to agonistic interactions, changes in foraging behaviours or intraguild predation (Griffen, 2006; Griffen and Byers, 2006a; 2006b; Griffen and Williamson, 2008; Wong et al., 2010). Alternatively, crabs can exhibit risk enhancement for prey, which has been attributed to stimulated foraging behaviours due to increased chemical cues in the presence of other crabs (Wong et al., 2012).

Studies investigating the effects of interactions between green crabs and rock crabs on their combined predation are limited, but have demonstrated that individual

predation rates either do not change or are reduced in the presence of heterospecifics (Bélair and Miron, 2009a; Gregory and Quijón, 2011; Chapter 2). Multiple predator effects of green crabs and rock crabs are likely influenced by the presence of alternative prey species and different prey sizes. For example, green crabs exhibit a diet shift in the presence of the Asian shore crab (*Hemigrapsus sanguineus*) and rock crabs alter their mussel size selection in response to chemical cues from live green crabs (Griffen et al., 2008; Matheson and Gagnon, 2012a). Consequently, multiple predator studies incorporating a diverse prey field are necessary in order to predict the effects of green crabs and rock crabs in natural systems.

I conducted a manipulative field experiment to examine multiple predator effects of green crabs and rock crabs on a soft-sediment community on Caribou Island, southern Gulf of St. Lawrence, NS. Green crabs have likely been present on Caribou Island since 1999 (Audet et al., 2003), where they overlap with rock crabs (A. Cheverie, pers. obs.). In soft-sediments within its invaded range, green crabs can cause significant declines in native prey populations (Grosholz et al., 2000; Floyd and Williams, 2004; Gregory and Quijón, 2011). Rock crabs can reduce infauna abundance and species richness in a laboratory setting and may reduce species richness in the field, suggesting that rock crabs are likely also important predators in soft-sediment communities (Quijón and Snelgrove, 2005a; 2005b). My study was designed to examine the role of these crab species, both in isolation and combined, in regulating the structure of a benthic macrofauna community. Specifically, my objectives were to determine (1) if green crabs and rock crabs (alone or combined) influence community structure based on abundance and biomass, and if so (2) whether green crab and rock crab predation produces independent or non-independent multiple predator effects on total macrofauna (> 1mm) community abundance and biomass, (3) whether predation by green crabs and rock crabs causes independent or non-independent multiple predator effects on the abundance and biomass of common taxa, and (4) in the event that non-independent multiple predator effects on prey are detected, whether the magnitude of non-independence differs between conspecific and heterospecific pairs (i.e., an emergent effect).

3.3 Materials and Methods

3.3.1 Study Site and Experimental Materials

A manipulative field experiment was conducted from September to November 2009 in the low intertidal zone at Caribou Island, NS, located on Caribou Harbour in the southern Gulf of St. Lawrence (Fig. 3.1). The experimental area was only exposed during spring tides, for a maximum of ~1.5 hrs. The study site was a homogeneous sand-flat, bordered by a seagrass bed to the south and rocks interspersed in sand on the north, west, and east sides. This site was chosen because green crabs and rock crabs overlap in distribution. Both crab species were collected during trapping surveys in July, August and September 2009 (A. Cheverie, unpubl. data). Preliminary sampling indicated that the soft-sediment community was dominated by small bivalves and polychaetes, of which many species appear in the diets of green crabs and rock crabs (e.g., Hudon and Lamarche, 1989; Stehlik, 1993; Cohen et al., 1995).

Cages (1 m long x 1 m wide x 0.55 m high) were constructed of black knotless nylon netting (1.9 cm mesh size) covering a PVC pipe frame (1.3 cm diameter) (Fig. 3.2). This mesh size was selected to restrict the movement of only large mobile predators into and out of the cages, including flatfish and adult crabs, and to limit potential cage artifacts, such as reduced water flow and shading. PVC pipes were tied to the bottom of the mesh to ensure that it remained buried during the experiment. Mesh was dug ~20 cm into the sand to prevent crabs from burrowing in and out of cages.

Green crabs and rock crabs were collected with baited conical crab pots (0.9 m diameter) at the study site and in the two adjacent coves on Caribou Island in September and October 2009. To prevent potential sex biases, only male crabs with intact chelae and walking legs were retained. Green crabs and rock crabs ranged from 51-60 mm in carapace width (CW) and 85-97 mm CW, respectively, measured as the distance between the notches anterior to the most distal marginal teeth. Crabs within these size ranges were the most abundant at the study site based on trapping data collected in July, August and September 2009, where green crabs measured 53.9 ± 5.9 mm CW (mean ± SD, n=122) and rock crabs measured 88.9 ± 11.2 mm CW (n=130) (A. Cheverie, unpubl. data). Prior to the experiment, crabs were separated by species and held in different crab

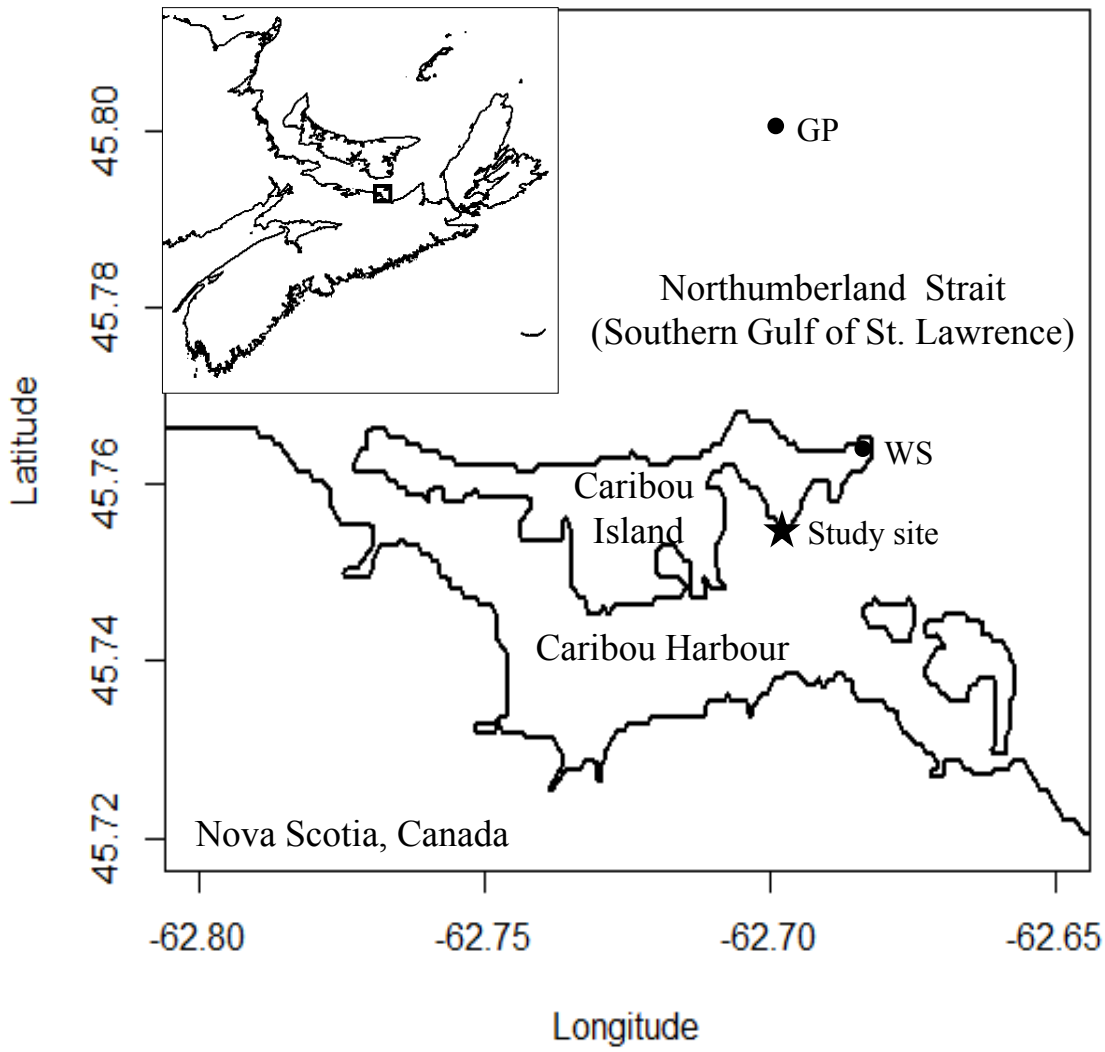


Figure 3.1 Location of study site and weather station (WS) on Caribou Island and grid point for significant wave heights (GP) in the Northumberland Strait.

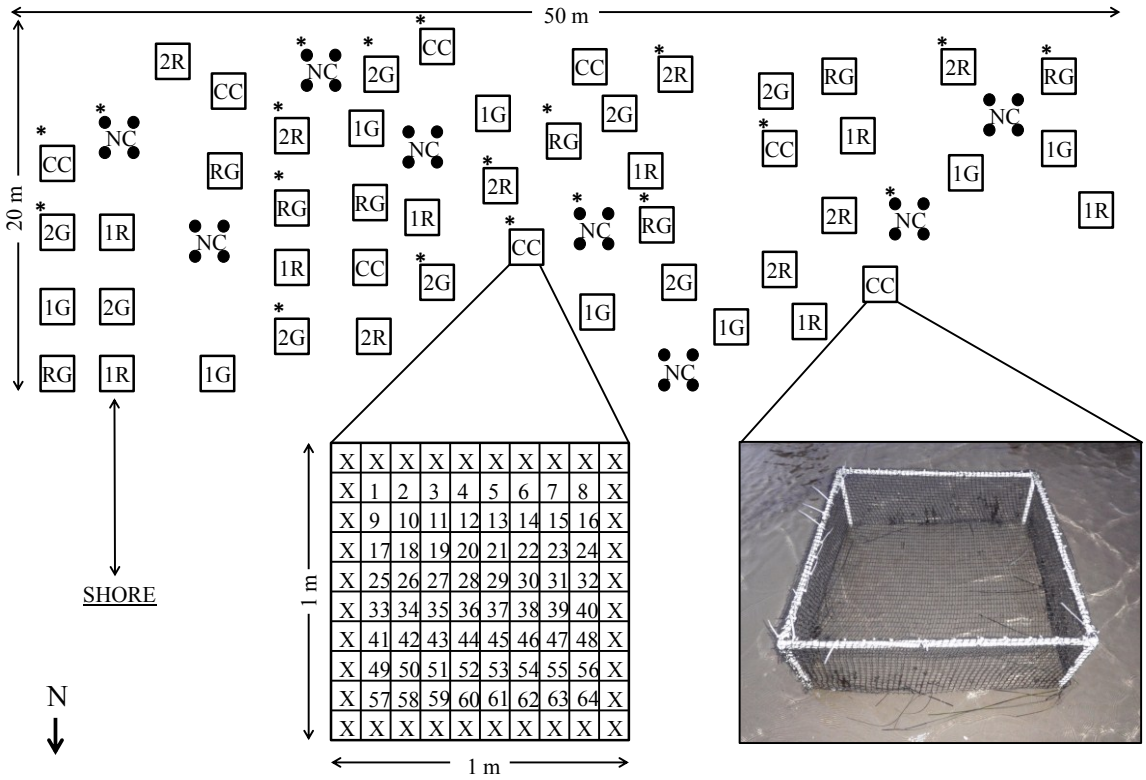


Figure 3.2 A representation of the experimental design (not drawn to scale). The top figure depicts the layout of the treatments at the experimental site. Cages (boxes) and open plots (four circles) from which macrofauna samples were processed are indicated by *. Treatments include a natural control (NC), cage control (CC), single green crab (1G), single rock crab (1R), green crab conspecific pair (2G), rock crab conspecific pair (2R) and heterospecific pair (RG). The bottom illustration shows the sampling grid, with X's specifying regions which were not sampled and numbers 1-64 identifying possible sampling positions chosen at random. An installed cage can be seen in the bottom-right.

pots near the experimental area. Crabs were fed frozen or canned fish every 1-3 days and were starved 1-2 days before they were added to experimental cages. As some crabs escaped or died during the experiment, trapping continued during the experiment and replacement crabs were stored in crab pots near the study site.

3.3.2 Experimental Design

To assess green crab and rock crab multiple predator effects on macrofauna, I established 7 treatments: open plot (natural control), no crabs (cage control), single green crab, single rock crab, green crab conspecific pair, rock crab conspecific pair and heterospecific pair. Natural controls were designated by a PVC pipe at each corner of a 1 x 1 m plot. Although crab densities within cages (1or 2 crabs m^{-2}) exceeded those observed at the study site (A. Cheverie, pers. obs.), these densities fall within the range observed in the southern Gulf of St. Lawrence (Gregory and Quijón, 2011). Forty-eight cages and eight natural controls were installed in a 50 x 20 m area of the sand-flat. Cages and natural controls were distributed haphazardly and separated by 1-1.5 m. Treatments levels were randomly assigned to cages, generating eight replicates of all treatments (Fig. 3.2). Cages and natural controls were exposed for similar durations; the study site was generally inundated and the maximum difference in exposure time was < 30 min.

Cages and natural controls were installed on 20-26 September and crabs were randomly assigned to cages on 3-10 October. Macrofauna samples were collected on four occasions: 28 September – 2 October (prior to crab addition), 21-28 October (17-22 days after crab addition), 6-12 November (32-37 days after crab addition) and 21-22 November (42-50 days after crab addition). Experimental set-up, crab addition and sampling were conducted over several days due to limited exposure at low tide and stormy weather, which prevented access to the experimental area. Due to a lack of observable predation effects during the late October (hereafter October) and late November (hereafter November) sampling rounds (see 'Results'), macrofauna samples collected before crabs were added to experimental treatments (late September - early October) and in early November were not processed. Cages were monitored weekly to ensure that crabs were accounted for and cages were clear of debris (e.g., drift algae).

During the experiment, 26 crabs escaped (predominantly green crabs) and 6 died out of a total of 81. Crabs were replaced during the late October and early November sampling rounds. On eight occasions, other large predators (fish and crabs) gained access to the cages and were removed.

Five samples of benthic macrofauna were collected from every cage (after pulling back the cage top) and natural control using a hand core (10 cm diameter, 12 cm depth) during each sampling round. Prior to sampling, a 1 m^2 PVC frame with a 10 x 10 grid of polyethylene twine was placed on the cage or natural control to locate the randomly assigned sampling positions (see Fig. 3.2). To limit edge effects associated with caging, samples were not taken within 10 cm of the perimeter of the treatments. Additionally, samples were not collected from the same position or in areas directly beside a sampled area in the previous sampling round. Sediment directly outside of cages or natural controls was used to fill in holes produced by sampling. Samples were cooled with ice packs and/or refrigerated at ~4ºC until they were rinsed through a 1 mm sieve with salt water. Remaining materials were preserved in a 5% buffered formalin solution and transferred to 70% ethanol ~ 2 weeks later.

For the October and November sampling rounds, three macrofauna samples were processed from four replicates of natural controls, cage controls, green crab conspecific pair, rock crab conspecific pair and the heterospecific pair. I began by processing samples from the paired predator treatments to determine if a predation effect was apparent. Because predation effects were not detected (see 'Results'), I did not process samples from single predator treatments. Power analyses on abundance data from the November sampling round indicated that I had low power (<30%) to detect a 50% decline in bivalves, polychaetes, gastropods and total macrofauna abundance (A. Cheverie, unpubl. data). Consequently, I did not process the other two macrofauna samples collected from each replicate because it was unlikely that this additional data would alter the results. All replicates of caged treatments could not be used as two cages disappeared, some crabs escaped and other adult crabs or fish occasionally gained access to cages. The selected replicates had few crab escapes (3) or deaths (3) and were not accessed by other large predators throughout the experimental period. Replicates of

natural controls were chosen to represent the entire experimental area. Using a dissecting microscope, animals were identified to the lowest taxonomic unit and counted. Bivalves, gastropods, amphipods and isopods were grouped according to genus or species; polychaetes to family; tanaidaceans to order and nemerteans to phylum. Although other organisms were present in macrofauna samples, they were excluded from analyses because they were either inadequately sampled (large mobile epifauna, meiofauna) or were not representative of a soft-sediment benthic community and were considered a chance encounter (e.g., barnacles, hydroids, bryozoans, caprellids, serpulidae, planktonic larvae). For each sample, biomass was obtained for every taxonomic group by drying specimens at 60ºC for ~24 hrs. Shell material was removed from molluscs prior to drying using 10% HCl. For animals retained as vouchers, dry mass was determined from wet mass using conversion factors from a data bank (Brey, 2001; Brey et al., 2010). Abundance and biomass data were converted to individuals per m^2 and g per m^2, respectively.

Large mobile epifauna were capable of moving in and out of cages. Because these animals were not adequately represented in cores, their abundance in all treatments was recorded during the early November and late November sampling rounds. Considering that the sediment was predominantly submerged throughout the experiment but large epifauna were documented during sampling when the sediment was often exposed, data may not reflect the actual abundances or the full complement of large epifauna which accessed the study site. Consequently, this data was only used to identify some of the taxa which frequented the treatments. Abundance of large epifauna was not documented between sampling rounds due to poor visibility inside submerged cages.

3.3.3 Environmental Conditions

To assess the sediment characteristics of the study site, sediment particle size distribution and organic content was determined in the four natural controls from which macrofauna samples were processed. During the October and November sampling rounds, two sediment samples were collected directly beside macrofauna samples using a 60mL syringe with the end cut off, pushed 11cm into the sediment. Sediment samples

were then frozen. For particle size and organic content analyses, one sediment sample was randomly selected from each natural control in both sampling rounds and oven dried at 60ºC for 48 hrs, then processed according to Bale & Kenny (2005). Samples (~25 g) were disaggregated with sodium hexametaphosphate (6.2g / L) and wet-sieved to separate sediment into gravel (>2mm), coarse and medium sand (250µm – 2mm) and fine sand (63-250µm) fractions. Fractions were dried at 60ºC for ~48 hrs and weighed. The % of gravel, coarse and medium sand or fine sand was calculated as (fraction mass/total mass) x 100 and % loss was attributed to silt and clay (<63 µm). Organic content was determined following a modified protocol of Wong et al. (2011). Samples (~0.5 g) were combusted in a muffle furnace at 500ºC for 7 hrs and subsequently oven dried at 60ºC for 2 hrs and weighed. Percent organic content was calculated as (initial dry mass-mass after combustion/initial dry mass) x 100.

Water temperature was monitored hourly throughout the experimental period using 5 Tidbit® v2 water temperature data loggers UTBI-001 (Onset Computer Corporation). Loggers were attached ~ 30cm above the sediment to 4 cages and 1 natural control, which were distributed throughout the site. In order to exclude air temperature readings, I only retained temperatures from ± 1 hr of the nearest hour to high tide. Water temperatures were calculated as the mean of all readings recorded within each 2 hr high tide period. The nearest hour to high tide was determined with the predicted time of arrival of each high tide in Pictou, NS (Station no. 1630, 45.68°, -62.70°), provided by the Canadian Hydrographic Service, Fisheries and Oceans Canada.

Although my field site is located in an embayment, it is likely influenced by both large scale and local scale disturbances. Caribou Harbour is most affected by conditions in the Northumberland Strait (southern Gulf of St. Lawrence) during northeasterly winds, which can result in large waves and sediment redistribution within the harbour (A. Sweet, pers. comm.). Within Caribou Harbour, southeasterly to southwesterly winds could contribute significant waves to my study site (G. Manson, pers. comm.; P. MacAulay, pers. comm.). To assess wind conditions at the study site, I obtained hourly wind speeds and wind directions from the Caribou Point weather station (climate identifier: 8200774, Environment Canada, 2012) located ~1.5 km from the site (Fig. 3.1). I obtained

predicted hourly significant wave heights, defined as the average height of one-third of the highest waves, from the MSC wind and wave hindcast of the North Atlantic Ocean for a grid point (M6009250) ~5 km north of the study site (Fig. 3.1). Data were provided by Integrated Science Data Management, Fisheries and Oceans Canada.

3.3.4 Cage Effects

The physical structure of cages can alter the hydrodynamic regime, resulting in cage artifacts. For instance, changes in water flow may increase erosion or sediment deposition, as well as enhance the settlement of planktonic larvae (Hulberg and Oliver, 1980; Virnstein, 1978). To assess the potential influence of cages on water motion, I compared the relative dissolution rates of plaster in all 8 natural controls and 8 randomly selected cages which were distributed throughout the site (e.g., Muus, 1968; Doty, 1971). Dissolution standards were ~21 g hemispheres (4-cm diameter) of DAP® Plaster of Paris (Dry Mix) attached to polyethylene twine. Standards were added to natural and cage controls on November 21 or 22, and exposed for 21 hrs or 25 hrs, respectively. In natural controls, standards were suspended in the centre of plots. In cages, they were located in a corner furthest from shore, to detect the maximum effect of cages on water flow. Before and after exposure, standards were dried at 85ºC for 24 hrs and weighed. Proportion of mass loss from plaster standards was calculated as initial mass – final mass/initial mass. A linear relationship exists between flow velocity and plaster weight loss (Jokiel and Morrissey, 1993). Thus, mass loss from standards within cages would be lower than in natural controls if cages impede water flow.

To determine whether cages altered the underlying sediment properties relative to natural controls, I also conducted particle size and organic content analyses on sediment samples taken from the four cage controls from which macrofauna samples were processed. Sediment samples from the October and November sampling rounds were collected and processed following the protocols described in section 3.3.3.

To assess the effect of caging on shading, light levels within and just outside of 37 cages were measured using a light meter (Milwaukee® SM700 portable lux meter with waterproof probe). Light levels were collected from October 22-28; however, readings

from inside and outside of each cage were conducted immediately after one another to ensure that changes in environmental conditions were not responsible for differences in light levels.

3.3.5 Statistical Analyses

For both the October and November sampling rounds, I pooled abundance data and biomass data from macrofauna samples within each treatment replicate (i.e., a single cage or natural control). Similarities between treatment replicates for both sampling rounds were calculated with the Bray-Curtis coefficient (Bray and Curtis, 1957) on transformed abundance and biomass data. Abundance data were square-root transformed, placing most weight on taxa of high or intermediate abundance in subsequent analyses (Clarke and Green, 1988). I applied a fourth root transformation to biomass data, which down-weights the contribution of dominant species (i.e., species with high biomass) and increases the importance of rare species (i.e., species with low biomass) (Clarke and Green, 1988). This transformation was utilized to ensure that numerically abundant taxa contributed to biomass analyses, some of which had low biomass and to reduce the importance of taxa which were not abundant but had high biomass.

3.3.5.1 Community Response to Treatments over Time

To test for differences in both community abundance and biomass between treatments (5 levels) and sampling rounds (2 levels), I employed two-way crossed Analyses of Similarities (ANOSIM, 999 permutations, Clarke, 1993). The null hypothesis for ANOSIM is that rank similarities between treatments (or sampling rounds) and within treatments (or sampling rounds) are the same on average. The *R* test statistic is calculated by:

$$R = (\bar{r}_B - \bar{r}_W)/(n(n\text{-}1)/4)$$

where $\bar{r}_B$ is the average of rank similarities between replicates between treatments (or sampling rounds), $\bar{r}_W$ is the average of rank similarities between replicates within

treatments (or sampling rounds) and *n* is the sum of replicates from each group. For each factor, an $\bar{R}$ test statistic is obtained by calculating an *R* value at each level of the other factor and averaging these values. The $\bar{R}$ test statistic ranges from +1 to -1. Positive $\bar{R}$ values indicate greater similarities within than between treatments (or sampling rounds), values close to zero support the null hypothesis and negative values demonstrate greater similarities between than within treatments (or sampling rounds). The null $\bar{R}$ distribution is created based on permutations of replicates within each level of the other factor.

3.3.5.2 Patterns in Community Structure

To visually assess patterns in community abundance and biomass across treatments and sampling rounds, I conducted non-metric multidimensional scaling (MDS, 50 restarts) using rank similarities and hierarchical agglomerative clustering (CLUSTER) with group-average linking on similarities. Kruskal's stress formula 1 was used to measure the goodness-of-fit of the two-dimensional MDS plots (Kruskal and Wish, 1978). Results from ANOSIM suggested that community abundance exhibited spatial and temporal patterns (see 'Results'). Consequently, I tested for patterns in community abundance and biomass by conducting similarity profile (SIMPROF, Clarke et al., 2008) tests in conjunction with CLUSTER analyses. SIMPROF is capable of detecting gradients among replicates and tests the null hypothesis that all replicates have the same community structure. Beginning at the top of a dendrogram, a SIMPROF test is conducted at each node until a non-significant ($p>0.05$) result is obtained, indicating that the group contains replicates with similar community structure. No further testing is then performed on that branch. For a group of replicates, the π test statistic is calculated as the area between its similarity profile (similarities plotted against their ranks) and the mean of 1000 permuted profiles, and then compared to the null π distribution. The π null distribution is produced by comparing each similarity profile from an additional set of 999 permutations to the mean permuted profiles (for additional information on SIMPROF, see Clarke et al., 2008). To determine which taxa contributed to differences in community structure between groups of replicates identified as significantly different by SIMPROF tests, I employed similarity percentages (SIMPER, Clarke, 1993) analyses, which calculate the average contribution of each taxa to the average dissimilarity between

two groups. Only taxa included in ≤70% of the cumulative percent contribution to average dissimilarities among SIMPROF groups were examined.

3.3.5.3 Multiple Predator Effects

Multiple predator effects on prey would be evaluated if crabs had significant effects on community structure based on abundance or biomass according to ANOSIM or SIMPROF tests. Because conspecific green crab pairs, conspecific rock crab pairs and heterospecific pairs did not influence community structure (see 'Results'), I did not test for multiple predator effects on prey.

3.3.5.4 Environmental Conditions

The Bio-Env procedure (Clarke and Ainsworth, 1993) was utilized to assess which environmental variables (% organic content, % gravel, % coarse and medium sand, % fine sand, % silt and clay) could 'best explain' patterns in community structure observed for abundance data. Bio-Env compares the biotic similarity matrix to abiotic similarity matrices for each possible combination of environmental variables. Spearman's coefficient (ρ_s) was used to calculate a rank correlation between each set of matrices. The optimal subset of environmental variables (i.e., with the highest ρ_s value) constitutes the best match to the biotic data. Only abundance data collected from natural controls and cage controls were utilized for these analyses. Biotic and abiotic data were averaged across sampling rounds, following Clarke and Ainsworth (1993), and the biotic similarity matrix was calculated as above. For environmental variables, log(x+0.1) transformations were applied to all variables to improve multivariate normality, which was assessed with draftsman plots. Similarities were calculated between treatment replicates with Euclidean distance using normalized data, which ensures that variables with larger variances do not contribute more to the results (Quinn and Keough, 2002). Following Clarke and Ainsworth (1993), only one representative environmental variable was included in Bio-Env when variables were mutually correlated (> 0.95 or < -0.95) according to standard product-moment correlations. To determine whether a statistically significant linkage between biotic and abiotic data was present, I employed the global BEST test (999 permutations, Clarke et al., 2008), which tests the null hypothesis that

there is no relationship between the biotic data and the optimal subset of environmental variables generated from Bio-Env. This test produces permutations of the environmental matrix (all variables included) and calculates ρ_s values with the Bio-Env procedure. The highest ρ_s value generated from each permutation is included in the null ρ_s distribution.

3.3.5.5 Cage Effects

To assess the influence of caging on water flow, I compared the proportion of mass loss from plaster standards in natural controls and cages with an independent samples t-test (2-tailed) for each date that standards were exposed. I ran separate analyses because the experimental conditions on both dates were not consistent due to different exposure times. Assumptions of normality and homogeneity of variance were assessed with normality Q-Q plots and boxplots (Quinn and Keough, 2002).

Percent organic content and percent fine sand were each analyzed with a univariate RM ANOVA to determine if the presence of cages altered sediment characteristics compared to natural controls. Fine sand was selected to test for changes in grain size because it was the dominant size fraction in the experimental area. Plot was the subject, treatment (natural control, cage control) was the between-subjects factor and sampling round (October, November) was the within-subjects factor. Plot was a random factor, while treatment and sampling round were fixed factors. Normality and homogeneity of variance were examined with normality Q-Q plots of residuals and plots of residuals versus fitted values, respectively (Draper and Smith, 1998). To assess these assumptions for each level of the between-subjects factor, I obtained residuals from a 1-way ANOVA with percent organic or fine sand averaged across sampling rounds as the dependent variable and treatment as a fixed factor (Quinn and Keough, 2002). Because the assumption of sphericity is not applicable when a within-subjects factor has only two levels, I tested for homogeneity of variance for the within-subjects factor using residuals from the RM ANOVAs.

I employed a paired t-test (1-tailed) to compare differences in light levels inside and outside of cages. I chose a 1-tailed test because I am only interested in determining if light levels were lower inside than outside of cages, which would indicate a shading

artifact. Normality was assessed with a normality Q-Q plot of differences. Light levels were square-root transformed to improve normality.

Multivariate analyses were performed in PRIMER (Plymouth Routines in Multivariate Ecological Research) v. 6.1.6 (Clarke and Gorley, 2006). Univariate analyses were run in SPSS 20.0 (IBM Corporation, 2011). The significance level for all statistical tests was p=0.05.

3.4 Results

3.4.1 Benthic Macrofauna Community Composition

The macrofauna community was composed of bivalves, polychaetes, gastropods, crustaceans and nemerteans. In natural controls, total abundance ranged from 9549 – 23682 individuals m^{-2} in October and 8191 – 19014 individuals m^{-2} in November, while total biomass (shell free dry weight) ranged from 1.063 – 2.023 and 1.040 – 5.967 g m^{-2} in October and November, respectively. In October, bivalves dominated in terms of abundance and biomass (Fig. 3.3a, b). In November, bivalves were numerically dominant and had greater biomass than the other classes, except for polychaetes (Fig. 3.3a, b). Abundance and biomass of macrofauna classes remained fairly consistent for both sampling rounds, except for polychaetes, whose average biomass was higher and more variable in November (Fig. 3.3a, b). I considered a taxa to be common if ≥ 1 individual was found on average in natural controls during each sampling round. The most common species at the study site was the amethyst clam, *Gemma gemma*, which greatly surpassed all other frequently encountered taxa in both abundance and biomass (Fig. 3.4a, b). Other numerically dominant bivalves were soft-shell clams (*Mya arenaria*), Atlantic surfclams (*Spisula solidissima*) and tellins (*Tellina* spp.). Like *G. gemma*, these bivalves were predominantly small (≤ 5 mm). However, approximately one-third of *Tellina* spp. were > 5mm, which explains their higher biomass than comparably abundant *M. arenaria*. Polychaetes were numerically dominated by syllidae and spionidae, followed by cirratulidae and paraonidae (Fig. 3.4a). Members of these polychaete families were also quite small in size (≤ 10mm in length). Besides *Hydrobia minuta* (Fig. 3.4a, b), gastropods were generally not abundant. The abundance and

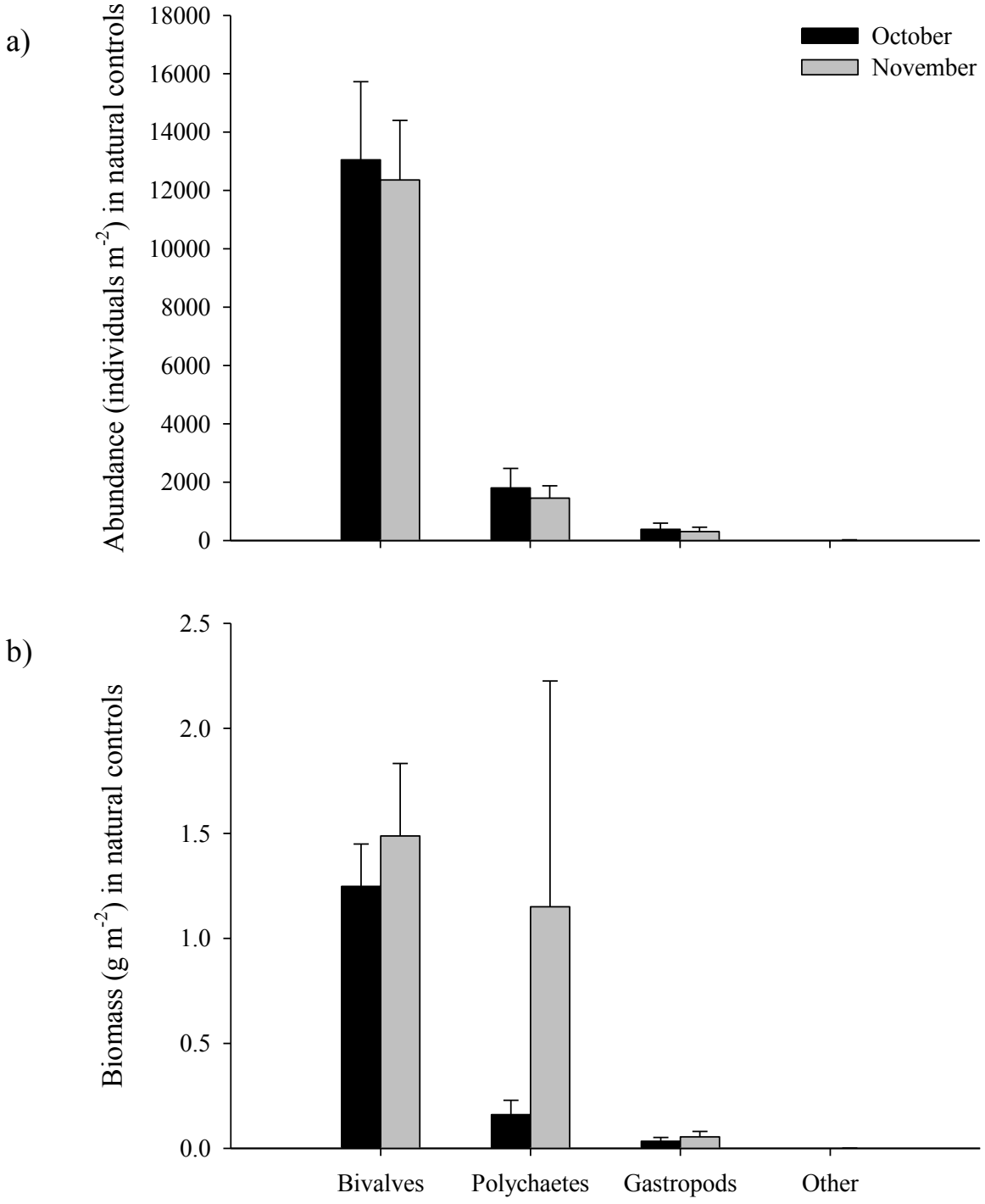


Figure 3.3 a) abundance and b) biomass (shell free dry weight) of macrofauna classes collected in cores from natural controls during the October and November sampling rounds (mean + SE, n = 4).

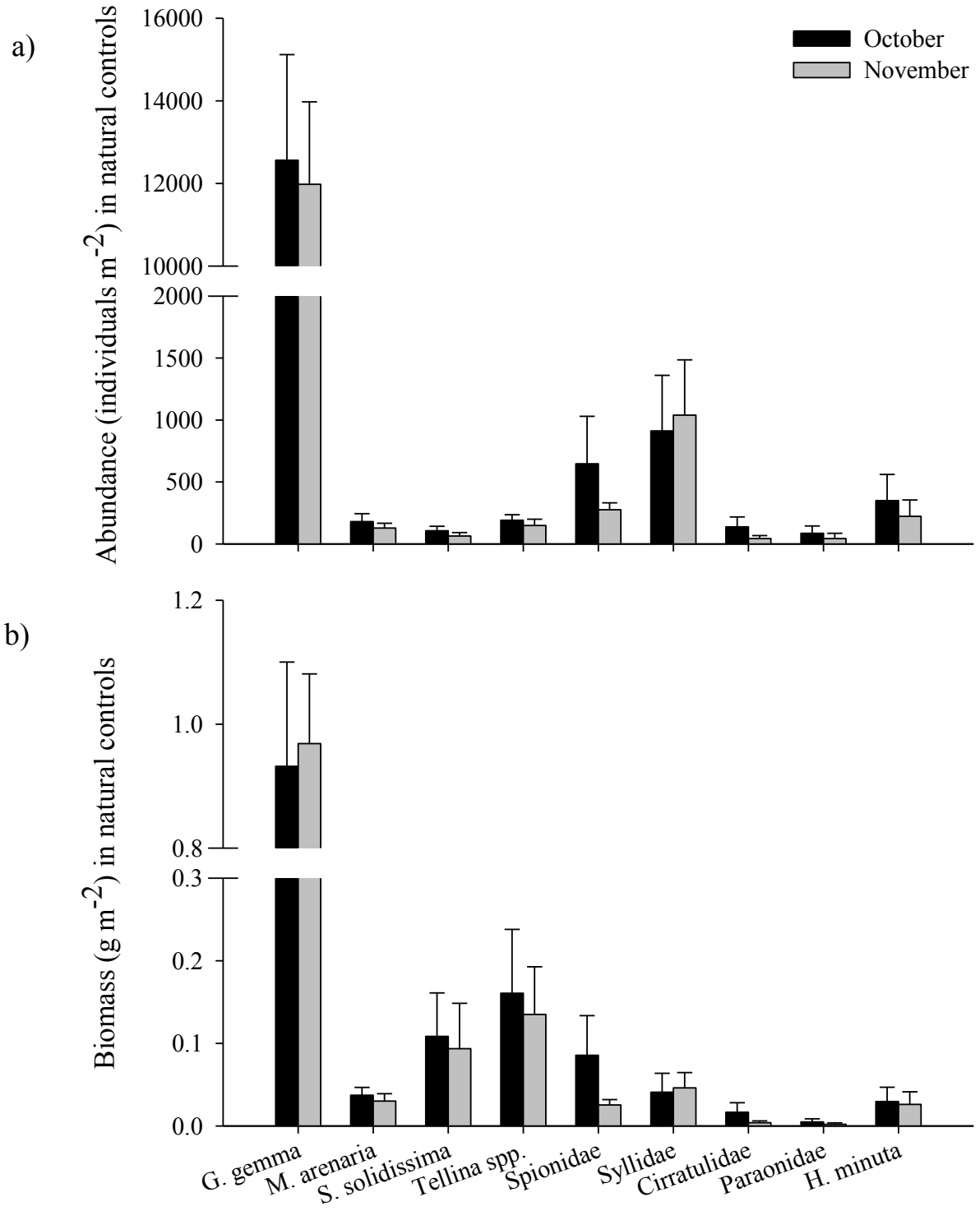


Figure 3.4 a) abundance and b) biomass (shell free dry weight) of common macrofauna taxa collected in cores from natural controls during the October and November sampling rounds (mean + SE, n = 4). Bivalves = *G. gemma*, *M. arenaria*, *S. solidissima*, *Tellina* spp.; polychaetes = spionidae, syllidae, cirratulidae, paraonidae; gastropod = *H. minuta*.

biomass of common taxa were similar during both sampling rounds, except for spionidae and cirratulidae, whose average abundance and biomass was lower in November (Fig. 3.4a, b). Because the most abundant taxa were small, biomass could potentially be swamped by the presence of rare and substantially larger taxa. For instance, the highly variable and greater average biomass obtained for polychaetes in November (Fig. 3.3b) can be attributed to a large glycerid polychaete found in one natural control. Other rare taxa which may have contributed greatly to biomass in cages and natural controls include: *Periploma leanum*, *Mercenaria mercenaria*, maldanidae, nereidae and nemertea. A complete list of the macrofauna taxa collected in cores and included in statistical analyses can be found in table 3.1.

During the early and late November sampling rounds, the most widespread large epifauna capable of moving in and out of cages and natural controls were large gastropods (present in 89% and 85% of experimental plots in early and late November, respectively), shrimp (44% and 39%) and hermit crabs (33% and 57%). Sea stars were less common and were only observed in 19% and 9% of experimental plots in early and late November, respectively. Only a single juvenile crab and moonsnail were documented in experimental plots. Three large epifauna taxa were collected in core samples and identified as *Pagurus longicarpus*, *Nassarius trivittatus* and *Littorina littorea*. Shrimp were *Crangon septemspinosa*.

3.4.2 Community Response to Treatments over Time

Community abundance did not differ significantly across treatments (ANOSIM, $\bar{R}$ =-0.12, p<0.96) or sampling rounds (ANOSIM, $\bar{R}$ =-0.18, p<0.99). Similarly, no significant effect of treatment (ANOSIM, $\bar{R}$ =0.02, p<0.36) or sampling round (ANOSIM, $\bar{R}$ =-0.02, p<0.65) was detected for community biomass.

3.4.3 Patterns in Community Structure

Despite non-significant results from ANOSIM, additional information regarding the study system is provided by ANOSIM's $\bar{R}$ values. For community abundance data, negative $\bar{R}$ values were obtained for both treatment and sampling round, indicating

Table 3.1 Macrofauna taxa identified from cores and included in statistical analyses. Taxa are identified as prey for green crabs and rock crabs based on stomach contents (SC), consumption in the field (CF), or reduced abundance (RA) or reduced biomass (RB) in a field experiment.

Taxa	Prey for green crabs	Prey for rock crabs
BIVALVES		
Gemma gemma	SC[1]	
Mya arenaria	SC[1,2], RA[9]	
Mercenaria mercenaria		
Spisula solidissima	CF[3]	
Tellina spp.	SC[1]	SC[4,15]
Periploma leanum		
Pandora gouldiana		
Mulinia lateralis		SC[15]
Ensis directus	SC[1,2]	SC[6,15]
GASTROPODS		
Bittium alternatum	SC[7]	
Hydrobia minuta	SC[1,2,10]	
Skeneopsis planorbis		
Littorina spp.	SC[1,2]	SC[5,11]
Onoba aculeus		
Turbonilla spp.		
Acteocina canaliculata	RA[7], RB[7]	
Astyris lunata	SC[7], RB[7]	
POLYCHAETES		
Spionidae	RA[8,9]	
Syllidae		
Opheliidae		
Cirratulidae	RA[9]	
Paraonidae		
Maldanidae	SC[1]	
Nereidae	SC[1,2,14], RA[9,13]	SC[4,12,15]
Phyllodocidae		
Glyceridae	SC[1,7]	SC[4]
Capitellidae	SC[10], RA[9]	
Nephtyidae	RA[8]	SC[6]
Orbiniidae	RA[17]	
OTHER		
Isopoda (*Chiridotea caeca*)	SC[1,2,10]	SC[12]
Tanaidacea		
Amphipoda (*Phoxocephalus holbolli*)	SC[1,10,14]	SC[2,4,6,12,15]
Nemertea		

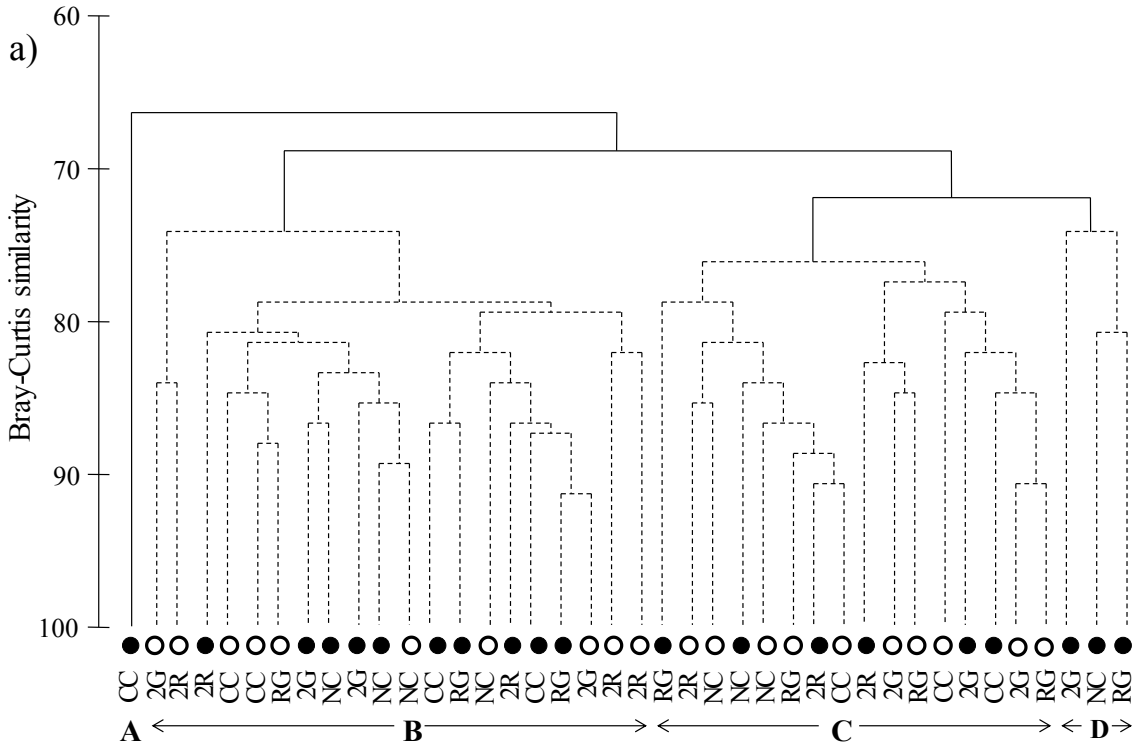
[1]Ropes 1968, [2]Elner 1981, [3]MacKenzie et al. 1985, [4]Hudon & Lamarche 1989, [5]Odeja & Dearborn 1991, [6]Stehlik 1993, [7]Thompson 2007, [8]Fernandes et al. 1999, [9]Scherer &

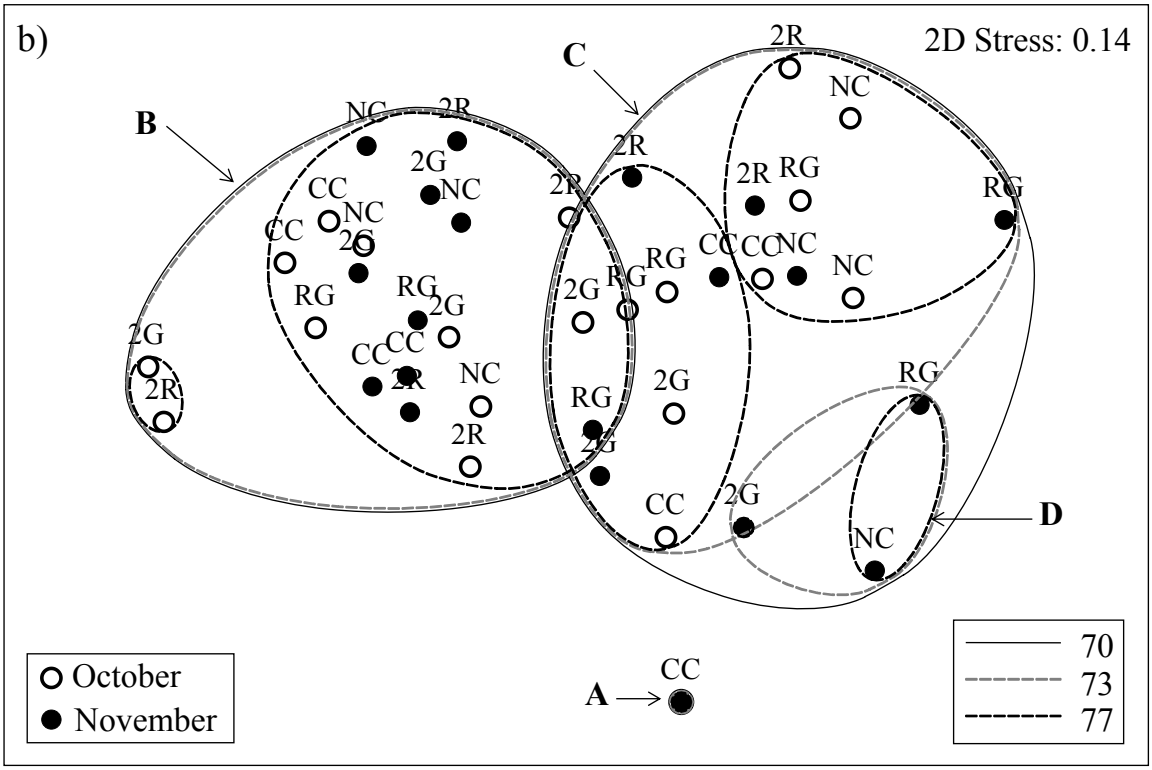
Reise 1981, [10]Wong unpubl., [11]Drummond-Davis et al. 1982, [12]Scarratt & Lowe 1972, [13]Gregory & Quijón 2011, [14]Raffaelli et al. 1989 [15]Stehlik et al. 2004

greater similarities between treatments (or sampling rounds) than within treatments (or sampling rounds) (Clarke, 1993). Negative $\bar{R}$ values have been observed for particular spatial and temporal patterns in community structure (Chapman and Underwood, 1999). Spatial patterns which could be responsible for the negative $\bar{R}$ value for treatment include patchiness within treatments and stratification of replicates within treatments. The negative $\bar{R}$ value obtained for sampling round could have occurred if the community was highly variable between replicates within treatments at each sampling round, but similar variability was observed at both sampling rounds, or if replicates within treatments divided into groups with different community structure and these groups persisted at both sampling rounds. In contrast, for community biomass data, $\bar{R}$ values were near zero for both treatment and sampling round, indicating that similarities between and within treatments (or sampling rounds) were comparable (Clarke, 1993). Thus, ANOSIM results suggest that community biomass did not follow the spatial and temporal trends exhibited by community abundance.

To test for spatial and temporal patterns in community abundance and biomass, I employed SIMPROF tests. Results for community abundance are shown in the dendrogram (Fig. 3.5a) and the corresponding MDS plot (Fig. 3.5b). Positions of replicates in the MDS plot were generally consistent with groups produced by CLUSTER analysis. Additionally, the MDS plot had a stress of 0.14 (Kruskal's stress formula 1), indicating that relationships among replicates were adequately represented (Clarke, 1993). SIMPROF tests identified four groups of replicates that differed in community structure. A cage control sampled in November (group A) split from all other replicates at 66.4% similarity (π=1.4, $p<0.001$). Group B separated from groups C and D at a similarity of 68.8% (π=1.4, $p<0.001$) and the split between groups C and D occurred at a similarity of 71.9% (π=1.0, $p<0.01$).

The two largest groups (B and C) deemed significantly different by SIMPROF each contain replicates from all treatments and sampling rounds suggesting that there


a)
Bray-Curtis similarity
60
70
80
90
100
CC 2G 2R 2R CC CC RG 2G NC 2G NC NC CC RG NC 2R CC RG 2G 2R 2R RG 2R NC NC NC RG 2R CC 2R 2G RG CC 2G CC 2G RG 2G NC RG
A
B
C
D


b)
2D Stress: 0.14
A
B
C
D
October
November
70
73
77

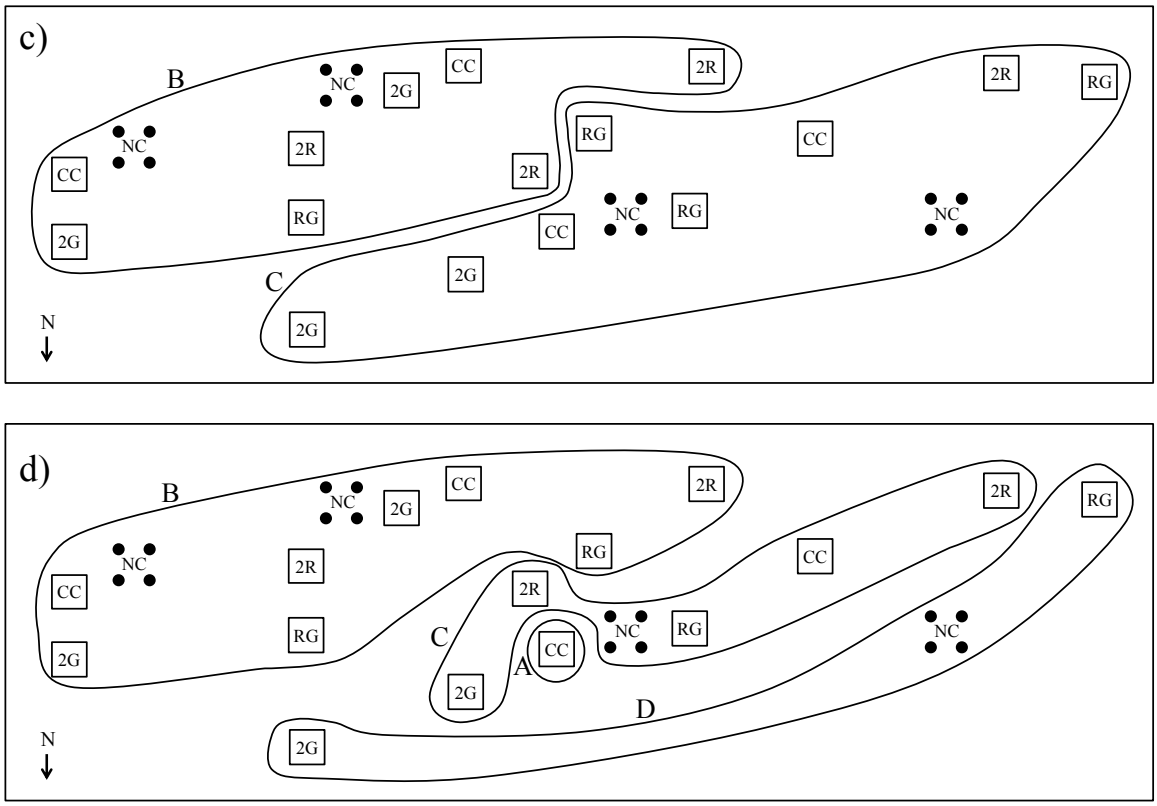


Figure 3.5 a) CLUSTER analysis and b) MDS plot of macrofauna abundance in each treatment replicate during the October (open circle) and November (closed circle) sampling rounds. Data were square-root transformed and similarities calculated with the Bray-Curtis coefficient. Contours in MDS plot correspond to groups from CLUSTER analysis at similarity levels of 70, 73 and 77%. Groups identified as significantly different ($p<0.05$) by SIMPROF tests (A, B, C, D) are shown by solid lines in the dendrogram and the 73% contours in the MDS plot. In c) and d), significantly different groups are outlined on a reduced map of the experimental site (not drawn to scale) for the October and November sampling rounds, respectively. NC = natural control; CC = cage control; 2G = green crab conspecific pair; 2R = rock crab conspecific pair; RG = heterospecific pair.

were no differences in community structure among treatments or sampling rounds. Instead, the groups reflect the spatial position of treatment replicates at the experimental site. Group B, located in the left of the MDS plot (Fig. 3.5b), contains treatment replicates found towards the southeast (SE) of the site, whereas the three right-hand groups (A, C and D) correspond to treatment replicates located towards the northwest (NW). The spatial stratification of treatment replicates from SE to NW is apparent when examining the groups produced by SIMPROF superimposed on the field site for each sampling round (Fig. 3.5c, d). Treatment replicates located towards the SE of the site are consistently grouped at both sampling times, except for one replicate each for conspecific rock crabs and heterospecific crabs. Treatment replicates towards the NW of the site are homogeneous in October, but these replicates separate into three groups in November, demonstrating increased stratification. Thus, ANOSIM's negative $\bar{R}$ value for treatment can be attributed to the stratification of replicates within treatments, which resulted in greater similarity between treatments than within treatments. Similarly, because spatial stratification resulted in high variability within sampling rounds but there was little variability between sampling rounds, stratification was also responsible for the negative $\bar{R}$ value obtained for sampling round. Repeated sampling of the same experimental unit (i.e., non-independent sampling) is expected to produce negative $\bar{R}$ values for time effects when there is little variability between times (Chapman and Underwood, 1999). However, a negative $\bar{R}$ value should also have been obtained if I had employed independent sampling because the persistent spatial stratification at both sampling rounds would have resulted in high variability between replicates within each sampling round and low variability between sampling rounds. Negative $\bar{R}$ values can also occur when outliers are present (Chapman and Underwood, 1999), suggesting that the cage control (November) isolated from all other replicates (group A) may have contributed to negative $\bar{R}$ values.

The taxonomic groups responsible for the observed spatial and temporal patterns captured by SIMPROF groups were explored with SIMPER analyses (see Appendix, Table A.1). Many of the same taxa proved to be important in discriminating groups B, C and D. When comparing the two largest groups (B and C), *G. gemma*, *H. minuta*,

spionidae, syllidae, cirratulidae, paraonidae and *S. solidissima* were the top contributors to the average dissimilarity. In addition to *M. arenaria* and *Tellina spp*., these taxa were also important in discriminating groups C and D. Similarly, *G. gemma*, *H. minuta*, syllidae, *M. arenaria*, cirratulidae and *Tellina spp.* contributed to the dissimilarity between groups B and D. Taxa contributing to differences among groups B, C and D demonstrated diverse patterns in abundance across the study site (Table 3.2). For example, *G. gemma* and syllidae were more abundant to the SE (group B) than the NW (group C) in October. Similarly, in November, abundance declined from the SE to the NW portion of the site (group B > C > D). In contrast, cirratulidae abundance was higher in the NW (group C, D) than the SE (group B) during both sampling rounds. Group A consists of a single replicate (cage control in November) and appears to be an outlier. Unlike comparisons between groups B, C and D, where only the common taxa were important in differentiating groups, approximately half of the taxa contributing to the average dissimilarities between group A and each other group were rare, and had their highest abundance in group A (e.g., *B. alternatum*, *Littorina* spp., *A. lunata*, capitellidae). Additionally, some common taxa were absent from group A (e.g., spionidae, cirratulidae).

Table 3.2 Patterns in abundance of macrofauna across groups deemed significantly different by SIMPROF tests (excluding group A). Listed taxa contributed up to 70% of the average dissimilarity between groups for at least one pairwise comparison of groups B, C and D by SIMPER. Raw abundances (individuals m^{-2}) from all treatments within each group are provided (mean ± SE, n=3 (D), 16 (C) or 20 (B)). + = highest average abundance; 0 = median average abundance; - = lowest average abundance.

Taxonomic group	Group 'B'	Group 'C'	Group 'D'
Gemma gemma	+ (19534 ± 1017)	0 (10175 ± 528)	- (7484 ± 123)
Hydrobia minuta	+ (637 ± 156)	- (32 ± 9)	0 (57 ± 57)
Spionidae	- (176 ± 31)	+ (716 ± 162)	0 (198 ± 51)
Syllidae	+ (809 ± 152)	0 (623 ± 114)	- (198 ± 51)
Cirratulidae	- (15 ± 8)	+ (135 ± 32)	0 (127 ± 88)
Mya arenaria	+ (323 ± 44)	0 (164 ± 21)	- (28 ± 14)
Paraonidae	0 (15 ± 13)	+ (95 ± 27)	- (0 ± 0)
Tellina spp.	0 (166 ± 21)	+ (167 ± 22)	- (71 ± 51)
Spisula solidissima	0 (149 ± 21)	+ (271 ± 32)	- (113 ± 14)

For community biomass data, SIMPROF results are shown in the dendrogram of fig. 3.6a. Unfortunately, the MDS plot (Fig. 3.6b) could not be interpreted because it likely did not adequately display the relationships between replicates, as suggested by a stress of 0.23 (Kruskal's stress formula 1) and was not consistent with results from CLUSTER analysis (Fig. 3.6a) (Clarke, 1993). SIMPROF failed to reject the null hypothesis that all treatment replicates from both sampling rounds were similar in community structure (similarity=59.2%, π=0.5, $p<0.37$). Consequently, it is invalid to interpret the groups produced by CLUSTER analysis (Clarke et al., 2008) and the inability to consider the MDS plot is therefore inconsequential. ANOSIM's near zero $\bar{R}$ values for both treatment and sampling round reflect homogeneous community structure in terms of biomass across all replicates.

3.4.4 Multiple Predator Effects

Significant predation effects on community structure in terms of abundance and biomass were not detected with ANOSIM or SIMPROF tests. Therefore, it was not logical to determine crab consumption rates on the total community abundance and biomass or the abundance and biomass of common taxa. Consequently, I did not test for multiple predator effects on prey.

3.4.5 Environmental Conditions

Sediment in natural controls (n = 4) was predominantly composed of fine sand, ranging from 52.3-65.4%, and coarse and medium sand, from 32.1-45.8%, with little to no silt and clay (1.9-3.0%) or gravel (0-0.1%). Organic content ranged from 0.6-1.0% (Fig. 3.7). Bio-Env and the global BEST test were utilized to determine whether there was a relationship between sediment characteristics and patterns in community abundance. Because fine sand and coarse and medium sand were correlated (< -0.95) based on standard product-moment correlations, only fine sand was included in the analysis. According to Bio-Env, silt and clay constituted the best match to community abundance data ($\rho_s = 0.42$), but this environmental variable was not significantly linked with biotic data based on the global BEST test ($p<0.14$). Consequently, patterns in sediment characteristics are independent of patterns in community abundance.

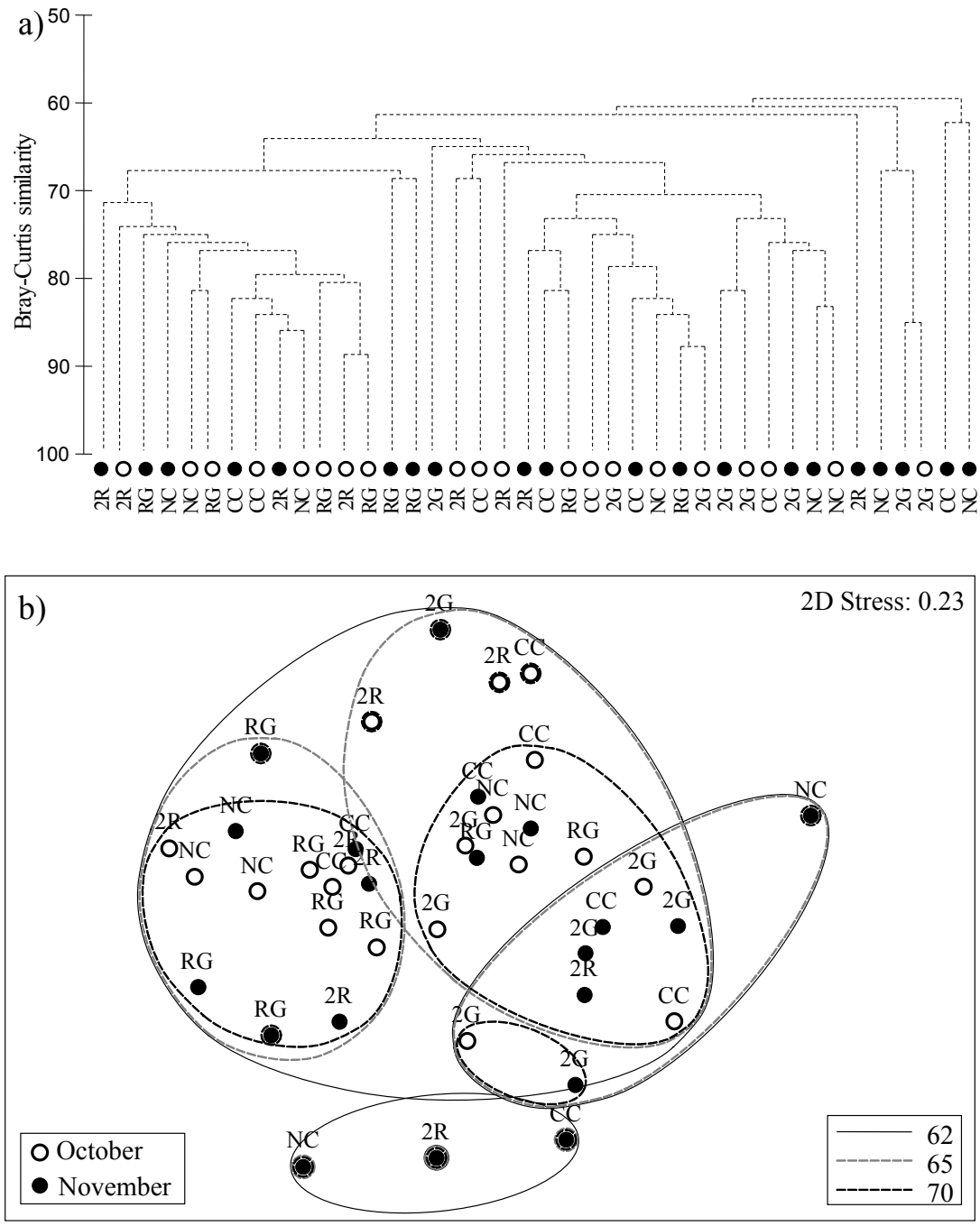


Figure 3.6 a) CLUSTER analysis and b) MDS plot of macrofauna biomass in each treatment replicate during the October (open circle) and November (closed circle) sampling rounds. Data were fourth root transformed and similarities calculated with the Bray-Curtis coefficient. Contours in MDS plot correspond to groups produced by CLUSTER analysis at similarity levels of 62, 65 and 70%. Dashed lines in the dendrogram indicate that groups do not differ significantly ($p>0.05$) based on SIMPROF tests. NC = natural control; CC = cage control; 2G = green crab conspecific pair; 2R = rock crab conspecific pair; RG = heterospecific pair.

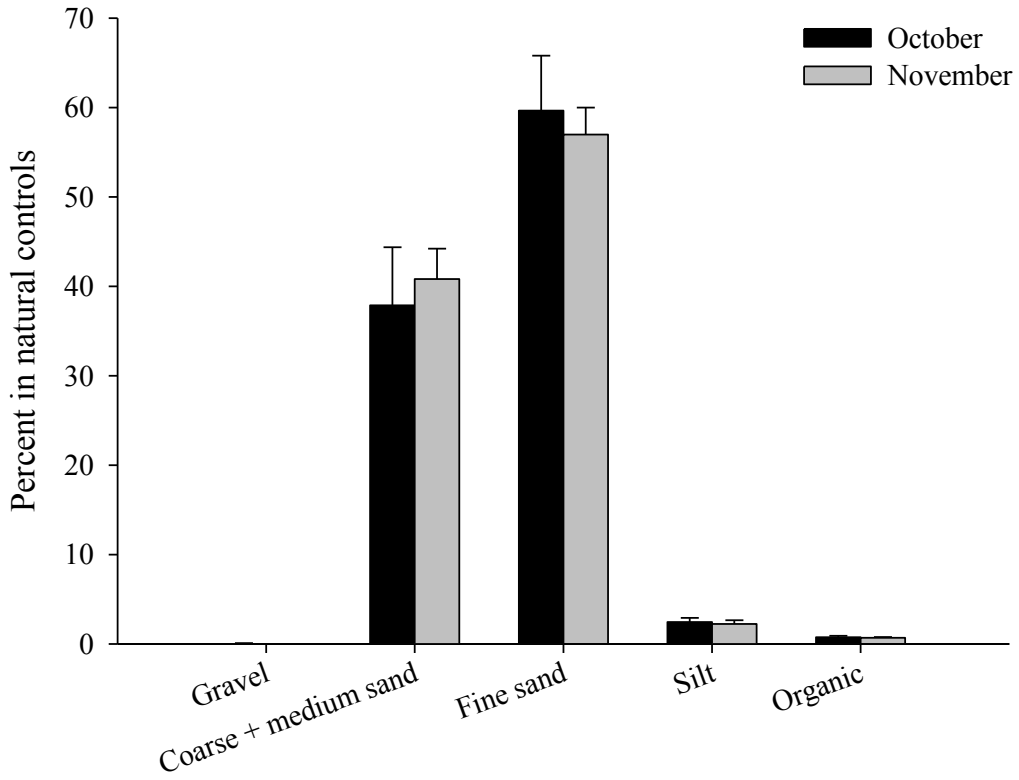


Figure 3.7 Grain size and organic content in natural controls during the October and November sampling rounds (mean % + SE, n = 4).

Crabs were exposed to a broad range of water temperatures throughout the experimental period (see Appendix, Fig. A.1). From the first day crabs were added to experimental treatments until the end of the October sampling round, water temperature ranged from 7.32 to 15.46°C (10.81± 2.22°C, mean ± SD, n=750). Between the October sampling round and the last day of the November sampling round, water temperature varied from 4.82 to 10.03°C (7.22 ± 1.16°C, mean ± SD, n=705).

The study site was exposed to substantial storms during the experiment. Storms were only documented by chance, i.e., when I could not access the study site at low tide because the water level did not fully recede due to significant wave action. Consequently, it is possible that storms influenced the study site at other times during the experiment. Storms were noted on 8, 15, 23 October and 6 - 7 November. I observed sediment redistribution at the study site due to the 15 October storm. These storms were associated with hourly maximum wind speeds ≥ 194 m s^{-1}, blowing from the north-

northwest to northeast and hourly maximum significant wave heights ≥ 0.99 m in the Northumberland Strait (Table 3.3). Although the 23 October storm occurred during the October sampling round, treatment replicates sampled before and after the storm fell within the same SIMPROF group, suggesting that the storm did not alter macrofauna community abundance at my study site. Likewise, despite a storm between the October and November sampling rounds (6 - 7 November), spatial patterns in community abundance were similar at both times. Consequently, storms likely do not explain the persistent spatial patterns in macrofauna community abundance at the study site.

3.4.6 Cage Effects

Proportion of mass loss from plaster standards did not differ between natural controls and cages on the first day of exposure ($t_{0.05(2),4}$=2.610, p=0.059) or the second ($t_{0.05(2),8}$=1.556, p=0.158). Therefore, cages did not appear to alter water flow. Percent organic and percent fine sand were not affected by treatment or sampling round (Table 3.4), suggesting that sediment characteristics were not altered due to caging and were consistent across sampling rounds. In contrast, the difference in light levels inside and outside of cages was significantly different from zero, with lower levels observed in cages (2685 ± 736 lux, mean difference ± SE, $t_{0.05(1),36}$=4.847, p<0.001).

3.5 Discussion

I conducted a manipulative field experiment to examine the effects of green crab and rock crab predation on a soft-sediment macrofauna community. Throughout my study, conspecific green crab pairs, conspecific rock crab pairs and heterospecific pairs

Table 3.3 Wind and wave conditions associated with storms documented during the experimental period.

Storm	Hourly maximum wind speed (m/s)	Wind direction (°) of maximum wind speed	Hourly maximum significant wave height (m)
October 8	220	40	1.06
October 15	194	340	0.99
October 23	194	30	1.17
November 6-7	205	350	1.32

Table 3.4 Repeated-measures ANOVA results for the percent of organic content and percent of fine sand in natural controls and cage controls during the October and November sampling rounds. df_1 = numerator; df_2 = denominator; MS_1 = numerator; MS_2 = denominator; T = treatment; S = sampling round.

Dependent variable	Source of variation	Error term	df_1, df_2	MS_1, MS_2	F-value	P-value
% organic	**Between-subjects**					
	T	plot(T)	1, 6	0.001, 0.02	0.04	0.848
	Within-subjects					
	S	S x plot(T)	1, 6	0.003, 0.01	0.32	0.593
	T x S	S x plot(T)	1, 6	0.005, 0.01	0.52	0.500
% fine sand	**Between-subjects**					
	T	plot(T)	1, 6	0.31, 20.45	0.02	0.906
	Within-subjects					
	S	S x plot(T)	1, 6	14.45, 8.64	1.67	0.243
	T x S	S x plot(T)	1, 6	2.54, 8.64	0.29	0.608

had no influence on community structure in terms of abundance or biomass. Due to the lack of predation effects, I did not test for multiple predator effects on prey. Although mobile epibenthic predators can alter the abundance of marine infauna in shallow, unvegetated soft-sediment habitats (Peterson, 1979; Wilson, 1991), a review of studies within this habitat revealed that 44% of experiments showed strong increases in infauna density due to predator exclusion (Ólafsson et al., 1994). Similar results have been observed in field experiments using green crabs, with some studies demonstrating significant crab impacts on soft-sediment macrofauna, and others exhibiting little or no effect (e.g., Thrush, 1986; Raffaelli et al., 1989; Grosholz and Ruiz, 1995; Fernandes et al., 1999). It is therefore possible that green crab and rock crab predation may not be important in regulating the macrofauna community at my field site.

Multiple factors may have contributed to the lack of predation effects in this system. The presence of another predator may have influenced crab behaviours and reduced their prey consumption (e.g., Griffen and Byers, 2006a). For instance, when crabs are paired with another species, they may spend less time foraging and consequently consume less prey due to vigilance (Wong et al., 2010). Additionally,

aggressive interactions between crabs can reduce predation effects (e.g., Mansour and Lipcius, 1991; Clark et al., 1999; Wong et al., 2010). This has been observed when green crabs forage with conspecifics or heterospecifics (Griffen, 2006; Smallegange et al., 2006; Griffen and Williamson, 2008). However, interactions between crabs may not always be important in regulating green crab and rock crab predation rates considering that some studies have observed independent effects when these crab species forage together or with conspecifics (Bélair and Miron, 2009a; Wong et al., 2012; Chapter 2). Studies conducted in an eelgrass bed and a sandy habitat in the southern Gulf of St. Lawrence have detected significant predation effects on soft-sediment macrofauna when green crabs forage with conspecifics or rock crabs at similar or lower densities than were used in my study (Thompson, 2007; Gregory and Quijón, 2011). Consequently, it seems unlikely that interactions between crabs completely suppressed foraging in my experiment. However, interactions between crabs could have combined with other factors (see below) to produce non-significant predation effects.

Environmental conditions in my study may have reduced crab predation rates relative to other field experiments that detected significant predation effects by these crab species. My study was conducted during the fall, with water temperatures declining from ~15 to 5°C during the experiment. Both green crab and rock crab predation rates tend to increase with temperature (Wallace, 1973; Elner, 1980; Barbeau and Scheibling, 1994; Bélair and Miron, 2009a; Matheson and Gagnon, 2012a). Consequently, predation was probably reduced relative to studies conducted in warmer waters (e.g., Floyd and Williams, 2004; Gregory and Quijón, 2011), but it was likely not completely suppressed because these crab species can forage at the lowest temperatures recorded in my study (Matheson and Gagnon, 2012a). Additionally, my study site was exposed to significant wave action during the experiment, which may have hindered crab foraging relative to studies conducted in more sheltered areas (e.g., Thompson, 2007). In a Maine estuary, predation effects of green crabs and rock crabs were significantly lower in high flow sites than low flow sites, despite their greater abundance in high flow areas (Leonard et al., 1998). High water flows and turbulence can inhibit crab mobility and searching efficiency, reducing foraging success (Weissburg and Zimmer-Faust, 1993; Martinez,

2001; Powers and Kittinger, 2002; Jackson et al., 2007). Consequently, wave action may have reduced crab predation rates at my study site.

The lack of predation effects in my experiment may have also resulted from the community composition. Macrofauna were predominantly small (≤ 10mm), consisting of juveniles or small species. It is possible that the common taxa which have been negatively affected by crab predation in other studies (*G. gemma*, *M. arenaria*, *S. solidissima*, *Tellina* spp., *H. minuta*, spionidae, cirratulidae, see Table 3.1) were not readily consumed due to their size distribution or because they were not a preferred prey item. For example, Gregory and Quijón (2011) found that conspecific green crabs (2.2 m^{-1}) reduced the density of bivalves (mostly *M. arenaria* and *G. gemma*) > 5mm SL, but did not affect smaller clams. Consequently, bivalves in my study, which were mostly ≤ 5mm, may not have been readily consumed by green crabs. Additionally, crabs may have reduced their predation on common taxa if they consumed the larger mobile epifauna that moved in and out of experimental plots (i.e., large gastropods, shrimp, hermit crabs), which are prey items for these crab species (e.g., *Pagurus* spp., *Littorina* spp., *N. trivittatus*, *Crangon* spp., Crothers, 1968; Ropes, 1968; Elner, 1981; Drummond-Davis et al., 1982; Stehlik et al., 2004). Unfortunately, crab predation effects on larger epifauna could not be determined due to difficulty in assessing their abundance and biomass throughout the experiment (see 'Materials and Methods'). Finally, some abundant macrofauna may simply not be prey items for green crabs and rock crabs (e.g., syllidae, paraonidae), while many taxa which are consumed by these crab predators were likely not affected due to their low abundance (e.g., *E. directus*, nereidae, glyceridae) (see Table 3.1).

Alternatively, crabs may have had predation effects, but other factors may have prevented the detection of these effects, such as prey mobility (e.g., Raffaelli and Milne, 1987; Frid and James, 1988). Models of prey movement demonstrate that prey moving randomly over even small distances (mm h^{-1}) can immigrate into enclosures or emigrate from exclosures, masking predation effects (Frid, 1989; Hall et al., 1990). Prey in my study likely exhibited active dispersal, for instance by burrowing (e.g., syllidae, spionidae) or crawling on the sediment surface (e.g., gastropods) (e.g., Shull, 1997), and

may have moved in and out of cages. Consequently, my ability to detect predation effects may have been compromised by mobile taxa. However, because some taxa had limited mobility, including the most abundant species *G. gemma* (Belt and Commito, unpubl. data in Commito et al., 1995a), active dispersal likely does not explain the total absence of predation effects in my experiment. Other important mechanisms of dispersal in soft-sediment systems are bedload and water column transport, which have been observed for bivalves, polychaetes and gastropods (e.g., Emerson and Grant, 1991; Commito et al., 1995a; 1995b; Cummings et al., 1995; Shull, 1997; Commito et al., 2005; Jennings and Hunt, 2009). In my study, macrofauna may have been susceptible to dispersal associated with substrate movement because macrofauna were predominantly small, located near the sediment surface and the study site was exposed to strong wave action (e.g., Emerson and Grant, 1991; Thrush et al., 1996). Yet, even the presence of storms did not alter spatial patterns in community abundance. Because it is unlikely that dispersal due to hydrodynamic forces generates persistent spatial patterns (Hewitt et al., 1997), bedload and water column transport may not have masked predation effects.

Results of my study could have been influenced by aspects of the experimental design, such as caging artifacts. The hydrodynamic artifact of caging can potentially alter sediment characteristics and community structure in cages established in soft-sediments (see review by Ólafsson et al., 1994). However, this caging artifact was not observed in my study; water flow, percent fine sand and percent organic did not differ between natural controls and cage controls. Hydrodynamic conditions were likely not influenced by caging due to the large mesh size and because detritus did not become trapped against the cages, which can hinder water flow. Another caging artifact arises when predators modify their behaviour as a result of being restricted to cages (Virnstein, 1978). Although it is possible that crab foraging was affected by caging, this behavioural artifact does not explain the lack of predation effects considering that adult crabs at a comparable density in cages of similar size have been shown to have significant predation effects (Gregory and Quijón, 2011). Cages can also influence the behaviour of other mobile fauna, which may be attracted to cages and increase in abundance relative to natural plots (Virnstein, 1978; Summerson and Peterson, 1984). This artifact could not be controlled and likely occurred in this system; cages were accessed by mobile epifauna

(e.g., shrimp, hermit crabs, large gastropods). Finally, I did detect a shading artifact which could have affected macro- and micro-algae, for instance (Peterson, 1979). Yet, community structure did not differ between natural controls and cage controls, suggesting that shading, behaviour of the mobile fauna and other potential caging artifacts did not have a significant effect on macrofauna. Consequently, I am confident that results from my study were not due to caging artifacts.

The detection of significant predation effects on community abundance with ANOSIM and SIMPROF analyses may have been obstructed by the persistent spatial stratification of community abundance across the study site. Consistent with my study, infauna exhibit spatial patterns in density (e.g., patches, gradients) ranging from cms to kms (e.g., Volckaert, 1987; McArdle and Blackwell, 1989; Thrush et al., 1989; Morrisey et al., 1992). Over small scales, spatial patterns in soft-sediment communities may be generated by abiotic (e.g., grain size, beach slope) and biotic (e.g., intra- and interspecific interactions, predation, mobility) processes (see reviews by Thrush, 1991; Defeo and McLachlan, 2005). Physical conditions appeared to be homogeneous across the study site and spatial patterns in community abundance were not related to sediment characteristics (grain size, organic content) or hydrodynamic conditions, suggesting that biotic factors may be important in regulating macrofauna density. Further research is required to determine the cause of spatial patterns at this site. ANOSIM demonstrated higher variability in community abundance within treatments than between treatments because spatial stratification resulted in positive correlation between treatments (i.e., non-independence), which inflates the type II error rate (Underwood, 1997; Chapman and Underwood, 1999). Consequently, if crabs had predation effects which did not alter community structure to a greater extent than spatial stratification, then predation effects would be undetectable by ANOSIM. Had I known that spatial stratification was present at the study site prior to the experiment, I would have employed a randomized block design, which would likely have increased the power to test for treatment effects. Low statistical power may have also influenced results from SIMPROF tests. As SIMPROF tests proceed down the nodes of a dendrogram, tests are performed on groups with fewer replicates; reduced power would be expected for groups with smaller sample sizes (Clarke et al., 2008). SIMPROF separated replicates into groups based on their spatial

position in the study site. Consequently, differences in community structure due to treatments would only be detectable within each spatial group. However, power may have been too low to observe such effects because each group had few treatment replicates. However, spatial stratification was not observed for community biomass and non-significant treatment effects were detected. Consequently, spatial stratification alone is not responsible for the lack of predation effects in this study. This result provides some support for the hypotheses that crabs did not have important predatory impacts on the community or that predation effects were confounded by other processes.

In conclusion, I examined the predation effects of green crabs and rock crabs on a soft-sediment macrofauna community. Crab predation rates may have been suppressed by the combined influence of interactions between crabs, harsh environmental conditions and macrofauna community composition. Alternatively, crabs may have exhibited some predation effects which could not be detected due to prey movement in and out of cages or low statistical power. Without further data, it is not possible to determine with certainty whether or not crab predation was important in structuring the macrofauna community. Macrofauna samples from single crab treatments could aid in explaining the lack of predation effects. If single crabs affected community structure, this would suggest that interactions between crabs reduced predation rates. Crab stomach contents could also provide insight into the causes of non-significant treatment effects. For instance, if stomach contents contained few prey or were dominated by the larger epifauna, then it is likely that crabs did not exert significant predation effects on the community. Emergence traps, bedload traps or defaunated plots could be used to examine prey mobility (e.g., Frid, 1989; Emerson and Grant, 1991; Shull, 1997).

The lack of predation effects in my study does not preclude the importance of green crabs and rock crabs in regulating soft-sediment communities under different conditions. Other field enclosure experiments have demonstrated that green crab predation can significantly reduce macrofauna abundance (Grosholz and Ruiz, 1995; Thompson, 2007; Gregory and Quijón, 2011), indicating that they can be important predators in soft-sediments. Additionally, although multiple predator effects on prey were not evaluated, interactions among green crabs and rock crabs can alter their

predation effects (but see Bélair and Miron, 2009a, Chapter 2). Gregory & Quijón (2011) observed reduced infauna density when green crabs and rock crabs foraged together at a low density, but not at high density, and suggested that aggression between crabs or avoidance behaviours reduced predation effects in the high density treatment. Additionally, I detected risk reduction for soft-shell clams (*Mya arenaria* L.) when green crabs and rock crabs foraged together in artificial seagrass, which likely occurred because rock crabs exhibited reduced foraging efficiency as green crabs depleted clam abundance (Chapter 2). Consequently, rock crabs may be negatively affected by the green crab invasion in the Gulf of St. Lawrence and multiple predator effects of these crab species on soft-sediment communities should be re-evaluated. Other studies investigating multiple predator effects on marine soft-sediment communities are limited (but see Martin et al., 1989; Ross et al., 2004) and have not included the appropriate treatments to test for emergent effects on prey. Further research is therefore required to determine the importance of multiple predator species in structuring soft-sediment communities.

3.6 Appendix

Table A.1 Results from SIMPER analyses on groups of replicates deemed significantly different by SIMPROF tests conducted on community abundance data. Taxa which are included contributed up to 70% of the average dissimilarity between groups. $\bar{\delta}$ = average dissimilarity between groups; $\bar{\delta}_i$ = average contribution from the *i*th species to $\bar{\delta}$.

Comparison	$\bar{\delta}$	Taxonomic groups	$\bar{\delta}_i$	$\bar{\delta}_i$/SD($\bar{\delta}_i$)	$\bar{\delta}_i$ %	$\sum\bar{\delta}_i$ %
Groups A and B	36.0	*Gemma gemma*	11.8	4.1	32.8	32.8
		Hydrobia minuta	3.6	1.6	9.9	42.6
		Spionidae	2.6	1.8	7.1	49.7
		Syllidae	2.5	1.3	6.8	56.6
		Bittium alternatum	2.3	2.6	6.5	63.0
		Capitellidae	2.1	11.4	5.7	68.7
		Littorina spp.	2.0	5.4	5.5	74.2
Groups A and C	31.7	Spionidae	5.7	2.0	17.9	17.9
		Gemma gemma	3.9	1.8	12.2	30.1
		Bittium alternatum	2.4	2.4	7.3	37.6
		Cirratulidae	2.3	1.4	7.2	44.8
		Capitellidae	2.2	5.0	6.8	51.6
		Littorina spp.	2.0	3.7	6.4	58.0
		Paraonidae	1.8	1.3	5.8	63.8

Comparison	$\bar{\delta}$	Taxonomic groups	$\bar{\delta}_i$	$\bar{\delta}_i$/SD($\bar{\delta}_i$)	$\bar{\delta}_i$ %	$\sum\bar{\delta}_i$ %
Groups A and C	31.7	Syllidae	1.7	1.1	5.5	69.3
		Astyris lunata	1.5	3.7	4.7	74.0
Groups A and D	28.2	Spionidae	3.8	5.0	13.6	13.6
		Mya arenaria	3.3	2.6	11.6	25.3
		Littorina spp.	2.6	17.2	9.1	34.4
		Bittium alternatum	2.5	2.0	8.7	43.1
		Cirratulidae	2.4	1.0	8.4	51.5
		Capitellidae	2.0	1.8	7.0	58.5
		Astyris lunata	1.8	17.2	6.4	65.0
		Hydrobia minuta	1.8	17.2	6.4	71.4
Groups B and C	30.4	*Gemma gemma*	7.9	2.2	25.9	25.9
		Hydrobia minuta	3.7	1.6	12.3	38.2
		Spionidae	3.1	1.4	10.2	48.3
		Syllidae	2.5	1.5	8.2	56.6
		Cirratulidae	1.8	1.4	5.9	62.5
		Paraonidae	1.6	1.3	5.1	67.6
		Spisula solidissima	1.3	1.3	4.4	72.0
Groups B and D	35.2	*Gemma gemma*	12.0	4.0	34.0	34.0
		Hydrobia minuta	4.2	1.6	11.9	45.9
		Syllidae	3.1	1.3	8.7	54.6
		Mya arenaria	3.0	2.2	8.4	63.0
		Cirratulidae	1.9	1.3	5.4	68.4
		Tellina spp.	1.7	1.4	4.7	73.1
Groups C and D	28.1	*Gemma gemma*	3.7	1.7	13.3	13.3
		Spionidae	3.2	1.5	11.6	24.9
		Syllidae	2.6	1.3	9.1	34.0
		Mya arenaria	2.2	1.8	7.6	41.7
		Cirratulidae	2.0	1.2	7.0	48.7
		Paraonidae	1.9	1.3	6.8	55.6
		Tellina spp.	1.8	1.5	6.4	61.9
		Spisula solidissima	1.5	1.9	5.5	67.4
		Hydrobia minuta	1.5	1.2	5.3	72.6

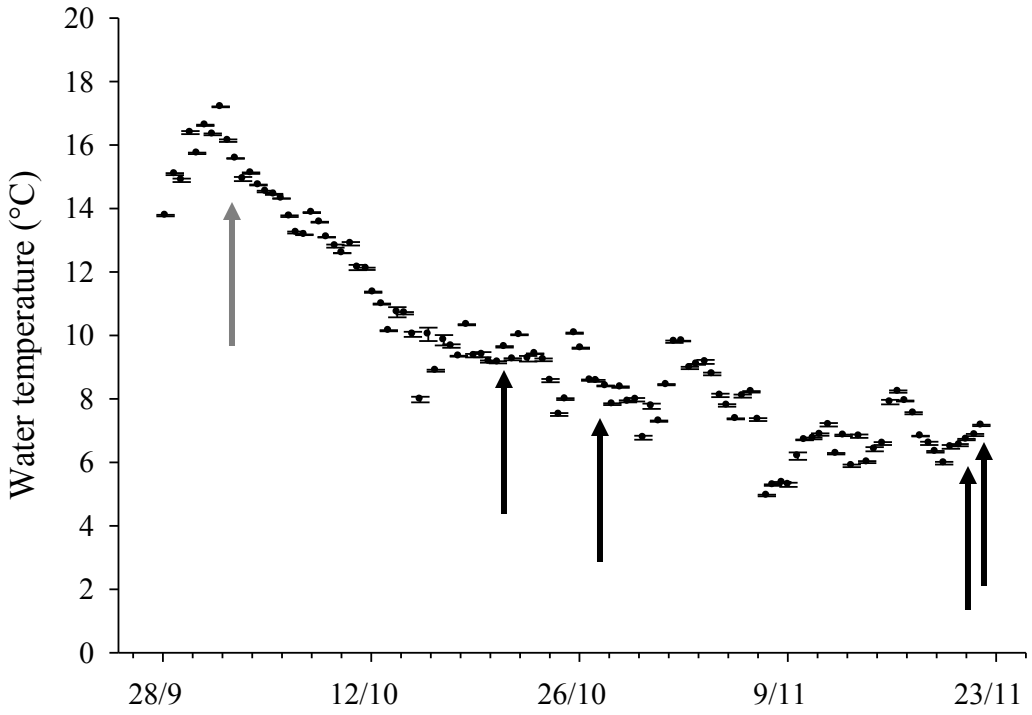


Figure A.1 Water temperature recorded for the closest hour to high tide ± 1 hr at five treatments (mean ± SE, n = 15) throughout the experimental period. The grey arrow demonstrates the first day crabs were added to treatments. Black arrows indicate the beginning and end of the October and November sampling rounds.

CHAPTER 4

Conclusions

Predation is an important force in structuring communities (e.g., Connell, 1975), and it is therefore of great importance to be able to predict the impacts of predation in a particular system. It is widely recognized that predation effects can be modified by the presence of other predator species (see reviews in Sih et al., 1998; Schmitz, 2007). Predators may be negatively influenced by other predators and reduce their foraging, and subsequently their per capita predation, as a result of vigilance, aggressive interactions or intraguild predation (Griffen and Byers, 2006a; Griffen and Williamson, 2008; Wong et al., 2010). Alternatively, prey may be more vulnerable to predation in a multi-predator system if prey behaviours or habitat use in the presence of one predator increases its vulnerability to the other predator, in which case predators benefit from the presence of another predator and increase their per capita consumption (Soluk, 1993; Losey and Denno, 1998; Swisher et al., 1998). Consequently, in multi-predator systems which exhibit risk reduction or risk enhancement for prey, predation impacts cannot be predicted based on the predation rates of predators foraging in isolation (e.g., Sih et al., 1998). To further our understanding of multiple predator effects on prey, and consequently our ability to predict combined consumption, I examined a) the influence of habitat type on multiple predator effects and the underlying behavioural mechanisms, and b) multiple predator effects within a complete community.

In Chapter 2, I investigated multiple predator effects of green crabs and rock crabs on soft-shell clams in different habitat types (sand, sand with artificial seagrass) and conducted detailed behavioural observations of predator foraging and interactions between predators. Multiple predator effects on prey were affected by habitat type and behavioural observations were instrumental in explaining the observed predation effects. Most conspecific and heterospecific pairs in both habitat types generated independent multiple predator effects on prey, which could be explained by predator behaviours. Generally, predator foraging behaviours were not influenced by the presence of another predator. Foraging behaviours were not affected by encounters between predators

because interactions were short in duration, infrequent and mostly non-aggressive. These independent effects likely resulted from the ease with which crabs could detect and consume soft-shell clams. A non-independent multiple predator effect on prey (marginally significant) was detected for heterospecific crabs in artificial seagrass. Even with detailed behavioural observations, it was not possible to determine the mechanism for this effect, suggesting that behaviours responsible for the non-independent effect were more complex than could be assessed in this study. This highlights the need to incorporate behavioural observations into multiple predator studies.

In Chapter 3, I examined multiple predator effects on a soft-sediment macrofauna community. In this system, there were no significant predation effects of green crabs and rock crabs on the community and hence multiple predator effects on prey were undetectable. However, it was not possible to determine whether predation effects were lacking because crabs were not important predators in this system or if other factors, such as prey mobility or low statistical power, hindered my ability to detect significant effects.

In conclusion, my research contributes to our overall understanding of multiple predator effects on prey and the predatory impacts of green crabs and rock crabs on soft-sediment macrofauna. Chapter 2 demonstrates that habitat type is important in regulating multiple predator effects on prey and that mechanisms for multiple predator effects may be quite complex and therefore not predictable without detailed behavioural observations. Results also indicate that multiple predator effects of green crabs and rock crabs on prey may differ depending on the conditions in which they interact, which has also be suggested by other studies (see Bélair and Miron, 2009b; Gregory and Quijón, 2011). Consequently, predicting their combined impact in a particular system will likely require additional experimentation to determine whether or not independent multiple predator effects on prey are present. Unfortunately, it was not possible to assess multiple predator effects on prey when green crabs and rock crabs foraged on a sand-flat (Chapter 3). Consequently, further research is required to assess the multiple predator effects of these crab species on a soft-sediment macrofauna community. Although predation by mobile epibenthic consumers is often important in structuring marine unvegetated soft-sediment systems (Peterson, 1979; Wilson, 1991; but see reservations on caging artifacts in

Ólafsson et al., 1994), multiple predator studies are lacking in this habitat (but see Martin et al., 1989; Ross et al., 2004; Hughes and Grabowski, 2006; Wong et al., 2010). Consequently, the role of multiple predator effects in regulating soft-sediment marcrofauna requires further exploration.

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