

**When getting a meal may cost your life:
Exploring the incongruous distribution between the
green crab *Carcinus maenas* and its prey**

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Abstract

The green crab *Carcinus maenas* invaded the Gulf of Maine over a hundred years ago and has become a well-established member of intertidal communities. We surveyed the vertical distribution of *Carcinus*, other crabs, and their potential prey from the intertidal into the shallow subtidal. *Carcinus* was most abundant in the intertidal and decreased in the subtidal. In contrast, a preferred prey of *Carcinus*, the mussel *Mytilus edulis*, had highest densities in the shallow subtidal. Why isn't *Carcinus* most abundant where prey densities are highest? A previous experiment revealed a higher mortality rate for *Carcinus* tethered in the subtidal than in the intertidal. In the subtidal there are higher abundances of the American lobster *Homarus americanus* and Jonah crab *Cancer borealis*. We performed a laboratory experiment to investigate the effects of cohabitation with lobster and *C. borealis* on survival, shelter use, and behavior of *Carcinus*. Lobsters were the more effective predator on *Carcinus*, consuming 27% of the crabs during 24 hours. Only 5% of *Carcinus* were eaten by *C. borealis* and none by conspecifics used in control treatments. In the presence of lobsters, *Carcinus* showed significantly more climbing and deep burrowing behavior relative to controls. Our results suggest that the risk of predation by lobsters underlies the scarcity of *Carcinus* in subtidal communities.

Introduction

The invasion of the east coast of North America by the European green crab *Carcinus maenas* (henceforth referred to as *Carcinus*) began over 100 years ago. Since its initial introduction into New York and New Jersey, *Carcinus* has expanded its range northward into the Gulf of Maine (Audet *et al.* 2003, Taylor *et al.* 1957), becoming a major presence in intertidal communities. *Carcinus* is omnivorous and consumes a wide range of prey: bivalves (the mussel *Mytilus edulis* and soft-shell clam *Mya arenaria*); gastropods (*Littorina littorea* and *L. obtusata*); barnacles; amphipods; crabs (*Cancer irroratus*, *Carcinus*); and algae (Ropes 1968, Elner 1981, Seeley 1986, Rangeley and Thomas 1987).

In the Gulf of Maine, *Carcinus* shares its range with other abundant subtidal and intertidal decapods including the Jonah crab (*Cancer borealis*), rock crab (*Cancer irroratus*), and American lobster (*Homarus americanus* henceforth referred to as lobster).

All of these animals are in the same feeding guild and intraguild predation is known to occur (Hudon and Lamarche 1989, Sainte-Marie and Chabot 2002, Novak 2004). Lobster and *C. borealis* reach their highest densities in the subtidal zone (Novak 2004) but both species migrate into the intertidal (*C. borealis*, Ellis et al. *in press*; *H. americanus*, P. Jones, *unpubl. data*). In the intertidal zone, *Cancer* crabs and lobsters suffer high mortality through predation by gulls and terrestrial animals during low tide; in contrast, *Carcinus* appears to avoid predation through crypsis and behavioral responses (Dumas & Witman 1993; Ellis et al. 2005; Ellis, Rome, Allen *unpubl. data*).

Given the importance of *Carcinus* as a predator, we were interested in determining its vertical distribution across the intertidal and shallow subtidal zones. We wanted to compare this distribution to that of potential prey such as mussels, that are important sessile foundation species in this community (Bertness 2007). *Carcinus* suffers significantly higher mortality in the subtidal (C. Santamaria *in prep*) where lobsters and *C. borealis* are most common. Therefore, we also examined how these potential intraguild predators affect the behavior of *Carcinus* in laboratory trials.

Methods

Study Site

This research was conducted on Appledore Island, in the nine-island archipelago of the Isles of Shoals located in the Gulf of Maine, 10 km off the coast of Portsmouth, New Hampshire USA. The eastern side of the Appledore Island faces the open Atlantic Ocean and experiences high wave action and intense winter storms; the leeward western shore is more protected. All fieldwork was done on the protected side of the island at 6

locations (Figure 1). The shoreline is composed of stretches of bedrock ledges interspersed with cobble coves. The Isles of Shoals experience semi-diurnal tides of ~4m amplitude.

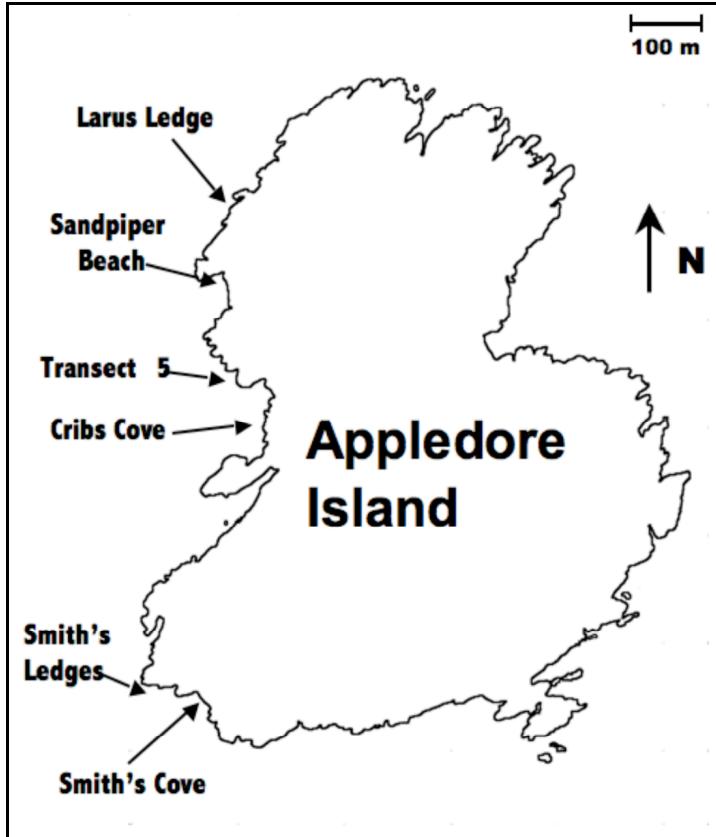


Figure 1: Appledore Island with study sites along the relatively protected western shore.

Distribution and demography of crab populations

To determine the shallow water distribution of *C. borealis*, *C. meanas*, and *C. irroratus*, we conducted a census of crabs in five vertical zones that encompassed the mid-intertidal (*Ascophyllum* and upper *Chondrus*), low intertidal (low *Chondrus*) and shallow subtidal [-1m and -2m relative to Mean Lower Low Water (MLLW)]. *Ascophyllum* and *Chondrus* are multicellular algae that are predominant in their respective zones. *Ascophyllum* is made of long thick strands that form beds in the mid-intertidal. It floats at high tide and forms a complex vertical habitat. *Chondrus* is next

down the intertidal below *Ascophyllum* and is a branching algae that forms a dense short canopy.

Crab distributions were studied at six sites, three from each of two kinds of habitats: cobble coves (Smith's Cove, Crib's Cove, Sandpiper Beach) and rocky ledges (Smith's Ledges, Transect 5, and Larus Ledge). The cove habitats were protected areas with bottoms that were comprised of large cobbles. Ledges had bottoms of large slabs of bedrock. Crabs were sampled in 1m² quadrats at high tide by SCUBA divers during the period of June 28-July 31, 2006; quadrats were randomly spaced along the tidal zone contour at each site. Randomization was accomplished by spacing the quadrat by a random number of kick cycles; the numbers were selected from a random number table. To ensure the accuracy of our crab censuses, we inspected crevices, turned over rocks, and carefully combed through algae. All crabs were sexed and measured (carapace width: ±0.5mm).

Abundances of all three species were very low within the 1m² quadrats (see results), so we summed the crab abundances of the 5 quadrats from each site. The sampling design then provided 3 replicates of each habitat type (cove and ledge) for each of the 5 vertical zones.

We used an ANOVA to examine the effects of habitat type, vertical zone, and their interaction on the transformed abundance of *Carcinus* and *C. borealis*. Crab abundances were transformed [log (x+1)] to produce residuals that were normally distributed with constant variance. Non-significant effects with p>0.25 were removed from the model and the analysis repeated.

C. irroratus densities were too low to use an ANOVA to analyze patterns across zones and habitats. Therefore, we used a binomial test to determine whether the number of individuals found in coves versus ledges differed from the expected proportion of 0.5, and whether the number of individuals found in the subtidal zones (-1m and -2m) differed from the expected proportion of 0.4 (2 of the 5 zones sampled).

We also analyzed the size and sex distribution of each crab species. *C. borealis* was relatively rare in the intertidal zones, so we restricted the analyses to individuals found in the two subtidal zones. For *Carcinus* we grouped the vertical zones into “intertidal” (*Ascophyllum*, upper *Chondrus*, lower *Chondrus*) and “subtidal” (-1m and -2m). For both species, we used a two-way ANOVA to examine the effects of zone, habitat (ledge vs. cove), and their interaction on crab size. Too few *C. irroratus* were available for a meaningful analysis of size distribution. For all species we used nominal logistic regression to determine whether sex is predicted by zone, habitat, size, and all possible interactions of these factors. We used two-sided binomial tests to determine whether the sex ratios differed from 1:1.

Shelter use of Carcinus maenas in the presence of potential predators

Carcinus maenas are potential prey of lobster, *C. borealis*, and larger conspecifics. We used a laboratory experiment to determine how *Carcinus* may alter use of shelter sites and behaviors in the presence of these potential predators. Our experiment included 10 replicates of 4 treatments (Table 1). Each treatment included one of these potential predator species or same-sized conspecifics as a control. The experimental design included three temporal parts (Table 1), each consisting of a 24 hr period: Part A: only 8 medium-size *Carcinus* (30-43 mm carapace width) present; Part B: potential

predator added (and 2 *Carcinus* removed); Part C: potential predator removed (and 2 medium-sized *Carcinus* added back).

TREATMENT	Lobster (72-79mm CL)	<i>C. borealis</i> (90-110mm CW)	Large <i>Carcinus</i> (50mm CW)	Medium <i>Carcinus</i> (30-43mm CW)
Part A	8 medium <i>Carcinus</i>	8 medium <i>Carcinus</i>	8 medium <i>Carcinus</i>	8 medium <i>Carcinus</i>
Part B	6 medium <i>Carcinus</i> + 1 lobster	6 medium <i>Carcinus</i> + 2 <i>C. borealis</i>	6 medium <i>Carcinus</i> + 2 large <i>Carcinus</i>	6 medium <i>Carcinus</i> + 2 medium <i>Carcinus</i>
Part C	8 medium <i>Carcinus</i>	8 medium <i>Carcinus</i>	8 medium <i>Carcinus</i>	8 medium <i>Carcinus</i>

Table 1: The experimental design for the habitat experiment. Part A is an introductory phase where 8 *Carcinus* are added to the tank and left for 1 day. Part B is the second day when two *Carcinus* are removed and replaced with the animals from one of the predator treatments or the control. Part C is the third day when the predators are removed and the original two *Carcinus* are replaced.

Small *Carcinus* were collected from the protected side of the island most often at “the swimming pool” beach. They were collected up to two days before the start of a trial and were kept in aquaria. To prevent stress they were given rocks for shelter and fed snail to prevent cannibalism. Large *Carcinus* were collected from the same location and kept separately; they were not feed prior to the trial. *C. borealis* was collected in deeper waters on the protected side of the island. They were kept in aquaria and were not fed for the two days prior to entering the trial. Lobsters were collected in early June and were kept with claws banded in a large sea table. They were fed snails regularly but were not fed to satiation.

To simulate a natural environment with shelter sites, we covered the bottom of four flow-through sea tables (180x86x55cm) with 3cm of gravel, placed three large rocks (20x20cm) in the central area, and two pipes (20cm long, 10 cm diameter) in tank corners (Figure. 2). The space under the L-shaped sea-table drainpipe was also available as shelter. The sea-tables were located under a porch and were shaded from direct sun but

underwent natural light and dark cycles. The treatments were randomly assigned to sea tables to prevent any tank bias. All crabs used in the experiment were labeled with numbered light pink flagging tape glued to the carapace and randomly assigned to treatments. In cases where *Carcinus* were found dead in the tank they were replaced with a new crab.

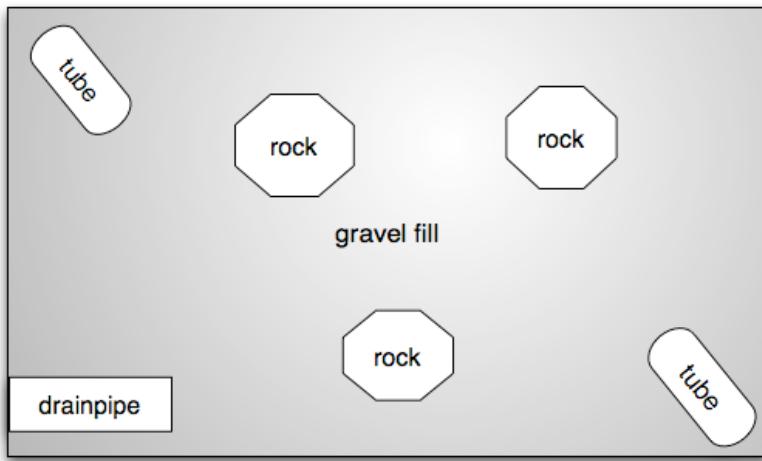


Figure 2: The experimental tank contained 3 rocks, 2 tubes, 1 drainpipe, and gravel available for shelter.

During each 24 hr phase of the experiment, the positions of the crabs and lobster were observed at 900, 1300, 1800, 2100, and 2300 hours. The day observations were considered to be 900, 1300 and 1800 and the other two were classified as night observations. All observations were made without moving any objects in the sea table. Tank manipulations (i.e. addition or removal of *Carcinus* or predators) were done one hour before observations were taken to allow time for acclimation. The sea-tables were located in a high traffic area and were continually exposed to people passing by. While collecting data the observer would be close to the tank and look into the tank from above. At night, a light covered with a red cellophane filter was used to help locate subjects with

minimal disturbance. The position/behavior of each animal was recorded and categorized as shown in Table 2. At the end of the experiment the sea-table was carefully searched for all remaining crabs. A missing crab was recorded as eaten and assumed to have died in the time period following its last sighting.

Behavior	Behavior description
Buried	Crab body mostly buried in gravel with only the carapace showing
Sheltered	Crab under a rock or pipe or in a pipe
Climbing	Crab on top of a rock or drain pipe or climbing on the wall
Exposed	Crab standing or walking on gravel surface
Not visible	Crab could not be located.
Hidden	Sum of buried, sheltered and not visible categories

Table 2: The categories on the left were used to summarize the data collected during observation periods.

To compare at the differences in mortalities between treatments we calculated proportion of *Carcinus* that were consumed in each trial. The consumption rates in the control and large *Carcinus* treatments were both zero. Therefore, we used t-tests to determine whether the rates in each of the other two treatments differed from a hypothesized mean of zero. We also used a t-test (assuming unequal variances) to compare consumption rates between the lobster and *C. borealis* treatments.

Carcinus behavior was analyzed to determine whether there were changes between day and night, phases of the experiment, and treatments. During the initial phase (Part A) of the experiment the conditions were the same in all treatments and we used observations during this phase to compare day and night behaviors and shelter use. Results from Phase B, when potential predators were present, were used to compare

Carcinus behaviors across treatments. Behaviors were averaged across the observations in the day and night categories. Data were analyzed in an ANOVA with day/night crossed within treatment. To determine whether effects of predators on *Carcinus* disappear after the predators are removed, we compared the results from Part C across treatments, and between Parts A and C within treatments.

Vertical distribution of small invertebrates

To determine the distribution of food vertically through the intertidal and subtidal zones we scraped down to bedrock in 15cmX15cm quadrats along the *Ascophyllum*, upper *Chondrus*, lower *Chondrus*, and at -1 and -2 below MLLW and collected all algae and animals. The samples were rinsed in 50% seawater to remove most mobile invertebrates from the algae, and then all invertebrates were carefully collected from the algae and rinse water. Invertebrates were then sorted and counted by species and size-class.

To analyze the distribution of each species across the 5 vertical zones and between the intertidal (3 upper zones) and subtidal (2 lower zones), we performed one-way ANOVAs on the transformed [$\log(x+1)$] densities. In most cases, these data transformations produced residuals that were normally distributed. However, differences in variance in mussel densities could not be satisfactorily resolved through transformations. Therefore, we used a t-test with unequal variances to compare densities between the subtidal and intertidal zones.

Feeding trials

To understand what size prey was available to different predators we offered mussel *M. edulis* to large *C. borealis* (max carapace width of greater than 90mm) and two

size classes of *Carcinus* (Small: 30-43mm Large: greater than 55mm max carapace width). The crabs were starved between 24 and 72 hours then placed in 37X28cm washtubs for a 30-minute acclimation period with a rock for shelter. They were then offered small (20-22mm max length) or large (29-31mm max length) mussels collected from the protected side of Appledore. The crabs were observed for an hour to see if they ate the mussel. After the hour had ended, if the crab had not eaten the mussel then the washtub, crab and mussel were placed together into a sea table with running water over night. In the morning we recorded which crabs had been successful in feeding. For crabs that had still not eaten, the mussel was cracked and given back to the crab to determine hunger level. If the crab ate the mussel after it had been cracked, the crab was marked as unable to open the mussel; if the crab did not feed, the trial was discarded. A minimum of eight trials were completed for each combination of crab and mussel type.

Results

Distribution and abundance of crab species

In total, in the 150 square-meter samples, we found a 155 *Carcinus*, 40 *C. borealis*, and 17 *C. irroratus*. Densities of *Carcinus* and *C. borealis* did not differ between habitats (coves vs. ledges) and there was no habitat by zone interaction effect (ANOVA: all $p>.5$). In contrast, densities varied strongly across vertical zones, but with opposite patterns in the two species (Figure 3). *C. borealis* was significantly more abundant in the two subtidal zones (-1m and -2m) compared to the intertidal *Ascophyllum* and upper *Chondrus* zones (ANOVA: zone effect, $F_{4,25}=11.02$, $p<0.0001$; Tukey's post-hoc tests, $p<0.05$). The *Carcinus* abundance showed a marginally significant zone effect

($F_{4,25}=2.57$, $p=0.063$). We performed a Tukey's post-hoc test to clarify the interactions between factors that made the ANOVA close to significant. We found that *Carcinus* density in the upper *Chondrus* was significantly greater than the density found at -2m (Tukey's post-hoc test, $p<0.05$).

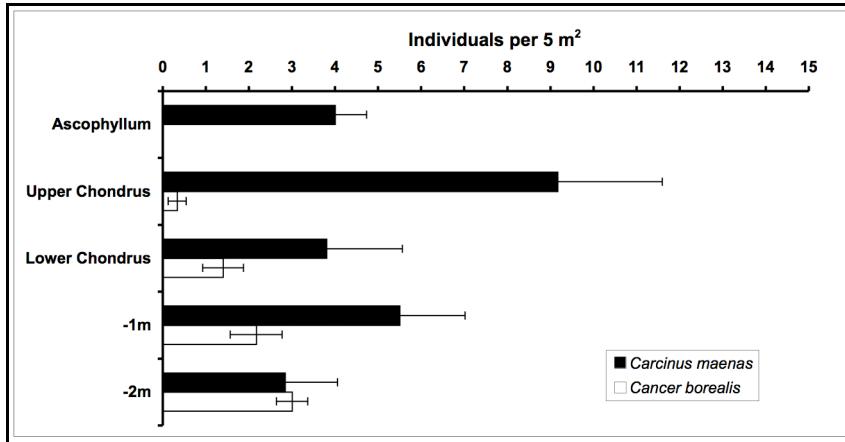


Figure 3: The number with standard error shown of *Carcinus* and *C. borealis* in 5m^2 across shoreline vertical zones. *Ascophyllum*, upper *Chondrus* and lower *Chondrus* are intertidal zones and -1m and -2m are subtidal zones.

In contrast to the other two crab species, *C. irrortatus* abundance differed among habitat types, with significantly higher numbers in ledge habitat (15 individuals) compared to cobble cove habitat (2 individuals) [2-sided binomial test: $p=0.0013$]. Additionally, *C. irrortatus* were primarily in the subtidal zones (13 individuals found at -1m or -2m) rather than in the intertidal zones (4 individuals in the upper and lower *Chondrus* zones) [2-sided binomial test: $p=0.0036$].

Size and sex distribution of crab species:

The size of *Carcinus* was significantly affected by habitat type, subtidal and intertidal zone, and their interaction (ANOVA: habitat type, $F_{1,151}=3.94$, $p=0.049$; zone, $F_{1,151}=23.53$, $p<.0001$; habitat-type x zone, $F_{1,151}=5.47$, $p=0.021$). *Carcinus* found in the intertidal ledge habitat were significantly smaller than those found in the subtidal ledge

habitat and intertidal and subtidal cove habitat (Tukey's post-hoc tests, $p<0.05$; Figure 4).

Males represented 63% of all *Carcinus* sampled, a highly significant deviation from an expected value of 50% (2-sided binomial test, $p=.0015$). Male and female *Carcinus* had similar distributions across habitats and zones (nominal logistic regression, likelihood ratio tests: both $p>0.2$). However, sex was significantly predicted by crab size (nominal logistic regression, likelihood ratio test: $p=0.0014$), with females larger than males (35.4 ± 1.3 mm vs. 28.5 ± 1.4 mm carapace width).

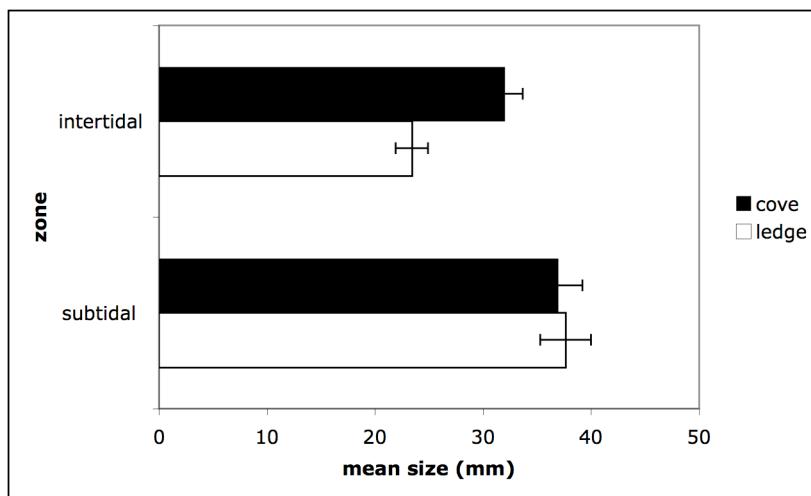


Figure 4: The mean size of *Carcinus* collected from intertidal and subtidal areas in cove and ledge habitats.

C. borealis were significantly larger at -2m (64.8 ± 5.7 mm carapace width) than at -1m (40.5 ± 6.9 mm) [ANOVA: zone effect, $F_{1,27}=9.09$, $p=0.006$]. Habitat type and its interaction with zone did not significantly affect crab size (both $p>0.1$). The sex ratio was significantly skewed: 70% of individuals were male (2-sided binomial test, $p=0.011$). The distribution of males and females across zones and habitat types did not differ (nominal logistic regression, likelihood ratio tests: all $p>0.1$). Females were larger than males (61.0 ± 7.4 mm vs. 45.0 ± 4.9 mm carapace width), but the difference was not statistically significant ($p=0.09$).

Of the 17 *C. irroratus* sampled, 71% were male; due to the small sample size, the deviation from an expected 50% was not significant (2-sided binomial test, $p = 0.09$). All individuals were relatively small (carapace width: $= 28.6 \pm 9.5$ mm; range 13–45 mm), with no size difference between males and females.

Results from laboratory habitat use experiment

Mortality and Shelter use of Carcinus maenas in the presence of potential predators

Carcinus mortalities occurred only in the lobster and *C. borealis* treatments, and all deaths occurred during part B of the experiment when the predators were present. In the lobster treatment, *Carcinus* deaths occurred in 9 of the 10 trials, with a total of 27% of the crabs being consumed. The mean *Carcinus* death rate differed significantly from the control treatment death rate of 0 (t-test, $t=5.2$, $df=9$, $p=0.0003$). In the *C. borealis* treatment, *Carcinus* deaths occurred in 2 trials with a total of 5% of the *Carcinus* consumed; this death rate was not significantly greater than 0 (t-test, $t=1.4$, $df=9$, $p=0.10$). However, a power analysis reveals a beta value of 0.64, making it unlikely that we could statistically detect a predation rate of 5%. A comparison of the lobster and *C. borealis* treatments showed that the 27% death rate when lobsters were present was significantly higher than the 5% seen in the *C. borealis* treatment (t-test with unequal variances: $t=3.5$, $df=16$, $p=0.003$) (Figure 5).

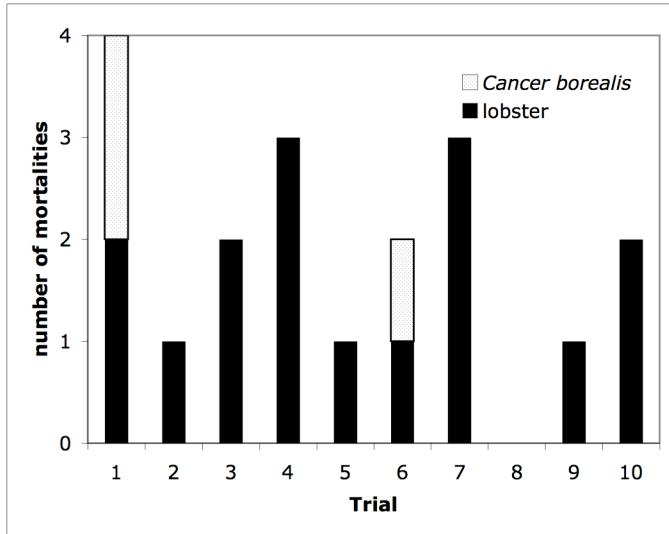


Figure 5: The number of *Carcinus* mortalities in the lobster and *C. borealis* treatments shown for each trial.

Shelter use during day versus night

In the day *Carcinus* were significantly more likely to be sheltered, buried, or not visible during Part A (ANOVA: all $p < .0001$). At night, *Carcinus* were significantly more likely to be climbing or exposed on the gravel surface (ANOVA: climbing $p = .0036$; exposed $p < .0001$) (Figure 6).

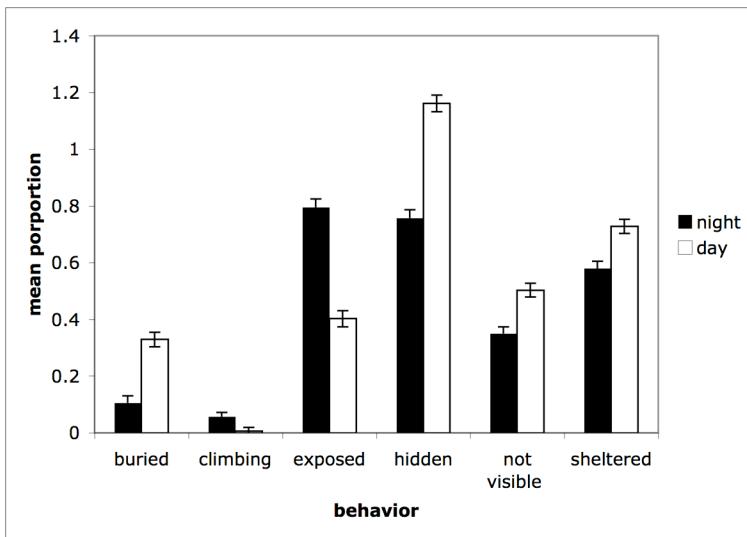


Figure 6: Night and day behavioral expression before predators were added.

Shelter use in the presence of a predator

When the predators had been added (Part B), we began to see differences between treatments (Figure 7). The proportion of *Carcinus* that were climbing, exposed, not visible, and hidden all varied significantly among treatments. *Carcinus* in the lobster treatment climbed or were not visible significantly more than crabs in all other treatments and were significantly less likely to be exposed (b, d figure 7) (ANOVA: climbing $f_{3,72}=2.98$, $p=0.0001$; Tukey's post-hoc test $p<0.05$; not visible $f_{3,72}=6.23$ $p=.0008$; Tukey's post-hoc test $p<0.05$; exposed $f_{3,72}=9.52$, $p<0.0001$; Tukey's post-hoc test $p<0.05$). Across most treatments exposed and climbing behaviors both showed significant variation between day and night (a, b figure 7) (ANOVA: climbing $f_{1,72}=8.234$, $p=.0054$; exposed $f_{1,72}=31.02$, $p=.0028$). The exception was in the lobster trial where exposed behavior was not significantly different and *Carcinus* were rarely exposed in both day and night (b figure 7) (Tukey's post-hoc test $p<0.05$). After the predators had been removed (Part C) all treatment effects were lost.

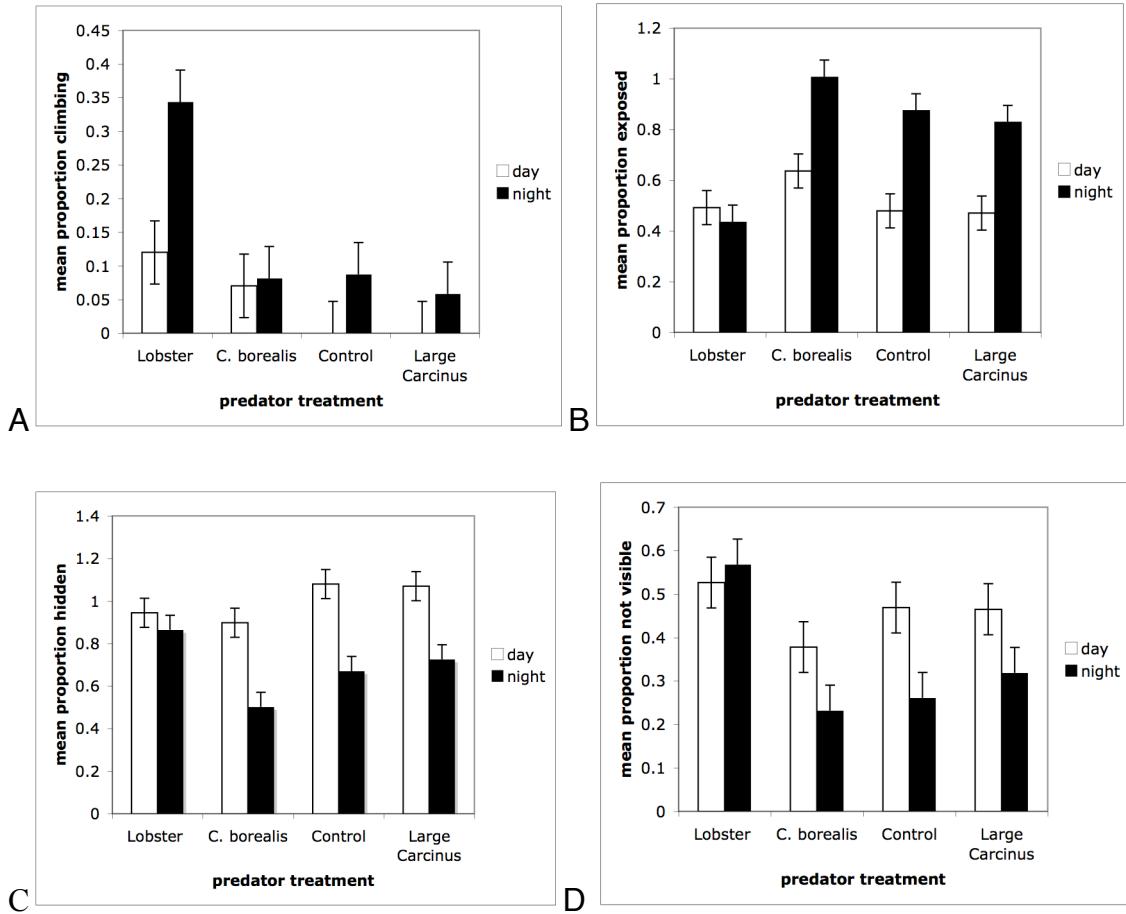


Figure 7: Behavioral expression for each treatment after the predators were added to the experiment.

Behavior	Effect	Significance
Climbing	More climbing in lobster treatment	ANOVA: $f_{3,72}=2.98$, $p=0.0001$
Shelter	Shelter was used more in the day	ANOVA: $f_{1,72}=17.50$ $p<.0001$
Exposed	Lobster treatment had the least exposed	ANOVA: $f_{1,72}=31.02$, $p<0.0001$ Tukey's post-hoc test: $p<0.05$
	Crabs were more exposed at night	ANOVA: $f_{1,72}=31.02$, $p=0.0028$
Hidden	All treatments were hidden more during the day. This was a significant difference for all except the lobster treatment	ANOVA: $f_{1,72}=40.83$ $p<0.0081$ Tukey's post-hoc test: $p<0.05$
Buried	Crabs were buried most in the day	ANOVA: $f_{1,72}=39.3$ $p<0.0001$
Not visible	Crabs were more often not visible in the lobster treatment	ANOVA: $f_{3,72}=6.23$ $p=0.0008$
	Crabs were more often not visible in the day	ANOVA: $f_{1,72}=20.27$ $p<0.0001$

Table 3. Summary of behavioral and shelter-use differences observed among treatments when predators were present.

Feeding trials

During the feeding trials we found that small mussels could be eaten by all of the crabs. The large *Carcinus* ate the highest percent of small mussels offered to them. Large *Carcinus* consumed 80%, small *Carcinus* consumed 40 % and *C. borealis* consumed 50% of offered small mussels. All crabs are equally likely to be able to eat a small mussel (Chi square test $p=0.1315$). The ability to access prey changed when large mussels were offered. Small *Carcinus* were only able to open 1 large mussel over the ten trials, large *Carcinus* opened 69% and *C. borealis* opened 100% (Figure 8). The ability of the crabs to get into the large mussels was significantly different (Chi-Square test $p=0.0005$) Large *C. borealis* were 40 times more likely to be able to consume a large mussel than small

Carcinus. Large *Carcinus* were 3.2 times as likely to eat large mussels compared to small *Carcinus*.

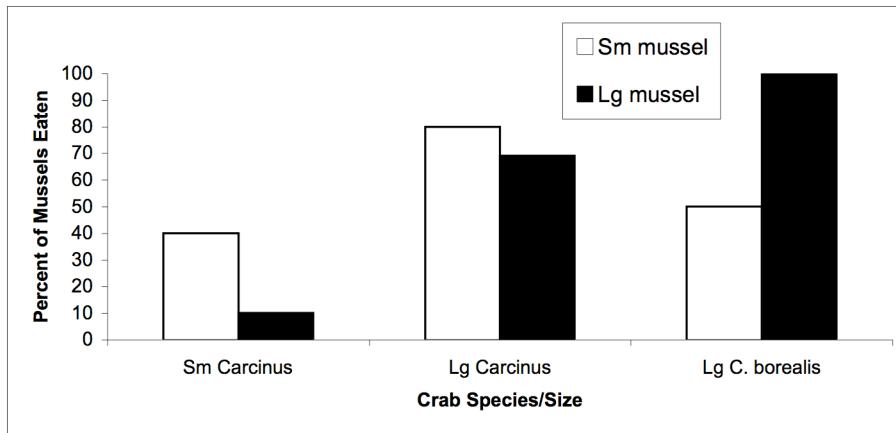
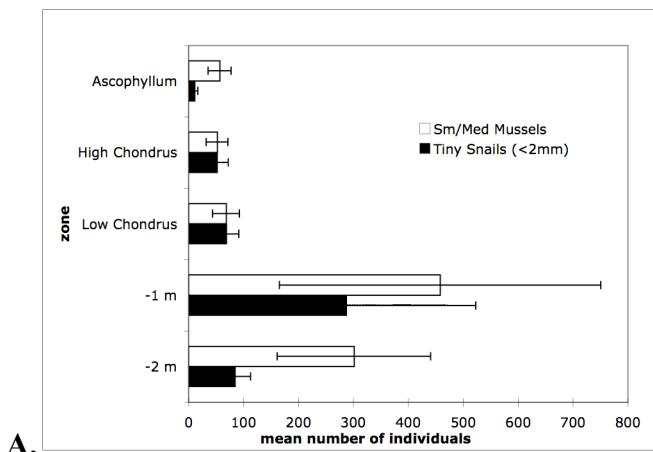


Figure 8. The percent of each mussel type successfully eaten by the three crab treatments.

Vertical distribution of small invertebrates

Mussels (small/medium), tiny snails, and amphipods all had higher mean abundances in the subtidal compared to the intertidal zone (Figure 9), but due to high variance the difference was only close to statistically significant for the mussels (t-test with unequal variances: $t=-2.02$, $p=.058$, $df=19.3$). In contrast, *Littorina littorea* and *L. obtusata* had higher abundances in the intertidal than the subtidal (ANOVA: *L. littorea* $p=.049$; *L. obtusata* ANOVA $p=.013$) (Figure 9). Both snails show low abundance in areas where they were present.



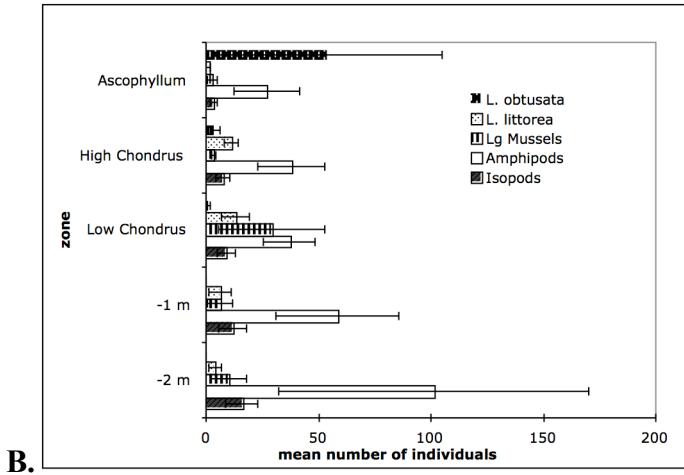


Figure 9: Densities (mean + SE) per quadrat (225 cm^2) of small invertebrates across intertidal and subtidal zones. Part A shows the distribution of the more abundant mussels and snails. Part B shows the distribution of less numerous invertebrates. *Ascophyllum*, Upper *Chondrus* and Lower *Chondrus* are intertidal zones and -1m and -2m are subtidal zones.

Discussion

There is an incongruent distribution between *Carcinus maenas* and its major prey species. *Carcinus* has its highest densities in the intertidal, while its prey items, particularly the mussel *Mytilus edulis*, reach highest densities in the shallow subtidal. Our experiments suggest that the low densities of *Carcinus* in the subtidal are due to interactions with the American lobster, *Homarus americanus*. Lobsters produce direct mortality of *Carcinus* and cause behavioral shifts that result in upshore movement.

Intraguild predation is defined as predation among members of a feeding guild. Guild members all feed on a common class of prey (HilleRisLambers and Dieckmann 2003, Krivan 2000). The decapods *Cancer borealis*, *C. irroratus*, lobster and *Carcinus* inhabit the Gulf of Maine and belong to the same shell-breaking feeding guild. They share the same primary prey, mussels, and they also all consume gastropods, polychaetes, sea urchins and other crabs (Ojeda and Deerborn 1991, Ropes 1968, Elner 1981, and

Sainte-Marie and Chabot 2002). In the case of intraguild predation where one member of the guild is both competing with and being preyed upon by other members, the situation is unstable and this species may have trouble persisting in the same habitat (HilleRisLambers and Dieckmann 2003, Krivan 2000).

An important part of the lobster's diet in the Gulf of Saint Lawrence is *C. irroratus* (Sainte-Marie and Chabot 2001) and in other regions the two *Cancer* species can comprise the largest component of lobster gut contents (Ojeda and Deerborn 1991). *Carcinus* has only recently expanded its range into the Gulf of Saint Lawrence (Audet et al. 2003), but in areas where its population is well established, it may provide a similarly high quality food source to lobsters. Lobsters have been found to eat *Carcinus* in the laboratory and in the field (P. Jones, *unpubl. data*; personal observation).

Lobsters are predominantly found in the subtidal, although they do venture up to the intertidal on nocturnal high tides (P. Jones *unpubl. data*). Previous work done at Appledore Island showed significantly higher mortality rates for *Carcinus* tethered in the subtidal when compared to mortality rates for those tethered in the intertidal (C. Santamaria *unpubl. data*). In our distribution study we see that *Carcinus* numbers are lower in the subtidal (-1 to -2 m depth). A previous study on Appledore had shown that *Carcinus* density is near-zero below -2 m (Lozyniak 2003). In subtidal areas interguild predation may be higher due to more abundant predators, in these deeper areas *Carcinus* may not be able to persist. Mortality in the lobster treatment of our habitat experiment was 25% in just 24 hours. In addition, we saw behavioral changes in *Carcinus* (burying deep in the gravel or climbing) that indicates a strong avoidance response. Climbing (moving upwards) may produce a shift of *Carcinus* into upshore, intertidal areas where

encounters with lobsters are fewer. Thus, lobsters may reduce *Carcinus* densities in the subtidal directly through predation and indirectly through behavioral effects. Both consumptive and trait-mediated indirect effects would reduce predation by *Carcinus* on small invertebrates in the subtidal zone, which would decrease the competition for food between *Carcinus* and lobster.

Predator effects on behavior of prey are well documented for many species. They are known to decrease foraging in fishes [plaice (Burrows and Gibson 1995), perch (Diehl and Eklov 1995), mammals [Pikas (Holmes 1990)], crustaceans [juvenile lobsters (Spanier et al 1998, Wahle 1992)] and snails [*Nucella lapillus* (Trussell 2006)]. These trait-mediated indirect effects occur when the presence of a predator induces a change in the behavior or growth of the prey species. These effects can in turn affect another species. We see this type of effect in the habitat experiment in the lobster treatment.

In our trials, in the presence of *C. borealis*, *Carcinus* did not increase its time in shelters. Though *C. borealis* is larger and capable of being predatory, *Carcinus* is the faster, more mobile crab. It may stay out of shelters because it is faster and can readily out-maneuver *C. borealis*. It may be safer out in the open rather than trapped in a shelter where it could be attacked and would be unable to escape. *C. borealis* has broader, more powerful chelae than *Carcinus*, and is more effective at opening large mussels (Moody and Steneck 1993; this study). In both laboratory and field studies, *Carcinus* has been seen approaching a feeding *C. borealis* and stealing food (Shulman *unpubl. data*). As long as *Carcinus* is out in the open and able to out-maneuver *C. borealis* it may benefit from a close association with *C. borealis*.

The rocky intertidal zone has low densities of lobsters and *C. borealis*. Intense diurnal predation by gulls keep large conspicuous decapods like lobster and *C. borealis* populations low in the intertidal and restrict them to a predominantly subtidal distribution (Ellis *et al.* *in press*, C. Santamaria *in prep*). In contrast, *Carcinus* are able to avoid predation by gulls due to cryptic coloration or some behavioral mechanism (Ellis *et al.* 2005, Dumas & Witman 1993, K. Allen, *unpubl. data*). Their ability to escape predation pressure from lobsters in the subtidal by moving to the intertidal where gulls keep predators at bay may be the explanation for the incongruent distribution of *Carcinus* and their major food resources.

My experimental results show that the larger predatory lobster can change how *Carcinus maenas* uses its habitat. These results show that interactions with lobsters are quite risky for *Carcinus* and frequently result in death or marked behavioral changes. Further, my field and laboratory results together suggest that *Carcinus* living in the intertidal may avoid considerable predation in the subtidal, while necessarily making less use of more abundant subtidal prey. The patterns I have found may explain how *Carcinus* can continue to persist as both competitor and prey in this system of interguild interactions.

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