INTRAGUILD AND EXTRAGUILD PREDATION: IMPLICATIONS FOR THE DIEL ACTIVITY AND DISTRIBUTION OF FOUR LARGE DECAPOD SPECIES

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Abstract. On the rocky shores of the Gulf of Maine, the American lobster, *Homarus* americanus, the Jonah crab, Cancer borealis, the Rock crab, Cancer irroratus, and the Green crab, Carcinus maenas, compose a guild of highly mobile predators. Although the species are potential competitors that consume the same prey and utilize the same shelters, lobsters also prey on crabs (i.e., lobsters are intraguild predators of crabs). During daytime low tides, crabs are also preved upon by Larus spp. gulls. In this study, I investigated the importance of avian and intraguild predation in influencing the diel and spatial (depth) patterns of decapod activity in the algal-covered lower intertidal and subtidal zones of Appledore Island, Maine, USA. During the summer months of 1999, the diel abundance and size distribution of active individuals was measured at several depths for each decapod species. Densities of active lobsters were highest at night and did not vary with depth. Contrary to prevailing knowledge, C. borealis and C. maenas were active almost exclusively during the day. While diurnal C. borealis were significantly more abundant in the deepest zone (9-11 m), C. maenas was not found at this depth and was most abundant in the shallowest zone (0-1 m). Day and night C. irroratus densities were not significantly different and showed no significant variation with depth. Only C. irroratus populations exhibited a diel difference in the mean size of individual crabs. The mean size of individuals observed during the day was larger than those observed at night. During the day, C. borealis were larger at depths of 9-11 m than at depths of 1-3 m, while C. maenas crabs were larger at depths of 5-7 m than at depths of 0-1 m.

The magnitude of avian predation was assessed by censuses of crab remains collected in the intertidal during periods of low tide. Results reinforce previous studies in suggesting that gulls are a major factor limiting the upper distribution of C. borealis. In the subtidal, the relative availability of potential shelters does not appear to account for the depth distributions observed among the species. The presence of a potentially sheltering *Codium* algal canopy at 1 to 7 m may be important for C. maenas and C. irroratus. A subtidal tethering experiment with C. borealis and C. irroratus revealed no diel or depth differences in crab survival. Overall, rates of predation were very low, but were significantly higher for small than for large crabs. Besides lobsters, no other predators were observed at the study site; predation on tethered crabs was therefore attributed to lobsters. In laboratory experiments exposing pairs of small and large C. borealis and C. irroratus to lobsters, small crabs were shown to be significantly more vulnerable to predation than large conspecifics; C. borealis and C. irroratus of similar size were equally vulnerable. Large crabs, however, were attacked 71 times more often than were small crabs. The results of this study reinforce concerns that traditional models of rocky shore community organization must be amended to include mobile predators. They indicate that competitive interactions between small crabs and lobsters may be unimportant relative to intraguild predation. For large crabs, perceived nocturnal intraguild predation pressures may be just as important as competitive interactions between guild members, especially in the recent absence of predatory fishes. These results underline the importance of understanding the ecological history of the community. They suggest that the overfishing of coastal fish populations has increased the relative importance of intraguild interactions and has thereby indirectly strengthened the link between marine and terrestrial ecosystems.

INTRODUCTION

The relative importance of competition and predation in determining the characteristics of individual organisms (e.g. behaviour), populations (e.g. demographics), and communities (e.g. species coexistence), has been a much debated topic in ecology. Reviews have shown that both the effects of predation (Hughes, 1980; Sih et al., 1985) and the effects of competition (Connell, 1983; Schoener, 1983) are frequent and important in natural systems. The majority of studies that have sought to address both interactions simultaneously have done so by comparing the relative importance of competition within a particular trophic level with that of predation by higher levels. Root's (1967 p. 335) definition of the ecological guild as "a group of species that exploit the same class of environmental resources in a similar way" allows us to simplify a system by simultaneously describing multiple species from the perspective of their common resources, but also enables us to focus on the interactions that occur within the guild. The development of the intraguild predation (IGP) concept has thereby sparked the recognition of additional complexities involved in species interactions. IGP differs from the classical concepts of predation and competition in that it combines the two – being the interspecific consumption of species that potentially compete for the same resources. IGP can therefore occur within a trophic level and can have more complex effects on organisms, populations, and communities than can either predation or competition alone (Polis et al., 1989). Consideration of IGP has been informative in studies of the behaviour of zooplankton (Gismervik and Anderson, 1997), the population dynamics of scorpions (Polis and McCormick, 1987), and the coexistence patterns of island spiders and lizards (Spiller and Schoener, 1988).

On the rocky shores of temperate zone marine systems, predation and competition have been studied extensively (Connell, 1961, 1970; Dayton, 1971; Lubchenco, 1978, 1985; Menge, 1976; Menge and Lubchenco, 1981; Ojeda and Dearborn, 1990, 1991; Paine, 1966, 1974). IGP has also been described in these systems (e.g. Paine, 1963). Most of these studies have examined interactions among sedentary organisms (e.g. algae, gastropods and echinoderms), with large mobile predators only recently garnering full attention. The work that has been done with highly mobile predators has shown that their role in communities can be significant (Ojeda and Dearborn, 1991; Robles, 1987; Witman and Sebens, 1992; Wootton, 1992), yet many of the interactions among them remain unresolved.

Lobsters and crabs constitute a dominant and abundant group of the large, highly mobile animals found along the rocky shores of the northwestern Atlantic's Gulf of Maine region. In part due to their economic importance, much has been learned concerning the biology of the American lobster (*Homarus americanus* Milne-Edwards), as well as of the three common crab species, the Jonah crab (*Cancer borealis* Stimpson), the Rock crab (*Cancer irroratus* Say), and the Green crab *Carcinus maenas* (L.). The four species constitute a guild by utilizing the same set of resources (shelters and prey) in a mechanically similar way – more so than any other syntopic species. Although these species have been previously described as belonging to a "guild" of mussel consumers that has included *Asterias* sea stars, and the gastropods *Buccinum undatum* and *Thais lapillus* (Menge, 1983; Witman, 1985), these classifications are more suitably considered "functional groups" in the original definition of the concept (Cummins, 1974) that does not focus on the method with which a resource is utilized – as does the original guild concept (Root, 1967; Simberloff and Dayan, 1991).

The diets of lobsters and the three crab species show a high degree of habitat-specific overlap with the predominant prey consisting of mollusks, polychaetes, echinoderms, and other crustaceans (Elner, 1980; Elner and Campbell, 1987; Ennis, 1973; Hudon and Lamarche, 1989; Ojeda and Dearborn, 1991; Ropes, 1989; Stehlik, 1993). The exception is that crabs are an important component of the lobster diet, while very little predation on lobsters by crabs appears to occur. All four decapods have consistently been described as nocturnal foragers that retreat to shelter during diurnal periods of inactivity (Aagaard et al., 1995; Burrows et al., 1999; Ennis, 1983, 1984; Fogarty, 1976; Gibson et al., 1998; Lawton, 1987; Naylor, 1958, 1960; Ojeda, 1987; Pottle and Elner, 1982; Rebach, 1985, 1987; Reid and Naylor, 1989; Stehlik et al., 1991; Wang, 1982; Witman, 1985).

Studies that have addressed the ecology of these decapods have often sought to explain their distributions and coexistence. However, hypotheses based on interspecific interactions have focused on the role of competition between the species. Studies have thus centered on finding dietary differences (Hudon and Lamarche, 1989; Stehlik, 1993) and differences in habitat utilization (Hudon and Lamarche, 1989; Jeffries, 1966; Stehlik et al., 1991), or have investigated competition for shelter (Richards, 1992; Richards and Cobb, 1986; Wang, 1982). Few studies have examined all species simultaneously.

These investigations have shown that *C. borealis* is competitively inferior to lobsters when it comes to shelter acquisition in the laboratory setting, regardless of the relative size of individuals

(Richards and Cobb, 1986). In some habitats, *Cancer* crabs have also been shown to broaden their diet in the presence of lobsters (Hudon and Lamarche, 1989). Experimental evidence for competition in the field, however, is tenuous: only after one of two periods of intensive lobster removal did Wang (1982) find a significant increase in the number of small *C. borealis* (< 50 mm carapace width), but not of *C. irroratus* or large *C. borealis*. The addition of shelters resulted only in a significant increase in the density of all decapods, suggesting shelter is a limiting resource for all four species, but not an important basis for competitive interactions.

Changes in the distribution and resource usage patterns of a species observed in the presence of other species cannot be solely interpreted as evidence of competition (Mac Nally, 1983); predatory interactions may have the same effect. Even in a guild, competition among members is not assured (Connell, 1980; Wiens, 1977). Real or perceived predatory pressures experienced at different intensities clearly may affect the behaviours and distribution patterns of species (Hines, 1982) and can be the primary factor affecting the activities and distributions of guild members, especially when IGP occurs (Wissinger et al., 1996, 1999). For the members of the decapod guild, both intraguild and extraguild predation may be important interactions. Good (1992) and Dumas and Witman (1993) have, for example, implicated avian predation in shaping the distributions of the three crab species in the intertidal and shallow subtidal. Using laboratory experiments, Richards (1992) has addressed the potential importance that predation by tautog fish has in influencing the habitat choices of lobsters and *C. borealis*.

Three types of interspecific interactions may therefore shape the activity patterns and distributions of a guild's constituent species: (1) competition among guild members, (2) intraguild predation, and (3) predation from outside the guild (i.e. extraguild predation). In this paper, I examine the importance of avian predation and asymmetric IGP by lobsters in affecting the distribution and timing of activity in the three crab populations. I address three main questions. (1) What are the diel patterns of activity and depth distribution among lobsters and the three crab species? (2) Can differences in predation pressure experienced by crabs in the (i) lower intertidal and (ii) subtidal zone explain the observed differences in their distributions and activity patterns? (3) Can differences in the vulnerability of crabs to asymmetric IGP by lobsters explain these differences?

MATERIALS AND METHODS

Site Description

Field studies were conducted on the northwest shore of Appledore Island, Maine, USA (42°58'N, 70°37'W; Fig. 1). Appledore Island is part of the Isles of Shoals situated 11 km off the mainland coast. The study site is relatively sheltered from the prevailing eastern swells that refract around the north side of the island. The gently sloping bedrock surface that extends to depths of \approx 14 m below Mean Low Water Level (MLWL) is dominated by macroalgae [*Ascophyllum nodosum* (L.), *Chondrus crispus* (Stackh.), *Codium fragile* (Suringar), *Fucoid* spp., *Laminaria* spp., *Polysiphonia* sp., and other reds]. Isolated clumps of *Modiolus modiolus* (L.) and individuals of *Agarum cribosum* (Mert.) kelp are found among the boulders and large rocks that occur between 13-15 m depths. Approximately 100 m from the shore at depths greater than \approx 14 m the substrate changes to a sandy bottom. Besides decapods, other mobile predators present around the Isles of Shoals are gulls [*Larus argentatus* Coues and *Larus marinus* (L.)] and several species of fishes, primarily cunner (*Tautogolabrus adspersus*), sculpin (*Myoxocephalus* spp.), juvenile pollock (*Pollachius virens*), skates (*Raja* spp.), striped bass (*Morone saxatilis*) and winter flounder (*Pseudopleuronectes americanus*).

Observational methods

Patterns of diel activity, depth distribution, and size structure. – To determine changes in the depth distribution and population size structure of the four decapod species over their diel periods of activity, censuses were conducted by myself and one other diver while snorkeling or using SCUBA. In the subtidal, five day and three nighttime censuses were performed from June to August 1999. Each subtidal census consisted of three 20 m long, 1 m wide transects haphazardly placed within each of three depth ranges (1-3 m, 5-7 m, and 9-11 m below MLWL). Nighttime censuses were conducted using lights covered by red cellophane filters to reduce startling effects and to better our own night-vision. Within each transect, active individuals (those not in shelters) were counted and measured to the nearest cm [carapace width (CW) for crabs, carapace length (CL) for lobsters]. During the low tide hours of three days (7/17/99, 7/30/99, and 8/3/99), I conducted ten 10 m long, 1 m wide snorkeling transects in the lower intertidal (0-1 m below the water surface). In total, 99 intertidal and subtidal transects were made during the summer months of 1999.



Figure 1. Map of the lower Gulf of Maine showing the location of the Isles of Shoals and the study site on the northwest shore of Appledore Island (inset).

After transforming densities $[\sqrt{(\text{density} + \frac{1}{2})}]$ to reduce heteroscedasticity, I compared the effects of time (day vs. night) and subtidal depth (1-3 m, 5-7 m, and 9-11 m) on the densities of each of the four decapod species using a two-way ANOVA. To include the 0-1 m deep intertidal transects that had only been conducted during the day, I also performed a one-way ANOVA for each species comparing daytime differences in densities across all the depth ranges. Due to the absence of individuals at particular times and depths I was not able to compare the effects of these factors on the size distribution of the decapod populations using a two-way ANOVA. I therefore used a one-way ANOVA on transformed sizes (\sqrt{CW} or \sqrt{CL}) for each species with either time or depth as the independent variable. I used Scheffe's (1953) *F* procedure of

unplanned *a posteriori* contrasts (SC) for comparing densities and sizes between the depth ranges.

Algal cover and shelter availability. – To quantify some of the habitat characteristics of the study site, I measured the algal cover and the relative availability of shelters at each of the three depth ranges. Six to twelve 0.0625 m^2 quadrats were randomly placed within a depth range. The dominant canopy algal species was recorded in each of the twenty-five 5 x 5 cm squares within the quadrat. I determined the effect of depth on percent algal cover (arcsine transformed) using a one-way ANOVA for each of four classified algal/substrate categories. These categories consisted of dominant, morphologically similar or rare algae and substrates, grouped as *Polysiphonia* sp., *Codium fragile*, bare rock and *Coralline* spp., and other (rare) algae.

The relative availability of potential shelters (crevices and holes larger than 5 cm in aperture) in each of the depth ranges was also assessed. One or 2 main reference lines on which 18-24 random points were chosen were placed at each depth. At each point the number of potential shelters intersecting a 1 m long length of rope, stretched perpendicular to the main reference line, was counted. I used a Kruskal-Wallace test to compare the number of shelters per meter-length counted in each of the three depth ranges.

Diurnal gull predation. – To address the potential importance of avian predators (primarily *Larus argentatus* and *L. marinus*) on the activity patterns, spatial distribution and size composition of the three crab populations in the intertidal, I indirectly assessed the magnitude of mortality that these predators exert by collecting the remains of their crab prey. Censuses were conducted between two hours after sunrise and one hour prior to sunset during the low tide on five days in June-August 1999. For each census the exposed intertidal zone (*Ascophyllum* and *Chondrus* zones) of the northwest shore of Appledore Island was scoured to collect all the remains (carapaces and appendages) of killed crabs. Molted carapaces which were easily distinguished from recently killed crabs containing remnant flesh were discarded. After the first search along the shore, a second search was made in the reverse direction to make sure all remains had been collected. Remains were identified to species and CW measured to the nearest mm.

For those remains where the carapace was not intact or present (all of which were *C. borealis* as identified by the shape and black colouration of the dactyloped), one chela was collected instead. Chela length (ChL) was measured as the length of the dactyloped, from the joint to the distal point. Measurements of the CW and ChL of 80 live *C. borealis* (29 to 132 mm CW, 6 to

40 mm ChL), collected from the subtidal of Appledore Island's southwest shore, were used to calculate an expression for CW as a function of ChL. This regression was used to convert the ChLs of collected remains to CWs. The calculated CWs were combined with the measured CWs to determine the size distribution of *C. borealis* crabs killed by the two gull species. Using an unpaired t-test, I compared the size distribution of prey *C. borealis* with the size distribution of live *C. borealis* observed in the 0-1 m deep intertidal transects.

Experimental methods

Diel predation intensity experiments. – To assess the relative risk that *Cancer* crabs experience in the subtidal during day vs. nighttime periods, I performed the following tethering experiment in July and August 1999. Three large *C. borealis* (80-100 mm CW, mean = 91.80 mm \pm 2.13 SE), were tethered to 1 m long weighted bars. Each crab was tethered by a 20-25 cm long, 2.5 mm thick, black vinyl-coated wire fastened to the posterior portion of the carapace by a cable tie loop embedded in a small amount of A-788 Splash Zone Compound (Z-Spar). These tethers provided a suitable alternative to monofilament line (which crabs were able to cut; *personal observation*), allowed equivalent freedom of motion, and required a force > 55 N to dislodge. One or two bars was placed at 2-3 m and 7-9 m below MLWL at the south end of Appledore Island's northwest shore. The survival of these tethered large *C. borealis* was monitored for a total of 16 days and 16 nights (balanced design for day/night and the two depths, n = 27 bars each) by retrieving the bars at the end of each day or nighttime period (within half an hour of sunrise and sunset) using lines that had been tied to surface floats. Missing crabs were replaced at the start of each time period.

The same procedure was concurrently used to assess the vulnerability of small (35 to 55 mm CW) *C. borealis* (43.12 mm \pm 1.09 SE) and *C. irroratus* (43.09 mm \pm 1.26 SE). Rather than wire, however, these small crabs were tethered using monofilament line (15-kg test) which they were not able to cut. I monitored the survival of small *C. borealis* a total of 9 days and 8 nights (unbalanced design with n = 18 bars for day, 16 for night, and 17 for each depth), and that of *C. irroratus* for 5 days and 5 nights (balanced design for day/night and the two depths, n = 5 bars each).

The relative risks of predation for large and small *C. borealis* and *C. irroratus* was compared across the depths and time periods with a two-way ANOVA. I performed the analyses using individual bars (three crabs) as the experimental unit because I assumed that the predation of crabs attached to the same bar were not independent events.

Crab vulnerability to predation experiments. – Several lobsters, ranging in size between 77 and 91 mm CL (81.33 ± 2.11 mm SE) were caught on the west side of Appledore Island and immediately transported to the laboratory. Individuals were maintained separately in covered, opaque aquaria (65 l) with flowing water at temperatures of 14-17 °C. Additional aquaria and sea-tables were used to maintain collections of large and small *C. borealis* and *C. irroratus* (Table 1).

Group	Mean	SE	Size range
Small C. borealis	42.03	1.35	31-55
Large C. borealis	87.30	1.53	72-99
Small C. irroratus	43.37	1.47	28-61
Large C. irroratus	85.26	1.50	72-98

Table 1. Mean carapace width (mm), standard error (SE) and size range of crabs with which vulnerability to lobster predation was examined.

To test the null hypothesis that crabs belonging to different species or size groups are equally vulnerable to predation by lobsters, I performed the following experiments. After an initial 24-hr period of starvation, each lobster was given up to 24 hrs to kill one of two crabs that had been placed simultaneously into its aquarium. The experimental combinations were: (A) large vs. small *C. borealis*, (B) small *C. borealis* vs. small *C. irroratus*, (C) large *C. borealis* vs. large *C. irroratus*, and (D) large vs. small *C. irroratus* crabs. During cross-species comparisons, crabs were paired to be of equal size (maximum of 6 mm CW difference, mean = 0.43 ± 0.41 mm SE, paired t-test: p = 0.295). Individual lobsters were given each combination of crabs three successive times with at least 24 hrs between trials. Trials were scored by species or size killed, both killed, or neither killed (when both crabs remained alive at the end of 24 hrs), but were ended as soon as the killing of one crab was noted. A Chi-square test was used for each experimental combination to detect unequal vulnerability of the crabs to lobster predation. Trials ending in both or neither crabs having been killed were excluded from these analyses.

During the first half hour of experiments B, C and D (see above), direct observations of lobster behaviour were made by recording the number of attacks (defined as any lunge or attempt at capture) each crab sustained. All trials, including those during which kills occurred before the end of this first half-hour, were used in paired t-tests comparing the number of attacks on the species or size groups in each crab-combination (n = 12, 12 and 4 trials, for experiments B, C and D, respectively).

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RESULTS

Observational studies

Patterns of diel activity, depth distribution, and size structure. – The four species of decapods exhibited three general patterns of diel subtidal activity (Fig. 2). Active lobsters were significantly more abundant during the night than the daytime (two-way ANOVA: F = 61.91, df = 1, p < 0.0001; Appendix 1; night mean = 0.20 m⁻² ± 0.03 SE, day mean = 0.02 m⁻² ± 0.00 SE). *C. borealis* were most active during daylight hours with a mean density of 0.11 m⁻² ± 0.016 SE during the day vs. 0.01 m⁻² ± 0.00 SE at night (two-way ANOVA: F = 20.3, df = 1, p < 0.0001; Appendix 2). *C. maenas* exhibited this pattern as well, with a mean diurnal density of 0.07 m⁻² ± 0.03 SE vs. 0.01 m⁻² ± 0.01 SE at night (two-way ANOVA: F = 7.85, df = 1, p = 0.007; Appendix 3). *C. irroratus*, however, did not exhibit significant diel differences in density (two-way ANOVA: F = 0.02, df = 1, p = 0.88; Appendix 4) and were observed at a mean density of 0.14 m⁻² ± 0.03 SE during the day and 0.12 m⁻² ± 0.02 SE at night.

Within these diel patterns of activity, only *C. maenas* and *C. borealis* exhibited significant differences in their depth distributions. During the day, *C. borealis* were significantly more abundant at the deepest depth of 9-11 m than at 0-1, 1-3 and 5-7 m (SC after one-way ANOVA: F = 7.13, df = 3, p = 0.0003; Appendix 2). Also by day, *C. maenas*, which were absent at a depth of 9-11 m, were significantly more abundant at a depth of 0-1 m than at deeper depths (SC after one-way ANOVA: F = 18.89, df = 3, p < 0.0001; Appendix 3). Lobsters and *C. irroratus* did not exhibit significant differences in their diurnal subtidal depth distributions (lobster two-way ANOVA: F = 0.09, df = 2, p = 0.91; Appendix 1; *C. irroratus* two-way ANOVA: F = 1.12, df = 2, p = 0.33; Appendix 4). These two species also did not exhibit a significant interaction between subtidal depth and time period (lobsters: two-way ANOVA: F = 0.58, df = 2, p = 0.56; Appendix 1; *C. irroratus*: two-way ANOVA: F = 0.16, df = 2, p = 0.85; Appendix 3). However, relative to other depths, densities of *C. borealis* were significantly higher at 9-11 m during the day than at night (two-way ANOVA: F = 3.16, df = 2, p = 0.049; Appendix 2). *C. maenas* densities at 0-1 m were also significantly higher during the day than at night relative to other depths (two-way ANOVA: F = 3.99, df = 2, p = 0.023; Appendix 3).



Figure 2. Diurnal and nocturnal depth distributions, expressed as the mean density of active individuals, for all crab species, lobsters, *Carcinus maenas*, *Cancer irroratus*, and *C. borealis* in the subtidal and lower intertidal transects conducted on the northwest shore of Appledore Island. Error bars represent ± 1 SE. See text and Appendices 1-4 for significance levels of within species diel and depth comparisons.

In the subtidal censuses there were no significant differences between the mean day and the mean nighttime sizes of lobsters, *C. borealis* or *C. maenas* (Table 2; Appendices 1-3, respectively). *C. irroratus* individuals observed during the day were significantly larger than those observed at night (one-way ANOVA: F = 7.71, df = 1, p = 0.006). *C. borealis* observed during the day were significantly larger at 9-11 m than those at 1-3 m (SC: p = 0.007, after one-way ANOVA), but were no different at other depths. *C. maenas* were also significantly larger at 5-7 m than those at 0-1 m during the day (SC: p = 0.032, after one-way ANOVA), but were no different at other depths. There was no significant relationship between depth and the daytime sizes of lobsters (Appendix 1) and *C. irroratus* (Appendix 4), or between depth and the nighttime sizes of lobsters, *C. irroratus*, and *C. maenas* (Appendices 1, 3 and 4, respectively). Although nocturnal *C. borealis* individuals observed at 5-7 m were significantly larger than those observed at 1-3 m (Appendix 2), the low sample size of this comparison (Table 2) gives little confidence to the ANOVA.

Table 2. Mean size expressed as carapace length for lobsters and carapace width for	crabs,
standard error (SE), size range, and total number (N) of individuals measured at the di	fferent
depths in all day and nighttime transects. See Appendices 1-4 for significance levels of	within
species comparison.	

	Daytime Size (cm)					Nighttime Size (cm)				
Species	Depth	Mean	SE	Range	Ν	Mean	SE	Range	Ν	
H. americanus	0-1 m	5.80	0.20	5-6	5					
	1-3 m	5.75	0.37	4-7	8	6.58	0.34	4-10	31	
	5-7 m	6.50	0.68	4-10	8	5.87	0.30	3-9	30	
	9-11 m	7.00	1.08	4-9	4	6.00	0.28	4-8	24	
C. maenas	0-1 m	3.79	0.12	1-9	140					
	1-3 m	4.20	0.24	2-10	40	4.41	0.67	2-6	7	
	5-7 m	5.57	0.61	4-9	7	-	-	-	0	
	9-11 m	-	-	-	0	-	-	-	0	
C. irroratus	0-1 m	5.25	0.37	4-7	8					
	1-3 m	4.95	0.25	2-7	37	3.86	0.31	2-8	29	
	5-7 m	4.57	0.21	2-7	35	3.94	0.32	2-6	16	
	9-11 m	4.91	0.41	2-9	23	5.44	0.94	2-11	9	
C. borealis	0-1 m	8.08	0.70	4-12	12					
	1-3 m	6.23	0.61	2-12	22	2.00	0.00	2	2	
	5-7 m	7.90	0.64	2-15	19	10.33	1.20	2-12	3	
	9-11 m	8.36	0.30	2-12	52	-	-	-	0	

Algal cover and shelter availability. – The type of algae/substrate that was dominant in a particular area was depth dependent (Fig. 3, ANOVA results in Appendix 5). *Codium fragile* was the most dominant canopy species in shallower depths, occupying 85% and 56% of the surface area at 1-3 m and 5-7 m, respectively. At depths of 5-7 m and 9-11 m, *Polysiphonia* sp. occupied 30% and 73% of the surface area, respectively. Coralline algae and bare rock, functionally similar substrates, together comprised between 9 and 15 % of the surface area across all depths. Remaining conspicuous algal species (such as *Agarum cribosum, Chondrus crispus*, and other reds) together covered 3% and 18% at 1-3 m and 9-11 m, respectively, but were virtually absent at a depth of 5-7 m.



Figure 3. Bathymetric variation in the percent cover $(\pm 1 \text{ SE})$ of the dominant algal/substrate types occurring in the subtidal area in which the decapod transects were conducted (Appendix 5). Legend: *Polysiphonia* sp. (P), *Codium fragile* (C), bare rock and coralline algae (B&C), and other algal species (O) including *Chondrus crispus*, *Agarum cribosum*, and other reds.

On average, the number of potential shelters at a depth of 9-11 m was 0.46 m⁻¹ \pm 0.15 SE (Fig. 4). At 1-3 and 5-7 m, the mean number of shelters was 0.78 m⁻¹ \pm 0.17 SE and 0.83 m⁻¹ \pm 0.15 SE, respectively. Nevertheless, the availability of potential shelters was not significantly different when considering all three depths simultaneously (Kruskal-Wallace test: H corrected for ties = 5.163, tied p = 0.076).



Figure 4. Bathymetric variation in the mean number (per meter, ± 1 SE) of potential shelters found in the subtidal area (> 1 m below MLWL) in which the decapod transects were conducted. Differences were not significant (Kruskal-Wallace test: H corrected for ties = 5.16, tied p = 0.076).

Diurnal gull predation. – Collections of crab remains over the five low tides yielded 103 carapaces and 114 chela of *C. borealis*, 15 carapaces of *C. irroratus*, and 9 carapaces of *C. maenas*. The mean CW of *C. irroratus* and *C. maenas* remains was 74.67 mm \pm 4.82 SE and 32.44 mm \pm 3.06 SE, respectively. After calculating the CWs of *C. borealis* for whom only a chela had been collected using the regression:

$$CW = (0.379ChL - 0.00476ChL^2 + 3.50)^2$$

 $(R^2 = 96.0\%)$ obtained from the 80 measured live *C. borealis*, the mean CW of all collected *C. borealis* remains was 90.45 mm ± 1.31 SE (Fig. 5). This mean was not significantly different from the mean CW of *C. borealis* measured during the daytime at a depth of 0-1 m (8.08 cm ± 0.70 SE; unpaired t-test: t = 1.55, df = 215, p = 0.12).



Figure 5. Size-frequency distribution of *C. borealis* crabs measured from intertidal remains of avian predators in the collections conducted along the northwest shore of Appledore Island during low tide. The arrow indicates the mean CW which was not significantly different from the mean CW of *C. borealis* measured in the 0-1 m transects (unpaired t-test: t = 1.55, df = 215, p = 0.12).

Experimental studies

Diel predation intensity experiments. – Over the course of the entire 16 day/16 night experiment tethering large *C. borealis*, only two individuals were ever lost (of a possible 324). While the first was the result of a molt, the second, occurring during the day at the shallower depth of 2-3 m, was unambiguously due to predation since only a broken piece of the carapace remained attached to the tether. No significant differences between day and night or between the 2-3 m and 7-9 m depths were thus observed (Fig. 6; ANOVA results in Appendix 6). Small *C. borealis* experienced a significantly higher total number of predation events than did large *C. borealis* (one-way ANOVA: F = 31.05, df = 140, p < 0.001). Twelve of a possible 192 small *C. borealis* and eight of a possible 120 small *C. irroratus* were lost. However, differences in the number of small *C. borealis* and small *C. irroratus* killed during the day vs. the night and shallow vs. deep depths were not significant (Appendix 6). The mean number of crabs killed during a given 12 hr period was 0.40 ± 0.18 SE for small *C. irroratus*, 0.35 ± 0.12 SE for small *C. borealis*, and 0.02 ± 0.01 SE for large *C. borealis*.



Figure 6. Mean number (\pm 1 SE) of large and small *C. borealis* (C.b.) and small *C. irroratus* (C.i.) that were preyed upon (per ~12 hrs) at the two depths of the tethering experiment during the day and the night. Small *C. borealis* were preyed upon significantly more often than were large *C. borealis*, however, rates during the day vs. the night or in shallow vs. deep water were not significant (ANOVA results in Appendix 6).

Crab vulnerability to predation experiments – Lobsters placed in an aquarium with small and large *C. borealis* were significantly more likely to kill the small crab (Fig. 7; $\chi^2 = 8.33$, df = 1, $\alpha = 0.005$). Injury to large crabs was observed, but rarely resulted in the death or subsequent consumption of the crab by the lobster. More small *C. irroratus* were killed than were large *C. irroratus*, but their differential vulnerability to lobster predation was not significant ($\chi^2 = 1.60$, df = 1, $\alpha = 0.1$). There were no significant differences in the frequency with which similar sized crabs were killed in the cross-species experiments where the combinations of large *C. borealis* and *C. irroratus* ($\chi^2 = 0.11$, df = 1, $\alpha = 0.1$) and small *C. borealis* and *C. irroratus* ($\chi^2 = 0.40$, df = 1, $\alpha = 0.1$) were made. A comparison of these two experiments reveals that it was significantly more likely that neither crab was killed when both crabs were large, and that both crabs were killed when they were small ($\chi^2 = 29.0$, df = 1, $\alpha = 0.001$).

The half-hour long periods of direct observation performed during the experiment comparing the rate of lobster attacks when small and large *C. irroratus* were placed into an aquarium, however, showed that large crabs were attacked at a significantly higher rate than were small crabs (Fig. 8; paired t-test: df = 3, p = 0.038). Rates of attack suffered by small and large *C. borealis* appeared to be qualitatively similar to those of small and large *C. irroratus*, respectively (*personal observation*). Observations during the comparisons of large *C. borealis* and C. *irroratus*, and of small *C. borealis* and C. *irroratus*, showed no significant differences in the number of attacks suffered by equal sized crabs (paired t-tests: df = 11, p = 0.37 for large and df = 11, p = 0.83 for small).



Figure 7. Relative vulnerability of large and small *C. borealis* (A), small *C. borealis* and *C. irroratus* (B), large *C. borealis* and *C. irroratus* (C), and large and small *C. irroratus* (D) when exposed to lobsters in the laboratory. Relative vulnerabilities are expressed as the proportion of trials in which each species or size-group was killed (grey bars). The proportion of trials in which both crabs and in which neither crabs were killed are shown as well (white bars). *n*, is the total number of trials performed. Statistical analyses comparing relative vulnerabilities of crabs within each combination were done excluding trials in which both or neither crabs were killed. The asterisk denotes a significant difference ($\chi^2 = 8.33$, df = 1, $\alpha = 0.005$).



Figure 8. Mean number of attacks (± 1 SE) incurred by crabs from lobsters in the first half hour of the laboratory vulnerability experiments comparing small *C. borealis* (C.b.) and *C. irroratus* (C.i.), large *C. borealis* and *C. irroratus*, and large and small *C. irroratus*. *n*, is the number of trials during which observations were made. The asterisk denotes a significant difference (paired t-test: df = 3, p = 0.0383). Observations were not recorded for small and large *C. borealis*.

DISCUSSION

Interspecific competition has long been assumed to be the major factor structuring guilds and has established itself in much of the theory concerning this guild of crabs and lobsters, as well as of guilds in general (Mac Nally, 1983). Densities of adult and subadult decapod populations are highest during summer months (Ojeda and Dearborn, 1990; Witman, 1985) in rocky habitats (Fogarty, 1976; Hudon and Lamarche, 1989; Stehlik et al., 1991). If occurring, competition is

therefore expected to have been high during this study, relative to other seasons and habitats. This study suggests, however, that for this guild of decapods, differential extraguild predation in the intertidal by gulls and size-dependent intraguild predation by lobsters in the subtidal, are interspecific interactions that are important factors influencing the different distributions and activity patterns of the three crab species.

Decapods in the intertidal community

Larus argentatus and L. marinus are primarily diurnal predators that feed mostly on crabs, urchins and mussels (T. Good, *personal communication*), preying upon 6-10 crabs or urchins per low tide cycle (Good, 1992). L. marinus is unable to dive below 1 or 2 m and obtains its prey at or near the surface (Pierotti, 1988). L. argentatus is similar in its opportunistic feeding habits, but appears not to dive as well as the larger L. marinus (Pierotti and Good, 1994). My intertidal carapace collections show that C. borealis was by far the predominant crab species consumed by gulls. The number of C. borealis remains collected was more than 10 times that collected of C. *irroratus* or *C. maenas*. The number of crabs of all species killed by gulls is likely to have been underestimated since gulls do not necessarily consume their prey in the intertidal (personal observation). Also, given that (1) the carapace of C. maenas is somewhat thinner than that of the *Cancer* species and (2) gulls can consume smaller crabs whole (*personal observation*), it is likely that the number of C. maenas preved upon is further underestimated considering that their average size in the 0-1 m transects was only 3.8 cm (Table 2). This may also be true for smaller individuals of the two Cancer species, especially for C. irroratus, which had a mean size considerably smaller than that of C. borealis but exhibited a similar mean density in the 0-1 m transects. Given that the mean size of *C. borealis* remains was not significantly different from the mean size observed in the 0-1 m transects however, I do not believe that the swallowing of small individuals introduced a major bias for this species. Furthermore, although gulls almost certainly consume crabs smaller than 2 cm whole, I did not note any *Cancer* crabs smaller than 2 cm in my transects. Relatively few C. maenas smaller than this size were noted.

Dumas and Witman (1993) have shown that in intertidal rock pools, *C. irroratus* is much more susceptible to predation by gulls than is *C. maenas*. They attributed this difference to the green carapace of *C. maenas*, which is more cryptic than the reddish-orange carapace of *C. irroratus*. One would predict that *C. borealis*, which has a colouration very similar to that of *C. irroratus* (*personal observation*), would suffer under equal pressure from these visual predators. Relative to the number of active individuals observed at 0-1 m (Fig.2), the difference in the

number of remains found for the two *Cancer* species is therefore somewhat surprising. The discrepancy may in part explain why *C. irroratus* is sometimes found in intertidal rock pools while *C. borealis* is not (Dumas and Witman, 1993). It is possible that since *C. irroratus* individuals were on average smaller than *C. borealis* within the 0-1 m transects, selection by these visual predators is simply based on crab size. This hypothesis is weakened by the observation that the mean size of *C. borealis* remains was not different from that of individuals observed at 0-1 m. Since the two species are likely to be equally non-cryptic, the difference in stereotypical defense behaviour may allow *C. irroratus* to escape predation by gulls more often. Unlike *C. borealis*, C. *irroratus* is predictably prone to retaliate by pinching when picked up by hand (*personal observation*, see discussion below).

While *C. maenas* densities were highest in the 0-1 m transects, both *Cancer* species showed considerably lower densities at 0-1 m than at deeper depths in the daytime (Fig. 2). Though he did not look at predation rates on *C. maenas* and *C. irroratus*, Good (1992) has already been able to experimentally implicate gulls as being a potential limiting factor for the upward distribution of *C. borealis*. Considering that the number of *C. borealis* remains found was very much higher than for *C. maenas* and *C. irroratus*, my censuses provide further evidence that predation by gulls is likely to limit the upper distribution of *C. borealis* during the day. If behavioural differences between the *Cancer* crabs does result in differential vulnerability to gull predation, the causes of the much lower 0-1 m *C. irroratus* density remains unclear. Nevertheless, as noted by Good (1992), the results for *C. borealis* imply that our traditional models of the organization of rocky shore communities must be revised – these models attribute the establishment of lower distributions to biotic factors, but the control of upper distributions to abiotic factors.

My results also reinforce the growing general concern that these models ignore the importance that mobile subtidal predators may play in structuring intertidal communities (Edwards et al., 1982). All three of the decapods (including lobsters) that are recognized as being predominantly subtidal were observed foraging in the intertidal during the 0-1 m censuses. Given the higher metabolic rates of these individuals relative to more sedentary predators, their impact may be quite important for the intertidal community, even though their densities are much lower relative to those observed in the subtidal.

Decapods in the subtidal community

Patterns of subtidal depth distribution. – C. maenas is generally noted as an intertidal species throughout the regions into which it has been introduced from Europe. Small individuals are commonly observed in tide pools and under rocks and algae during low tide (*personal observation*). The abundance and lower limit to the depth distribution of C. maenas in this study parallels that of *Codium fragile*, a densely growing exotic algal species that forms a thick canopy in the shallower subtidal. Neither is found below a depth of \approx 7 m (Figs. 2 and 3). Though it was beyond the scope of this study to investigate, it is possible that C. maenas is more vulnerable to predation in the subtidal than are the other species due to its smaller size and less protective carapace. It is also likely that C. maenas is a poorer competitor for shelter since, in general, an individual's size seems to be an important factor determining competitive success among crabs. Ironically, *Codium* may therefore serve C. maenas as a suitable refuge from predation for which it need not compete.

My findings concerning the subtidal distribution of *C. irroratus*, *C. borealis* and *H. americanus*, however, stand in contrast to those of Ojeda and Dearborn (1990) who studied these species in the rocky subtidal of Pemaquid Point, Maine. They report an increase in the abundance of lobsters and *Cancer* crabs with increased depth, as has generally been found across habitats at the regional scale (e.g. Stehlik et al., 1991). Ojeda and Dearborn (1990) propose two hypotheses to explain their observed decapod depth distributions: (1) that the increase in decapod abundance with depth is due to responses to strong water turbulence and wave surge, and (2) that decapod densities parallel the availability of shelters.

In this study, *C. borealis* densities were highest in the deepest transects, but lobsters and *C. irroratus* showed no significant variation in their depth distributions (Fig. 2). My site is much more protected than Pemaquid Point and my results can therefore not be used to test the first of their hypotheses directly. The fact that different depth patterns were exhibited by the different decapods, however, suggests that other factors are generally more important at my site. As the relative number of potential shelters at my study site did not vary significantly with depth (Fig. 4), my surveys do lend some support to their hypothesis that decapod densities in the subtidal may simply parallel the availability of shelters: both lobsters and *C. irroratus* did not show significant differences in their densities at the three subtidal depths. Though non-significant, *C. irroratus* did show a trend of decreasing abundance with depth. As with *C. maenas*, this may reflect the distribution of the alga *Codium*. The higher density of active *C. borealis* individuals at 9-11 m, however, is not only counter to the trend observed for the number of potential rocky

shelters, but also to expectations based on the lack of a sheltering algal canopy at this depth, where *Codium* is replaced by a sparsely growing, non-canopy forming *Polysiphonia* species. The site of Ojeda and Dearborn (1990) was located in an urchin barren and thus had no macroalgae.

To briefly summarize, the presence of *Codium* may explain the subtidal distribution of *C*. *maenas* as well as the trend of decreasing *C*. *irroratus* densities with depth at my site. As lobster densities did not vary with depth, algal cover appears to be irrelevant, but the importance of shelter availability remains inconclusive in explaining lobster distributions. The higher densities of *C*. *borealis* in the deepest transects cannot be explained by the importance of wave surge or the availability of rocky shelters and algal cover.

Patterns of subtidal diel activity. – Lobsters in this study were mostly restricted to nocturnal periods of activity, an observation in accord with other studies (Ennis, 1983, 1984; Fogarty, 1976; Lawton, 1987; Pottle and Elner, 1982; Wang, 1982; Witman, 1985). Lobsters exhibit an intimate association with their shelters and diurnal emergence from shelters in the laboratory has been observed only among subdominant lobsters in the presence of larger individuals or after periods of starvation (Lawton, 1987). In the subtidal transects of this study, 12.5 % of all active lobsters were observed in the daytime. However, mean lobster size was no different during the day than at night (Table 2), suggesting that it was not simply subdominant individuals that were diurnally active. The indication is thus that the shelters are not a limiting resource for lobsters, but because lobsters were observed during the day, other factors such as a low abundance of prey or a lack of diurnal predators may be important.

In contrast to lobsters, *C. maenas* and *C. borealis* populations exhibited much higher densities of active individuals by day than by night (Fig. 2). Even for *C. irroratus*, which did not show a diel difference in densities, the significant difference in the mean size of individuals during the two periods (Table 2) suggests that there was a diel pattern of activity within the population. Evidence for such patterns of diurnal activity among the three species has not previously been reported. *C. maenas* and both *Cancer* species have been consistently described as being primarily active at night (Aagaard et al., 1995; Burrows et al., 1999; Gibson et al., 1998; Naylor, 1958, 1960; Ojeda, 1987; Rebach, 1985; 1987; Reid and Naylor, 1989; Stehlik et al., 1991; Wang, 1982; Witman, 1985), with the only exception being that Hunter and Naylor (1993) did not detect a difference in the diel capture rate of *C. maenas* in directional traps placed in a

shallow sand estuary of North Wales, UK. Few studies, however, have reported similar direct comparisons of day and night activity patterns and many reports are of an anecdotal nature.

The patterns of diurnal crab activity observed in this study may be (1) a reflection of mortality due to predation, (2) a short-term behavioural response to avoid a perceived predatory or competitive pressure, or (3) an evolutionary response to these pressures. My crab tethering experiment suggests that it is not the first of these explanations. Similar to the rates observed by Witman and Sebens (1992) at their coastal sites, the rates of predation observed in my experiment were very low. Furthermore, predation rates did not differ significantly between night and day (Fig. 6) as would be necessary for this hypothesis to be correct.

One possibility for the lack of a diel difference in predation rates is that cannibalism within *C. borealis* is a significant source of diurnal mortality for small individuals. Unfortunately, the importance of cannibalism, an interaction that has been shown to be important for small individuals in some size-structured populations (Polis et al., 1989), as well as IGP between the crab species, have yet to be assessed and were beyond the scope of this study. Observations in the laboratory suggest that both do occur, even among individuals of the same size range (*personal observation*). A preliminary experiment indicates furthermore, that small *C. irroratus* and *C. borealis* are equally vulnerable to predation by "extra-large" *C. borealis* (> 100 mm CW).

The latter two explanations are more difficult to distinguish and will be more difficult to test in the future. How recent and how unique the diurnal activity of the *Cancer* species is to the study site is not known. A preliminary study in 1998 indicates that the diurnal activity is not novel to 1999, yet Witman (1985) documented higher nocturnal *C. borealis* and *C. irroratus* activity in the subtidal zone of the Isles of Shoals on the southern side of Star Island only 14 years previously. Discoveries of rapid evolutionary change occurring in the time scale of ecology are becoming increasingly common (Thompson, 1998). Where information on diel patterns of activity is available, the phylogeny of cancrid crabs suggests that the explicit diurnal activity observed at this study site is novel to the genus (e.g. Chatterton and Williams, 1994; Harrison and Crespi, 1999; Skajaa et al., 1998; but see Stevens et al., 1984). The presence and activity patterns of predators and potential crab competitors in these systems is unclear.

The diurnal activity of the crabs may be a direct or indirect consequence of the loss of diurnal predators in the community. The overfishing of large predatory fishes has already been implicated in increased urchin (Vadas and Steneck, 1995) and crab (Witman and Sebens, 1992) densities in the coastal regions of the Gulf of Maine. The recent absence of fishes such as cod,

which consume crabs as a large proportion of their diet (Bigelow and Schroeder, 1953; Witman and Sebens, 1992), may have released these coastal crabs from diurnal predation pressures with a concomitant increase in the relative importance of interactions with nocturnally active lobsters.

Whether or not the observed patterns of activity are in fact the expression of evolutionary change or of a short-term behavioural nature, an intriguing question remains concerning the difference in patterns exhibited by *C. borealis* and *C. irroratus* (Fig. 2). Many have remarked that *C. irroratus* often appears to be excluded from rocky subtidal habitats if both *H. americanus* and *C. borealis* exist together (Haefner and Terretta, 1971; Hudon and Lamarche, 1989; Jeffries, 1966; Stewart, 1971; Weiss, 1970; Winget et al., 1974). Jeffries (1966) attributed the division in habitat utilization he observed among the *Cancer* species to differences in their activity levels. *C. irroratus* is in general much more active that *C. borealis*, but it has also been conjectured that *C. borealis* is dominant to *C. irroratus* during shelter acquisition (*personal observation*; Jeffries, 1966). At this study site on Appledore Island where all three species coexist, the observed diel division of activities may be a critical factor that permits their syntopic existence.

C. irroratus also responds to direct confrontation with a stereotypical antagonistic lateral merus display that involves the extension of the chelipeds and a raising of the body off the substrate; *C. borealis* crouches down, folding its appendages to cover its mouth parts and ventral surface (*personal observation*). These behaviours have been interpreted to suggest that *C. irroratus* is less vulnerable to predation by fishes than is *C. borealis*, but relatively more vulnerable to (IG) predation by lobsters (Fogarty, 1976; Hudon and Lamarche, 1989; Jeffries, 1966). If this is correct, the recent reduction of diurnal fish predators would be more significant for *C. borealis* than *C. irroratus*. Nevertheless, since *C. irroratus* would therefore be more vulnerable to lobsters, this in itself cannot explain why it was equally active during the day and the night.

During the summers of both 1998 and 1999, day and night dives showed no predators other than lobster common or large enough to be of likely importance to crabs. Both the tethering experiment in the field and the laboratory experiments show that small crabs, regardless of species, are considerably more vulnerable to lobster IGP than are large crabs (Figs. 6 and 8). Similar results have been observed among many size-structured populations (Polis et al., 1989) and are not unexpected in this system (Richards, 1992). What is masked by the difference in the number of small and large crabs actually killed by lobsters in the laboratory (and presumably in the field), is the fact that large *C. irroratus* were attacked 71 times more often than were small *C*.

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irroratus (Fig. 8). The rates of attack were similarly distinct for small and large *C. borealis* (*personal observation*). Even in the across-species comparisons, two large crabs were on average 10 times more likely to be attacked by a lobster than were two small crabs (Fig 8). This suggests that antagonistic interactions with lobsters may be very important for large crabs, even if the result is not always death.

Smaller crabs are almost certainly inferior competitors for shelter relative to larger individuals, yet whether they must compete for prey with other members of the guild is uncertain. Although Hudon and Lamarche (1989) found differences in the diets of small and large *C. irroratus* at one of two sites, whether *Cancer* crabs exhibit a quantitative change in diet with ontogeny in general is not known. In the context of our present understanding therefore, the implication of this study is that small crabs are more likely to act as IG prey to lobsters. Lobsters, *C. borealis* and *C. irroratus* of similar size classes are more likely to interact either by asymmetric antagonistic interactions, or potentially, by asymmetric exploitative competition for shelter (where lobster > *C. borealis* > *C. irroratus*).

The larger size of diurnal *C. irroratus* individuals (Table 2) is in accordance with this general hypothesis that an interference of activities, or competition for shelter, is less significant for smaller crabs than for larger crabs: large *C. irroratus* "avoid" nocturnal lobsters more so than they do diurnal *C. borealis*. Presumably, *C. borealis* and large *C. irroratus* occupy the shelters made available at night by foraging lobsters. Small *C. irroratus* may simply be out-competed by both larger *C. irroratus* and *C. borealis* (even of similar small size) and are thus exposed to IGP from lobsters by night. This hypothesis may in part also explain the trend of the decreasing abundance of *C. irroratus* that paralleled the distribution of the potentially sheltering canopy of *Codium*: the prediction would be that one would see an increase in the mean size of crabs at the 9-11m depth where no such canopy exists – which, though observed in this study, was not significant.

Though the high rates of attack suffered by large crabs in the laboratory may have been both predatory or antagonistic in nature, IGP on large crabs by lobsters does occur, both in the laboratory, and in the field (*personal observation*). In the field, IGP is probably more commonly only an unrealized threat to large crabs that does not result in death when small crabs and other potential prey species are available. Nevertheless, even such a perceived threat may elicit the patterns of diel activity observed in this study. Since IGP causes death in the absence of a response, selective pressure caused by IGP may be much greater than that of competition alone

(Polis et al., 1989). In the past, IGP has been implicated in a diel separation of activity among African carnivores (Eaton, 1979), scorpions (Polis and McCormick, 1987), and raptors (Carothers and Jaksic, 1984; Jaksic, 1982).

For the lobster-crab association, IGP may be especially important since the absence of diurnal fish predation on crabs. By increasing the importance of intraguild predatory and competitive interactions between lobsters and crabs, the recent overfishing of crab predators appears to have been an important mechanism resulting in diurnal crab activity. Overfishing may thereby be indirectly strengthening the link between marine and terrestrial ecosystems in the Gulf of Maine (Fig. 9), affording gulls a higher abundance of crab prey. These and other rapid changes occurring within the Gulf of Maine marine community underline the importance of understanding the ecological history of the region and will need to be incorporated into future studies of the community and ecosystem dynamics of the region.



Figure 9. Recent changes in the relative importance of predatory (-) and competitive (--) interactions within the marine community resulting from the overfishing of predatory fishes may be strengthening the link between terrestrial and marine ecosystems in the coastal Gulf of Maine.

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Appendix 1 – ANOVA tables and Scheffe's a posteriori contrasts of the diel density and size composition of active <u>*H. americanus*</u> *individuals.*

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Day/Night	1	.149	.149	61.914	<.0001
Depth	2	4.306E-4	2.153E-4	.089	.9145
Day/Night * Depth	2	.003	.001	.575	.5655
Residual	63	.152	.002		

ANOVA Table for subtidal day vs. night *H. americanus* density by depth.

ANOVA Table for daytime *H. americanus* density by depth.

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Depth	3	.002	.001	.646	.5878
Residual	71	.062	.001		

ANOVA Table for day vs. night *H. americanus* size.

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Day/Night	1	.003	.003	.031	.8613
Residual	108	11.813	.109		

ANOVA Table for daytime *H. americanus* size by depth.

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Depth	3	.185	.062	.673	.5783
Residual	21	1.926	.092		

ANOVA Table for nighttime *H. americanus* size by depth.

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Depth	2	.332	.166	1.453	.2398
Residual	82	9.370	.114		

Model II estimate of between component variance: .002

Appendix 2 – ANOVA tables and Scheffe's a posteriori contrasts of the diel density and size composition of active <u>C. borealis</u> individuals.

ANOVA Table for subtidal day vs. night C. borealis density by depth.

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Day/Night	1	.056	.056	20.299	<.0001
Depth	2	.009	.005	1.729	.1858
Day/Night * Depth	2	.017	.009	3.158	.0493
Residual	63	.173	.003		

ANOVA Table for daytime C. borealis density by depth.

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Depth	3	.092	.031	7.130	.0003
Residual	71	.306	.004		

Model II estimate of between component variance: .001

Scheffe for C. borealis daytime density by depth.

Significance Level: 5 %

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	Mean Diff.	Crit. Diff	P-Value	
0-1m, 1-3m	022	.059	.7761	
0-1m, 5-7m	017	.059	.8781	
0-1m, 9-11m	095	.059	.0004	s
1-3m, 5-7m	.005	.069	.9980	
1-3m, 9-11m	073	.069	.0333	S
5-7m, 9-11m	078	.069	.0203	S

ANOVA Table for day vs. night C. borealis size.

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Day/Night	1	.324	.324	1.162	.2835
Residual	108	30.118	.279		

Model II estimate of between component variance: .005

ANOVA Table for daytime C. borealis size by depth.

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Depth	3	2.990	.997	4.364	.0062
Residual	101	23.066	.228		

Model II estimate of between component variance: .033

Scheffe for daytime C. borealis size by depth.

Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
0-1m, 1-3m	.383	.488	.1806	
0-1m, 5-7m	.049	.501	.9942	
0-1m, 9-11m	052	.435	.9897	
1-3m, 5-7m	333	.426	.1821	
1-3m, 9-11m	435	.346	.0070	s
5-7m, 9-11m	102	.364	.8892	

ANOVA Table for nighttime C. borealis size by depth.

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Depth	1	3.840	3.840	52.034	.0055
Residual	3	.221	.074		

Model II estimate of between component variance: 1.569

Appendix 3 – *ANOVA tables and Scheffe's a posteriori contrasts of the diel density and size composition of active* <u>*C. maenas*</u> *individuals.*

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Day/Night	1	.010	.010	7.848	.0067
Depth	2	.039	.019	15.611	<.0001
Day/Night * Depth	2	.010	.005	3.989	.0234
Residual	63	.079	.001		

ANOVA Table for subtidal day vs. night C. maenas density by depth.

ANOVA Table for daytime C. maenas density by depth.

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Depth	3	1.197	.399	18.890	<.0001
Residual	71	1.499	.021		

Model II estimate of between component variance: .021

Scheffe for daytime C. maenas density by depth.

Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
0-1m, 1-3m	.187	.132	.0019	s
0-1m, 5-7m	.269	.132	<.0001	s
0-1m, 9-11m	.289	.132	<.0001	S
1-3m, 5-7m	.083	.152	.4921	
1-3m, 9-11m	.102	.152	.3055	
5-7m, 9-11m	.019	.152	.9879]

ANOVA Table for day vs. night C. maenas size.

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Day/Night	1	.011	.011	.074	.7852
Residual	192	28.270	.147		

ANOVA Table for daytime C. maenas size by depth.

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Depth	2	1.493	.746	5.385	.0053
Residual	184	25.504	.139		

Model II estimate of between component variance: .017

Scheffe for daytime C. maenas size by depth.

Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	_
0-1m, 1-3m	110	.188	.4414	
0-1m, 5-7m	432	.407	.0324	s
0-1m, 9-11m	1.910	•	•	
1-3m, 5-7m	322	.430	.2202	
1-3m, 9-11m	2.020	•	•	
5-7m, 9-11m	2.342	•	•	

Too few observations to compute ANOVA Table for nighttime C. maenas by depth.

Appendix 4 – ANOVA tables and Scheffe's a posteriori contrasts of the diel density and size composition of active <u>C. irroratus</u> individuals.

ANOVA Table for subtidal day vs. night C. irroratus density by depth.

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Day/Night	1	2.044E-4	2.044E-4	.023	.8800
Depth	2	.020	.010	1.118	.3333
Day/Night * Depth	2	.003	.001	.160	.8529
Residual	63	.560	.009		

ANOVA Table for daytime C. irroratus density by depth.

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Depth	3	.084	.028	3.236	.0272
Residual	71	.618	.009		

Model II estimate of between component variance: .001

Scheffe for daytime C. irroratus density by depth.

Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value
0-1m, 1-3m	081	.084	.0642
0-1m, 5-7m	067	.084	.1721
0-1m, 9-11m	045	.084	.5200
1-3m, 5-7m	.014	.098	.9809
1-3m, 9-11m	.037	.098	.7631
5-7m, 9-11m	.022	.098	.9338

ANOVA Table for day vs. night C. irroratus size.

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Day/Night	1	1.154	1.154	7.709	.0062
Residual	155	23.204	.150		

Model II estimate of between component variance: .014

ANOVA Table for daytime C. irroratus size by depth.

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Depth	3	.217	.072	.562	.6413
Residual	99	12.740	.129		

ANOVA Table nighttime C. irroratus size by depth.

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Depth	2	.800	.400	2.158	.1259
Residual	51	9.448	.185		

Model II estimate of between component variance: .013

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 \mathbf{S}

<.0001

Appendix 5 – One-way ANOVA tables and Scheffe's a posteriori contrasts for arcsine transformed algal cover, grouped by morphological similarity.

ANOVA Table for Codium fragile

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Depth	2	7.580	3.790	50.597	<.0001
Residual	21	1.573	.075		
		61			

Model II estimate of between component variance: .495

ANOVA Table for Polysiphonia spp.

	DF	Sum of Squares	Mean Square	F-Value	P-Value	
Depth	2	4.233	2.116	25.148	<.0001	
Residual	21	1.767	.084			
Madel II actimate of between companent variance: 271						

Model II estimate of between component variance: .271

ANOVA Table for Bare rock and Corallines

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Depth	2	.075	.037	.585	.5657
Residual	21	1.341	.064		

Scheffe forCodium fragile Significance Level: 5 %

5-7m, 9-11m

Mean Diff. Crit. Diff P-Value 1-3m, 5-7m .402 .416 .0598 1-3m, 9-11m 1.288 .360 <.0001</td>

.887

.360

Scheffe forPolysiphonia spp. Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
1-3m, 5-7m	432	.441	.0558	
1-3m, 9-11m	998	.382	<.0001	S
5-7m, 9-11m	567	.382	.0032	s

Scheffe for Bare rock andCorallines Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value
1-3m, 5-7m	145	.384	.6173
1-3m, 9-11m	028	.333	.9752
5-7m, 9-11m	.117	.333	.6585

ANOVA Table for Other

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Depth	2	.479	.239	2.678	.0921
Residual	21	1.878	.089		

Model II estimate of between component variance: .02

Scheffe for Other

Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value
1-3m, 5-7m	.068	.455	.9249
1-3m, 9-11m	244	.394	.2849
5-7m, 9-11m	313	.394	.1374

Appendix 6 – One-way ANOVA tables for the subtidal predation intensity tethering experiments.

ANOVA Table for Large C. borealis							
	DF	Sum of Squares	Mean Square	F-Value	P-Value		
Day/Night	1	.009	.009	1.000	.3196		
Depth	1	.009	.009	1.000	.3196		
Day/Night * Depth	1	.009	.009	1.000	.3196		
Residual	104	.963	.009				

ANOVA Table for small C. borealis

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Day/Night	1	.180	.180	.878	.3561
Depth	1	.020	.020	.098	.7569
Day/Night * Depth	1	.255	.255	1.245	.2734
Residual	30	6.153	.205		

ANOVA Table for small C. irroratus

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Day/Night	1	.050	.050	.222	.6437
Depth	1	.050	.050	.222	.6437
Day/Night * Depth	1	.050	.050	.222	.6437
Residual	16	3.600	.225		