

PREDATION RISK, PREY ABUNDANCE, AND THE VERTICAL DISTRIBUTION OF THREE BRACHYURAN CRABS ON GULF OF MAINE SHORES

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ABSTRACT

Three large brachyuran species are common in the intertidal and shallow subtidal of New England rocky shores: two native crabs *Cancer borealis* (Jonah crab) and *Cancer irroratus* (rock crab), and the introduced crab *Carcinus maenas* (European green crab). For these three co-occurring species in the Isles of Shoals (Gulf of Maine, USA), we compared distribution and abundance to survivorship and prey availability along a depth gradient and examined stomach contents and prey preference. The three species show differences in vertical distribution: *Carcinus* is more abundant in the intertidal, while both species of *Cancer* are more abundant in the subtidal. Survivorship of both species of *Cancer* increases with increasing depth, while survivorship of *Carcinus* decreases with increasing depth, perhaps corresponding to differential vulnerability to predation by gulls in the intertidal and by decapods and fish in the subtidal. There were notable differences in laboratory prey preference experiments: *C. irroratus* consumed both small mobile and non-mobile prey (amphipods, small snails, and small mussels), while *Carcinus* consumed primarily small mobile prey (amphipods and isopods). In contrast, *C. borealis* consumed larger, heavier bodied prey (larger snails and mussels) but did not eat amphipods or isopods. However, differences in prey preference among crab species were greater than the differences in realized diets. Based on stomach content analysis, the blue mussel *Mytilus edulis* was the majority component of stomach contents for all three species. Some differences were evident in the remaining diet components: *Carcinus* was the most omnivorous (> 30% green algae), *C. borealis* consumed more snails and arthropods, and *C. irroratus* consumed the most mussels. Overall, species distribution does not track the distribution of the preferred prey of each species; rather, the distribution corresponds with patterns of survivorship, indicating predominant top-down control of crab distribution.

KEY WORDS: *Carcinus maenas*, *Cancer borealis*, *Cancer irroratus*, Gulf of Maine, Isles of Shoals, top-down and bottom-up control

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INTRODUCTION

On rocky shores, crabs are important predators on mollusks, crustaceans, and other invertebrates, and, in turn, are important prey for fishes, decapods, and terrestrial vertebrates. As predators, crabs can have important effects on community structure by influencing the behavior (Siddon and Witman, 2004), morphology (Seeley, 1986; Trussell and Nicklin, 2002), and abundance of their prey (Ropes, 1968; Siddon and Witman, 2004). As prey, differences in the behavior, morphology, and abundance of crab species make them differentially vulnerable to predation (Ellis et al., 2005; Richards and Cobb, 1986; Good, 1992). Crab species distribution reflects the joint response to prey distribution ("bottom-up" control) and predation ("top-down" control). Differences among co-occurring crab species in these ecological interactions influence community structure and function but have rarely been systematically explored. In this study, we combine experiments and descriptive data analysis to compare top-down and bottom-up control on the distribution of three co-occurring brachyuran crabs in the Gulf of Maine.

On the rocky shores of the Gulf of Maine, three large brachyuran crab species are common: *Cancer borealis* Stimpson, 1859, *Cancer irroratus* Say, 1817, and *Carcinus*

maenas Linnaeus, 1758. *Carcinus maenas* (European green crab; henceforth referred to as *Carcinus*) was introduced to eastern North America in the early 1800s and expanded its range north of Cape Cod in the early 1900s (Vermeij, 1982; Grosholz and Ruiz, 1996). *Carcinus* has the highest per capita prey consumption rate of any intertidal predator on the New England coast (Menge, 1983), and its introduction precipitated the rapid decline of *Mya arenaria* L. populations (Ropes, 1968) and a change in the shell morphology of *Littorina obtusata* L. (Seeley, 1986; Trussell and Smith, 2000). *Carcinus* is extremely abundant in the mid- to low intertidal zones but is rarely found at depths greater than 2 m below mean lower low water (MLLW) (Novak, 2004).

Cancer borealis (Jonah crab) and *C. irroratus* (rock crab) are widely distributed in their native northwest Atlantic: *C. borealis* is found from Newfoundland to Florida to depths of 750 m and *C. irroratus* is found from Labrador to South Carolina to depths of 550 m (Haefner, 1977; Stehlik et al., 1991). In the northern part of their range, both species are found in shallow waters (Haefner, 1977); they are commonly observed in the shallow subtidal in the Gulf of Maine during the summer months (Krouse, 1978; Jeffries, 1966) and are frequent bycatch in the lobster fishery (DFO, 2000b, a).

Despite their different distributions on a geographic scale, *Cancer borealis*, *C. irroratus*, and *Carcinus* all occur in the shallow subtidal in the Gulf of Maine (Novak, 2004). Here, we examine how differences in species' distributions from the intertidal to the shallow subtidal reflect differences in diet, prey preference, prey availability, and vulnerability to predation, and we discuss the different responses and impacts of each species on benthic community structure.

MATERIALS AND METHODS

Sites and Organisms

All experiments were conducted during the summers of 2004–2006 at the Shoals Marine Laboratory on Appledore Island, Isles of Shoals, Maine, USA (42°59'N, 70°37'W). The Isles of Shoals experience semi-diurnal tides of ~4 m amplitude. The shoreline of Appledore Island is composed of stretches of bedrock ledge interspersed with cobble coves. Field collections and experiments took place in rocky intertidal and subtidal habitat on the western, protected side of the island.

Distribution and Demography of Crab Populations

We made a census of *Cancer borealis*, *C. irroratus*, and *Carcinus* at six sites in two habitats: three cobble coves, and three rocky ledges. At each site, we sampled five vertical zones: three intertidal zones characterized by their dominant algal species (*Ascophyllum nodosum* (L.) Le Jolis, 1863 at ~1.3 m MLLW; upper *Chondrus crispus* Stackhouse, 1801 at ~0.5 m MLLW; and lower *C. crispus* at ~0 m MLLW) and two subtidal zones (-1 m MLLW and -2 m MLLW). In each zone, a census of the crabs was taken by SCUBA divers at high tide in five random 1 m² quadrats between June 28 and July 31, 2006; special care was taken to inspect crevices, turn over rocks, and carefully comb through algae. Crabs were counted, sexed, and measured (carapace width, CW; ± 0.5 mm). Abundances of all three species were low within the 1 m² quadrats and, therefore, were summed within each zone for analysis.

To test whether the relative frequency of the species were similar across zone (intertidal versus subtidal) and habitat (cove versus ledge), we analyzed a three-way contingency table (3 species × 2 zones × 2 habitat types) using a hierarchical log-linear analysis (Gotelli and Ellison, 2004) in Statistica 6.0 (StatSoft, 2002). We also examined the distribution of each species separately. For *Carcinus* and *Cancer borealis*, crab densities (per 5 m⁻²) were analyzed as a split-plot ANOVA with habitat (2 levels) as the whole-plot factor and zone (5 levels) as the within-plot factor (Gotelli and Ellison, 2004): $Density \sim Habitat_i + Site_{j(i)} + Zone_k + (Habitat \times Zone)_{ik} + (Site \times Zone)_{k(ji)}$. Densities were $\ln(x + 1)$ -transformed to meet the assumptions of ANOVA. Densities of *Cancer irroratus* were too low for ANOVA; therefore, we used a binomial test to determine whether the number of *C. irroratus* found in coves versus ledges differed from the expected proportion of 0.5, and whether the number of *C. irroratus* found in the intertidal versus subtidal zones differed from the expected proportion of 0.6 (3 of the 5 zones sampled). To test for an interaction between habitat and zone for *C. irroratus*, we analyzed a 2 × 2 contingency table with Yates-corrected χ^2 (Sokal and Rohlf, 1995).

The size and sex distribution of each crab species was also analyzed. For *Carcinus* and *Cancer borealis*, we used a split-plot ANOVA to test whether size varied by habitat type (whole-plot factor) or vertical zone (within-plot factor). *Cancer borealis* was relatively rare in the intertidal zones, so we restricted the size comparison to the -1 m and -2 m vertical zones. *Carcinus* had small sample sizes in some habitat × zone combinations, so we combined vertical zones into intertidal and subtidal. Too few *C. irroratus* were available for a meaningful analysis of size distribution. For each species, we tested for equal sex ratio using a binomial test (Sokal and Rohlf, 1995) and tested for a relationship between size and sex using logistic regression (Hosmer and Lemeshow, 2004).

Survivorship

To test for differences in survivorship between species along a depth gradient, 15–20 individuals of *C. borealis* (63–104 mm CW), *C. irroratus*

(53–102 mm CW), and *Carcinus* (27–61 mm CW) were tethered at depths 0 m, -2 m, and -7 m MLLW from 20 July 2005 to 27 July 2005. A stainless-steel wire tether (50 cm long, 0.5 mm diameter) was attached to the crab's carapace using epoxy (Z-spar Splashzone Compound A-788). Crabs were randomly assigned to depths and then either tethered to a brick (0 m) or a weighted trotline (-2 m and -7 m), with individuals spaced at least 1 m apart. Survivorship was recorded each day at both dawn and dusk. For overall patterns of survivorship, we estimated Kaplan-Meier survivorship for each species by depth. To test for effects of depth, species, and depth × species on survivorship, we used a Cox proportional hazards survivorship model with planned contrasts of species within depths and depths within species (Hosmer and Lemeshow, 1999).

Stomach Contents

Crabs for the stomach content analysis were collected between 11 July 2005 and 15 July 2005 from three sites on Appledore Island at depths of 0 to 7 m MLLW. Upon collection, crabs were injected with 4 mL of 10% formalin solution and placed on ice to stop digestion and preserve the stomach contents (Elner, 1981; Ledesma and O'Connor, 2001; Ropes, 1988). Crabs were frozen for at least 24 h and defrosted for 30 min prior to dissection. The cardiac stomach was dissected out of each crab, ranked for stomach fullness (0 = 0–20%; 1 = 21–40%; 2 = 41–60%; 3 = 61–80%; 4 = 81–100% full), and the contents washed into a small, gridded Petri dish using 10 mL of sea water. Stomachs of 26 *C. irroratus* (51–95 mm CW), 16 *C. borealis* (65–98 mm CW), and 39 *Carcinus* (25–54 mm CW) were >40% full and were included in the analysis. Stomach contents were recorded by point-intercept sampling of 50 points on the bottom of the Petri dish; contents were identified to the lowest taxonomic grouping possible. We compared stomach contents across species using MANOVA (Gotelli and Ellison, 2004). To meet the assumptions of MANOVA, we compared the ranked proportion of stomach contents in five categories: mussels, arthropods (including crabs, isopods, barnacles, and amphipods), green algae, other algae, and other (including urchins, snails, and unidentified). Although the analysis was performed on ranks, the figures are presented as proportions for interpretability.

Prey Preference Experiments

In laboratory experiments, we compared the preference of the three crab species across eleven potential prey types. The 11 prey types are common invertebrates in the shallow subtidal and intertidal: small (20–30 mm test diameter) and large (40–50 mm) sea urchins (*Strongylocentrotus droebachiensis* Müller, 1776; small (5–15 mm shell length) and large (35–50 mm) mussels (*Mytilus edulis* L.); small (8–13 mm shell height), medium (15–19 mm), and large (20–25 mm) *Littorina littorea* L.; small (6–8 mm) and large (9–11 mm) *L. obtusata* L.; isopod *Idotea balthica* Pallas, 1772; and amphipod *Jassa marmorata* Holmes, 1905. One of each of these eleven prey types were placed in a 30 × 36 × 18 cm (L × W × H) tub with mesh lid, which was immersed in a flow-through seawater aquarium. After 30 min of acclimation, a single small or large crab, which had been starved for 24 h, was added and prey items were counted after 6 h. Trials were run with 13 large (70–100 mm CW) and 13 small (50–70 mm CW) *C. irroratus*, 11 large (75–85 mm CW) and 11 small (55–65 mm CW) *C. borealis*, and 13 large (40–60 mm CW) and 13 small (15–25 mm CW) *Carcinus*. We also ran 15 control trials, in which no crabs were present, to determine whether prey escaped or ate one another; only amphipods (20% of trials) and isopods (15%) disappeared. We adjusted the amphipod and isopod consumption rates within crab treatments by subtracting the rate of disappearance observed in the control treatment. We excluded from analysis trials in which the crab did not eat. In a preliminary analysis, there was no difference in the probability of consumption of particular prey types between large and small crabs within any species; therefore, we excluded crab size from further analyses.

To determine whether overall prey selection differed among the crab species, we used a contingency table analysis to test whether the relative proportions of all 11 prey types consumed were similar across the 3 crab species. Then, for each prey type, we tested whether the observed frequency of prey consumed differed from expected between crab species, where the expected frequencies were the total number of prey items consumed by a crab species divided by eleven prey types. For most prey types, at least one cell had an expected value less than 5. Therefore, we used Monte Carlo simulations (3000 samples) (Lowry, 2009; El-Shaarawi

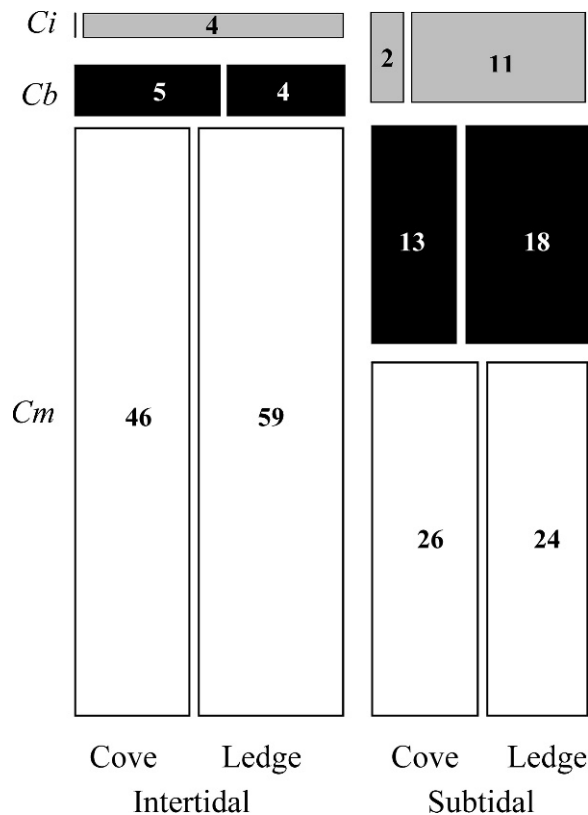


Fig. 1. Mosaic plot illustrating relative frequencies of *Cancer borealis* (Cb, black), *C. irroratus* (Ci, gray), and *Carcinus maenas* (Cm, open) by habitat type (cobble cove versus rocky ledge) and vertical zone (intertidal versus subtidal). Box size is proportional to the relative frequency of crabs in each species \times habitat \times zone cell; numbers in each box are actual crab counts; there were no *C. irroratus* in the intertidal cove habitat.

and Piegorsch, 2002) to calculate the P value and compared this to a Dunn-Sidak corrected $\alpha' = 0.0047$ (for 11 multiple comparisons). When a significant difference was found among the three crab species, we performed pair-wise goodness-of-fit tests with $\alpha' = 0.0169$ (3 multiple comparisons) to determine which crab species were different.

Vertical Distribution of Small Invertebrate Prey

To determine the vertical distribution of small invertebrate prey, we collected samples from each of the five vertical zones at five rocky ledges on the western shore of Appledore Island. In each zone, we scraped two 15 cm \times 15 cm quadrats down to bedrock and collected all algae and invertebrates. The samples were rinsed in 50% seawater, and invertebrates were carefully collected, sorted, and counted by species. *Mytilus edulis* and *Littoreia* were sorted into two size-classes (*M. edulis*: ≤ 20 mm and > 20 mm shell length; *L. littorea*: < 13 mm and ≥ 13 mm shell height). To analyze the distribution of each species across the vertical zones, we used a two-way (Site \times Zone) permutation ANOVA (PERMANOVA: Anderson, 2001; McArdle and Anderson, 2001; Anderson, 2005). PERMANOVA uses the permutation of residuals to calculate P values; unlike standard ANOVA, it is robust to the non-normality and zero abundances common to ecological data sets.

RESULTS

Distribution of Crab Species

In the 150 m² sampled across all zones and habitats, we found 155 *Carcinus*, 40 *Cancer borealis*, and 17 *C.*

irroratus. Relative frequencies of the three species differed between habitat types (log-linear model: Species \times Habitat, $L^2 = 7.3$, $P = 0.026$) and zones (log-linear model: Species \times Zone, $L^2 = 33.6$, $P < 0.0001$, Fig. 1). In single-species analyses, *Carcinus* and *C. borealis* abundances were unaffected by habitat type (split-plot ANOVA, *Carcinus*, $F_{1,4} = 0.048$, $P = 0.84$; *C. borealis*, $F_{1,4} = 0.32$, $P = 0.60$), while *C. irroratus* abundance was higher in ledge habitat (15 crabs) than cobble cove habitat (2 crabs) (binomial test: $P = 0.0013$). Densities of all three species varied with vertical zone (split-plot ANOVA, *Carcinus*, $F_{4,16} = 3.31$, $P = 0.037$; *C. borealis*, $F_{4,16} = 9.4$, $P < 0.001$; *C. irroratus*, binomial test, $P = 0.0036$) but with differing patterns (Fig. 2). *Cancer borealis* and *C. irroratus* were more abundant in the subtidal than the intertidal (Fig. 2). In contrast, *Carcinus* was more abundant in the upper *Chondrus* zone than at -2 m (Fig. 2). There was no habitat by zone interaction for any species (split-plot ANOVA, *Carcinus*, $F_{4,16} = 0.28$, $P = 0.89$; *C. borealis*, $F_{4,16} = 0.28$, $P = 0.88$; *C. irroratus*, $\chi^2 = 0.18$, $P = 0.7$). *Carcinus* found in the intertidal/ledge habitat were smaller than those in other zone/habitat combinations (Table 1), and *C. borealis* were larger at -2 m than at -1 m (Table 1). Relationships of sex and size are summarized in Table 1.

Survivorship

The mean survival times for *C. borealis*, *C. irroratus*, and *Carcinus*, respectively, were 110 h (Kaplan-Meier CI_{95%}: 97-125 h), 80 h (67-93 h), and 49 h (38-60 h), and the effect of depth on survivorship varied by species (Table 2, Fig. 3). *Cancer borealis* survivorship increased with depth: survivorship was 3.5 \times higher at -2 m depth than 0 m and 10 \times higher at -7 m than 0 m. *Cancer irroratus* survivorship also increased with depth: survivorship was 3.7 \times higher at -2 m than 0 m and 2.7 \times higher at -7 m than 0 m. In contrast, survivorship of *Carcinus* declined 66% from 0 m to -7 m.

Survivorship of the three crab species diverged with depth (Table 2, Fig. 3). At 0 m, there were no differences in survivorship among species. At -2 m, survivorship of *C. borealis* and *C. irroratus* were similar and were 4.8 \times and 3.5 \times higher than *Carcinus*, respectively. At -7 m, survivorship of *C. borealis* and survivorship of *C. irroratus* were 83 \times and 4.5 \times higher than *Carcinus*, respectively.

Stomach Contents

All three species consumed a wide variety of prey, but the main item in the diets of all species was the blue mussel (*Mytilus edulis*), which comprised over 50% of the stomach contents (Fig. 4). Despite this similarity, stomach contents differed between species (MANOVA, Wilks' $\lambda = 0.21$, $F_{10,148} = 17.3$, $P < 0.0001$, Fig. 4). Mussels were most abundant in the stomachs of *C. irroratus*, and arthropods were more abundant in *C. borealis* than *C. irroratus*. *Carcinus* was most omnivorous, with $> 30\%$ of its gut contents composed of green algae. *Cancer borealis* had the greatest proportion of "other" (primarily red) algae, but this comprised $< 5\%$ of gut contents.

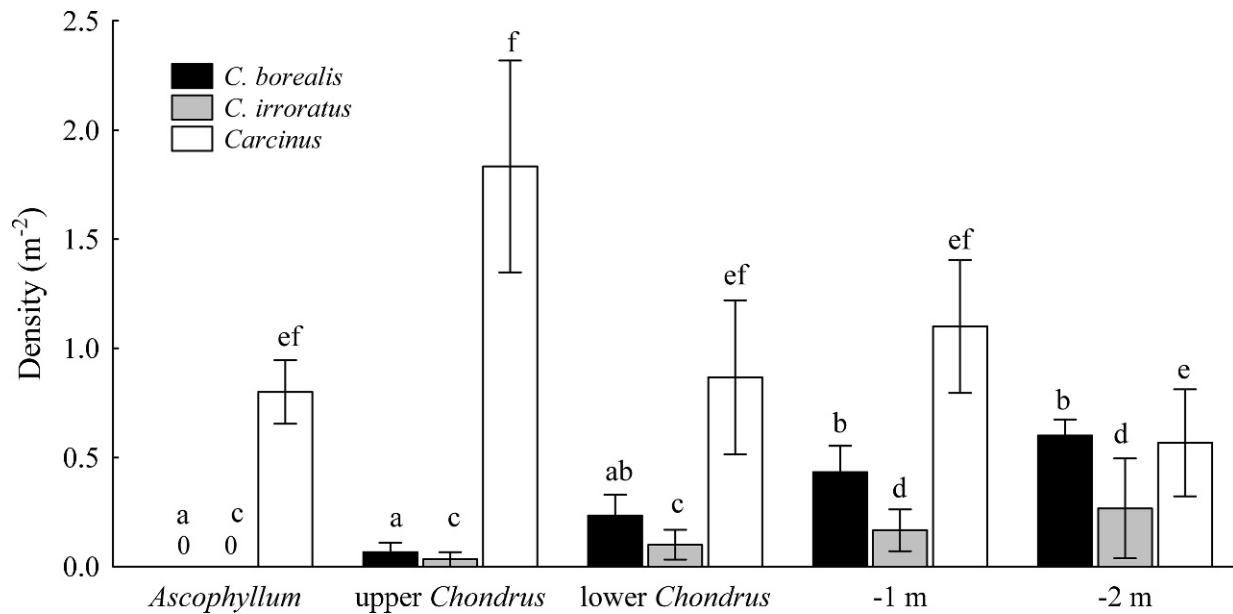


Fig. 2. Density (mean \pm SE) of *Cancer borealis* (black), *Cancer irroratus* (gray), and *Carcinus maenas* (open) for five depth zones. Different letters over *C. borealis* (a, b), *C. irroratus* (c, d), and *Carcinus* (e, f) denote significantly different densities within species across zones (post-hoc Tukey HSD $P < 0.05$ for *C. borealis* and *Carcinus*; binomial test $P < 0.05$ for *C. irroratus*).

Prey Preference

The three crab species differed significantly in the total amount of prey consumed during the experiment (goodness-of-fit test: $\chi^2 = 14.52$, $d.f. = 2$, $P = 0.0007$); *Cancer borealis* and *Carcinus* consumed similar numbers of prey (28% and 27%, respectively) while *C. irroratus* ate only half that number of prey (14%). The overall composition of consumed prey depended on crab species (contingency table: $\chi^2 = 68.0$, $d.f. = 20$, $P < 0.0001$), with significant differences for 8 of the 11 prey types (Fig. 5). *Carcinus* fed almost exclusively on small mussels and small crustaceans (isopods and amphipods). In contrast, *C. borealis* preyed upon all mollusk species and sizes at similar frequencies, but consumed fewer small mussels than *Carcinus* and did not eat isopods or amphipods. *Cancer irroratus* had a broader diet than *Carcinus*, consuming more snails, but

showing a similar preference for small mussels, isopods, and amphipods.

Vertical Distribution of Potential Invertebrate Prey

The density of littorines varied with depth zone (PERMANOVA zone effect, small *L. littorea*: $F_{4,25} = 6.98$, $P = 0.003$; large *L. littorea*, $F_{4,25} = 7.06$, $P = 0.003$; *L. obtusata*: $F_{4,25} = 3.94$, $P = 0.019$). Small *L. littorea* increased in abundance from the *Ascophyllum* zone to -1 m (Fig. 6a), large *L. littorea* were more abundant in the upper and lower *Chondrus* zones than the other three zones (Fig. 6a), and *L. obtusata* decreased in abundance from the *Ascophyllum* zone to -2 m (Fig. 6b). Small mussels, isopods, snails < 2 mm, and amphipods all had higher mean abundances in the subtidal than the intertidal

Table 1. Summary of demographic and ecological characteristics for populations of crab species co-occurring in the intertidal and shallow subtidal of the Isles of Shoals, Maine, U.S.A.

	<i>Cancer borealis</i>	<i>Cancer irroratus</i>	<i>Carcinus maenas</i>
Highest density zone & habitat	Shallow subtidal Ledge = Cobble Cove	Shallow subtidal Ledge > Cobble Cove	Mid-intertidal Ledge = Cobble Cove
Maximum density	0.6 m ⁻²	0.4 m ⁻²	1.8 m ⁻²
Size distribution by depth/habitat*	Larger at -2 m than -1 m	–	Smallest in intertidal ledge habitat
Mean size by sex†	♀ = 61.0 mm ♂ = 45.0 mm	♀ = ♂ = 28.6 mm	♀ = 35.4 mm ♂ = 28.5 mm
Sex ratio ♂:♀‡	2.3:1	2.4:1 ^{ns}	1.7:1
Highest mortality depth	0 m	0 m	-7 m
Primary Item in Gut	Mussels	Mussels	Mussels
Secondary Item in Gut (> 10% of contents)	Other Algae	None	Green Algae
Prey Preferences	All sizes of: snails, mussels, sea urchins	Small snails, small mussels, amphipods	Small mussels, isopods, amphipods

* *C. borealis* were larger at -2 m (64.8 ± 5.5 mm CW) than at -1 m (40.5 ± 7.2 mm) ($F_{1,29} = 7.5$, $P = 0.011$). *Carcinus* in the intertidal ledge habitat were smaller (23.4 ± 1.43 mm CW) than those found in the other zone/habitat combinations (34.5 ± 1.23) (Habitat \times Zone, $F_{1,4} = 8.13$, $P = 0.012$; Tukey post-hoc, $P < 0.001$).

† Logistic regression, *Carcinus*: $\chi^2 = 10.2$, $P < 0.001$; *C. borealis*: $\chi^2 = 2.9$, $P = 0.09$; *C. irroratus*: $\chi^2 = 0.03$, $P = 0.86$.

‡ Binomial tests: *C. borealis*, $P = 0.011$; *C. irroratus*, $P = 0.09$; *Carcinus*, $P = 0.0015$.

Table 2. Cox proportional hazards survival analysis: effect of species, depth, and species \times depth on survivorship, and planned contrasts of depths within species and species within depths. *Cb* = *Cancer borealis*; *Ci* = *Cancer irroratus*; *Cm* = *Carcinus maenas*. The hazard ratio of A to B is the relative risk of mortality for A compared to B (e.g., a hazard ratio of 0.5 means that A has 2 \times higher survivorship than B and a hazard ratio of 2 indicates that B has 2 \times higher survivorship than A). The equality and inequality signs in the first column reflect the result of the contrast.

Effects		Wald χ^2	df.	P			
Depth		7.93	2	0.019			
Species		2.87	2	0.238			
Depth \times Species		28.96	4	< 0.001			
Contrasts within Species	β	SE(β)	Wald χ^2	df.	P	Hazard Ratio	
<i>C. borealis</i>	2 m > 0 m	-1.24	0.41	9.30	1	0.002	0.289
	7 m > 2 m	-2.31	1.05	4.82	1	0.028	0.099
	7 m > 0 m	-3.56	1.03	11.98	1	< 0.001	0.029
<i>C. irroratus</i>	2 m > 0 m	-1.32	0.39	11.69	1	0.001	0.267
	7 m = 2 m	-0.31	0.41	0.57	1	0.452	0.735
	7 m > 0 m	-1.01	0.36	7.72	1	0.005	0.364
<i>Carcinus</i>	2 m = 0 m	0.50	0.39	1.66	1	0.198	1.645
	7 m = 2 m	0.58	0.37	2.47	1	0.116	1.79
	7 m < 0 m	1.08	0.39	7.86	1	0.005	2.945
Contrasts within Depth							
0 m:	<i>Cb</i> = <i>Cm</i>	0.17	0.36	0.23	1	0.628	1.191
	<i>Ci</i> = <i>Cm</i>	0.58	0.36	2.53	1	0.112	1.782
	<i>Cb</i> = <i>Ci</i>	-0.40	0.32	1.54	1	0.215	0.668
2 m:	<i>Cb</i> > <i>Cm</i>	-1.57	0.43	13.20	1	< 0.001	0.209
	<i>Ci</i> > <i>Cm</i>	-1.24	0.41	9.33	1	0.002	0.289
	<i>Cb</i> = <i>Ci</i>	-0.33	0.45	0.53	1	0.469	0.722
7 m:	<i>Cb</i> > <i>Cm</i>	-4.46	1.04	18.41	1	< 0.001	0.012
	<i>Ci</i> > <i>Cm</i>	-1.51	0.39	15.34	1	< 0.001	0.22
	<i>Cb</i> > <i>Ci</i>	-2.95	1.04	8.06	1	0.005	0.052

(Fig. 6a,b), but there was substantial variability among samples, and these differences were nonsignificant (PERMANOVA zone effect, small *M. edulis*: $F_{4,25} = 0.55$, $P = 0.68$; isopods, $F_{4,25} = 0.53$, $P = 0.73$; snails < 2 mm: $F_{4,25} = 1.19$, $P = 0.36$; amphipods: $F_{4,25} = 0.76$, $P = 0.55$).

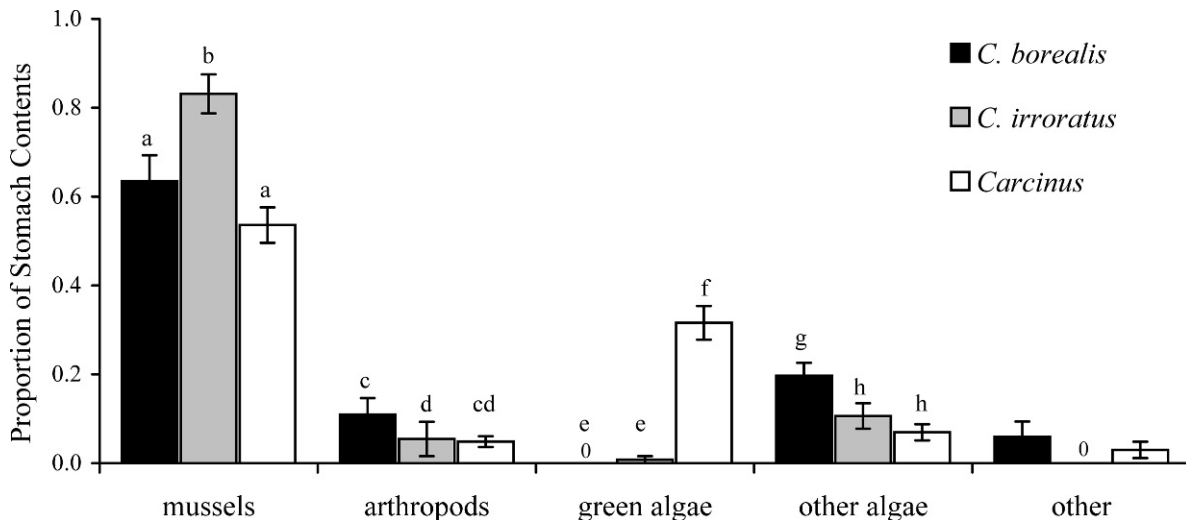


Fig. 4. Proportion (mean \pm SE) of gut contents composed of mussels, arthropods, green algae, other algae, and other for *C. borealis* (black), *C. irroratus* (gray), and *Carcinus* (open). Different letters within each prey category (mussels: a, b; arthropods: c, d; green algae: e, f; other algae: g, h) denote significantly different proportions between species for that prey category based on post-hoc Tukey comparisons of ranked gut contents ($P < 0.05$).

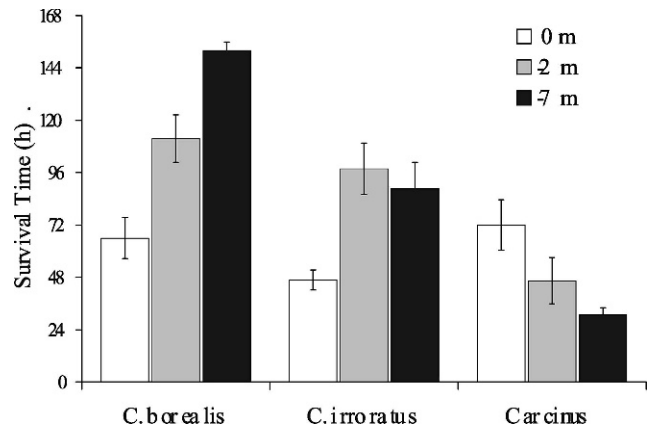


Fig. 3. Kaplan-Meier estimates of average survival time for *C. borealis*, *C. irroratus*, and *Carcinus* during a six day tethering experiment at 0 m MLLW (open), -2 m MLLW (gray), and -7 m MLLW (black). Error bars are ± 1 SE.

DISCUSSION

The three large brachyuran crab species on New England shores, the native *Cancer borealis* and *C. irroratus* and the introduced *Carcinus maenas*, show distinct differences in vertical and habitat distribution across the intertidal and shallow subtidal zones (Figs. 1, 2). *Carcinus* was most abundant in the mid-intertidal (upper *Chondrus*) zone, while the two *Cancer* species were most abundant at -2 m MLLW. According to previous work in the Isles of Shoals (Novak, 2004), these distribution patterns continue deeper into the subtidal: densities of *Carcinus* drop to zero by -7 m below MLLW, *C. irroratus* densities are similar from -2 m to -10 m, and *C. borealis* densities increase from -2 m to -10 m. The prey preference experiment and censuses of the vertical distribution of small invertebrate prey suggest that none of these species is strongly tied to the distribution of their preferred prey. Instead, patterns of abundance were most consistent with patterns of survivorship across depth zone (Fig. 7).

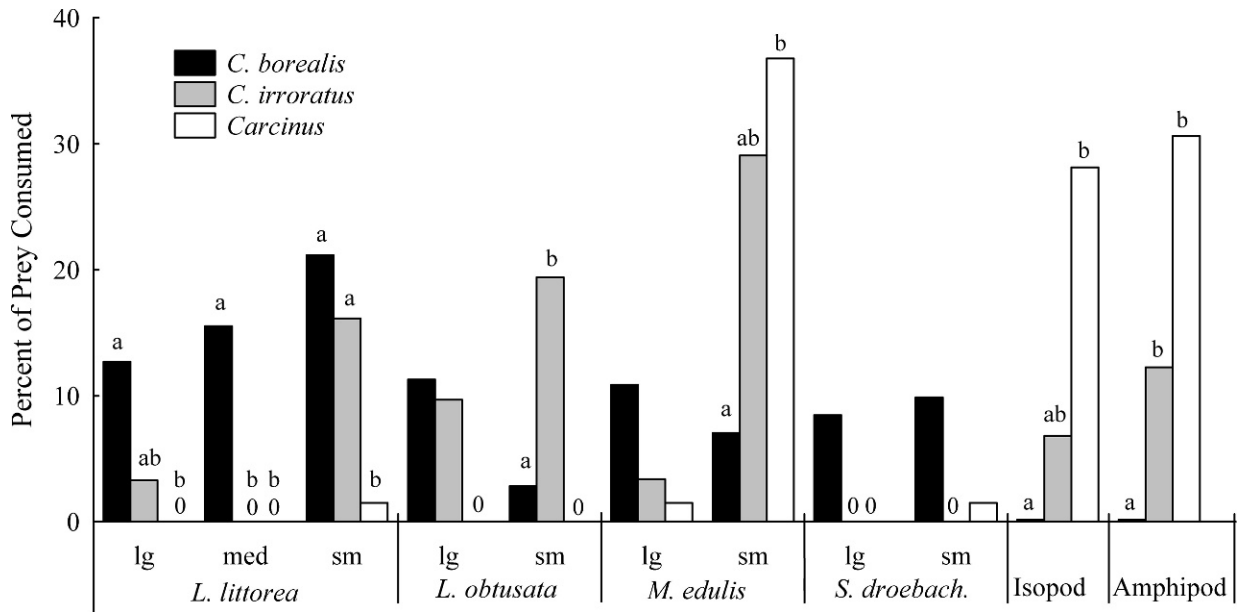


Fig. 5. Percent of each prey type consumed by *C. borealis* (black), *C. irroratus* (gray), and *Carcinus* (open) in laboratory prey preference experiments. The three crab species showed different preferences for 8 of 11 prey types; within each of these eight prey types, different letters indicate significantly different levels of preference between crab species (a χ^2 *P* value less than the Dunn-Sidak corrected alpha, $\alpha' = 0.0167$).

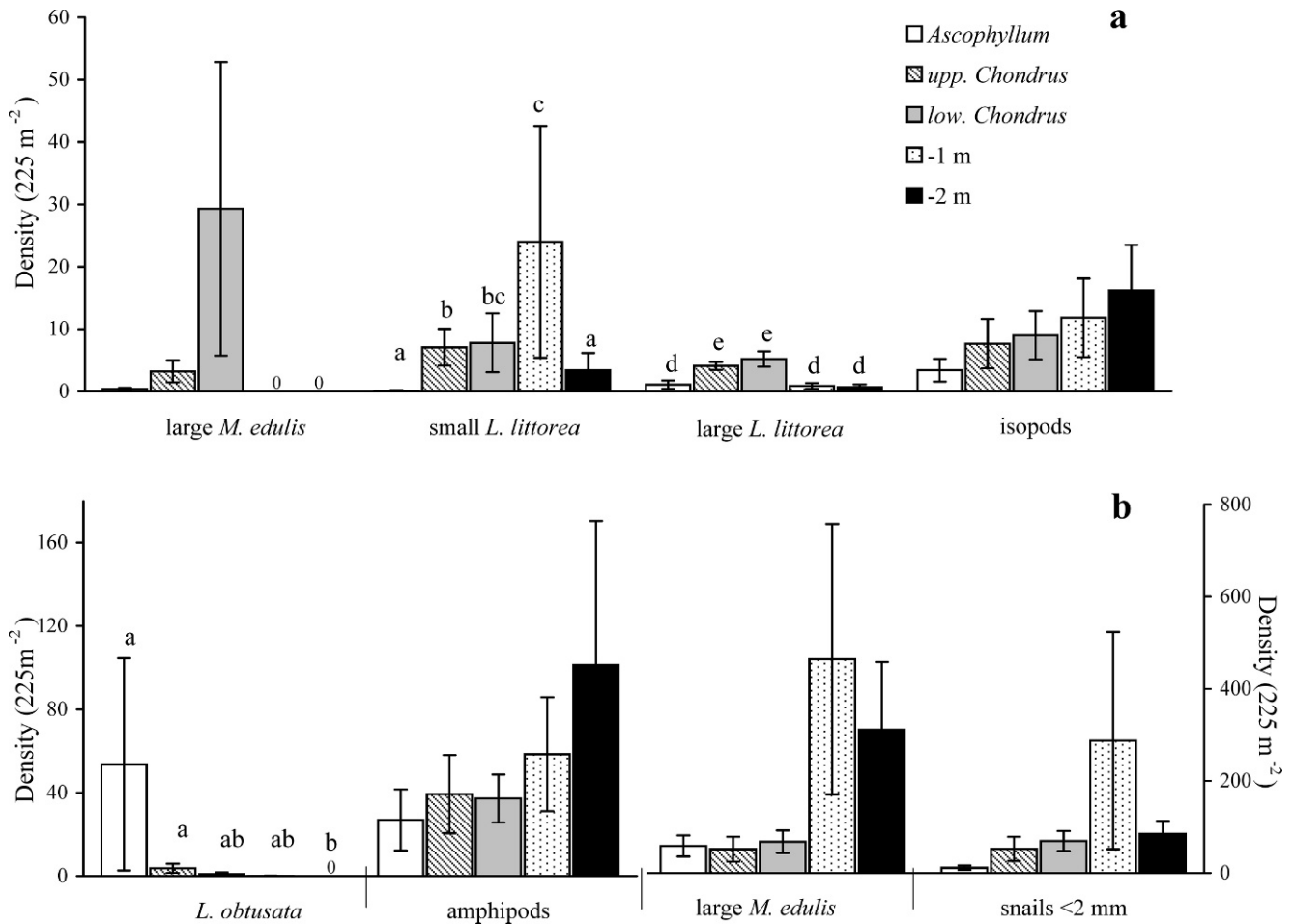


Fig. 6. Densities (mean \pm SE) per 225 cm² quadrat of (a) less abundant and (b) more abundant small invertebrates for five intertidal and subtidal zones. In (b), the right y-axis is for densities of small *Mytilus* and snails < 2 mm, and the left y-axis is for *L. obtusata* and amphipods. Different letters over *L. littorea* < 13 mm (a, b, c) and *L. littorea* > 13 mm (d, e), and *L. obtusata* (a, b) denote significantly different densities between zones within species (a post-hoc permutation test *P* value less than 0.05); there was no significant effect of zone for other invertebrate groups.

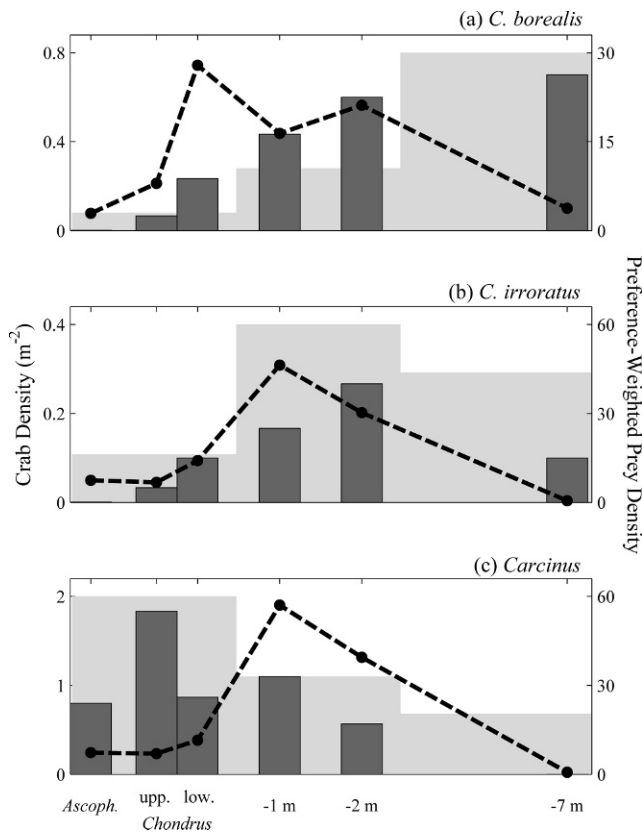


Fig. 7. Summary figure comparing crab density (bars, left axis), crab survivorship (gray background), and prey availability (line, left axis). Crab density is from Fig. 2 and, for the -7 m depth, from Novak (2004). Survivorship reflects the within-species hazard ratios (Table 2), normalized to the maximum survivorship for that species. Prey availability ($\text{kJ} \cdot 225 \text{ cm}^{-2}$) is prey density (225 cm^{-2} from Fig. 6) \times prey preference (proportion of experimental diet, Fig. 5) \times energy value (kJ per individual) of average sized prey in each category, based on energy-size relationships in the literature (*Strongylocentrotus*: Snellen et al., 2007; *Mytilus*: Elner and Hughes, 1978; littorines: Elner and Raffaelli, 1980; amphipods: Steimle and Terranova, 1985; Nair and Anger, 1979; *Idotea*: Fredette et al., 1990). Additional subtidal data (-7 m depth) for crab density is from Novak (2004) and for prey density is from Kredeit and Donahue (2009); both studies use similar methods to this study and were performed at similar sites in the Isles of Shoals.

Survivorship and abundance of *Carcinus* decreased with depth from the intertidal *Chondrus* zone into the subtidal, survivorship and abundance of *Cancer borealis* increased from the intertidal to the subtidal, and survivorship and abundance of *C. irroratus* increased from 0 m to -2 m and declined slightly (although not significantly) from -2 m and -7 m (Table 1, Figs. 2, 7). Gulls (*Larus argentatus* Pontopiddan, 1763 and *Larus marinus* L.) are important intertidal predators on crabs (Good, 1992; Rome and Ellis, 2004; Ellis et al., 2005; Dumas and Witman, 1993), while lobsters (*Homarus americanus* Milne Edwards, 1837) and fishes (*Tautoga onitis* L., *Gadus morhua* L., *Tautogolabrus adspersus* Walbaum, 1792) are important subtidal predators (Ojeda and Dearborn, 1991). Gulls can prey on crabs that are less than 1 m below the surface of the water (Ellis et al., 2005) and, therefore, had greatest access to crabs tethered at 0 m, some access to crabs tethered at -2 m, and no access to crabs tethered at -7 m. Previous studies demonstrate that gulls prefer *C. borealis* to *C. irroratus*

and *Carcinus*, and that *C. borealis* is a disproportionately large component of gull diet (pellets and remains on shore) (Rome and Ellis, 2004; Ellis et al., 2005). In the subtidal, *Carcinus* may be disproportionately affected by lobsters, which are at densities of 0.2 m^{-2} from -2 m to -10 m MLLW in the Isles of Shoals (Novak, 2004, 2732) and have both consumptive and non-consumptive effects on *Carcinus* (League-Pike and Shulman, 2009). In this study, predation on *C. irroratus* and *C. borealis* decreased in the subtidal, while predation on *Carcinus* increased, indicating that *Cancer* spp. were relatively more susceptible to predation by gulls and/or less susceptible to predation by lobsters and other subtidal predators.

Differences in laboratory prey preferences among crab species were greater than the differences in field-realized diets. In the prey preference experiments, *Carcinus* fed almost exclusively on small mussels and small crustaceans, while *C. borealis* preyed upon almost all mollusk species and sizes at similar frequencies but did not eat isopods or amphipods. *Cancer irroratus* had a broader diet than *Carcinus*, consuming more snails, but showed a similar preference for small mussels and amphipods. This division between preferences for larger, heavier-shelled prey (*C. borealis*) and smaller or mobile prey (*Carcinus* and *C. irroratus*) was predicted by Jeffries (1966), comparing agility of *C. borealis* and *C. irroratus*, and by Moody and Steneck (1993), who described *Carcinus* and *C. irroratus* as “similarly quicker, more dexterous, and capable of a greater diversity of shell opening tactics” in contrast to *C. borealis* and *H. americanus* that “utilized only shell crushing tactics.” Despite these differences, the stomach contents of field collected crabs in all species were $> 50\%$ blue mussel (Fig. 4), which was the most abundant prey item available (Fig. 6).

Overall, we find that crab distributions align more closely with the distribution of predation risk (top-down effects) than distribution of prey (bottom-up) effects (Fig. 7). This could have important implications for community structure both past and present. While there is little historical data available on the distribution of small invertebrates in a pre-*Carcinus* Gulf of Maine, this study indicates that the impacts of *Carcinus* on the intertidal community were probably novel, distinct from the impacts of the native *Cancer* species. *Carcinus*, with its high foraging rate (Menge, 1983), may deplete the intertidal of its preferred prey; this is supported by data available from the northward expansions of *Carcinus* (Seeley, 1986; Trussell, 2000; Ropes, 1968). In contemporary intertidal communities, prey distribution may also reflect top-down control: the preferred prey of *Carcinus* (small mussels, amphipods, and isopods) are more abundant in the subtidal; and prey available only to *C. borealis* (large *Mytilus* and large *L. littorea*) are more abundant in the intertidal. While further manipulative experiments would be necessary to demonstrate such trophic cascades, recent studies in this system have demonstrated a *C. borealis*-mediated trophic cascade (gulls \rightarrow *C. borealis* \rightarrow *L. littorea*) using a gull-exclusion experiment (Ellis et al., 2007), and the potential for cascading effects of *C. borealis* to kelp (*C. borealis* \rightarrow green urchin \rightarrow kelp) (McKay and Heck, 2008; Siddon and Witman, 2004). Perhaps a second cascade, due to the

dramatic consumptive and non-consumptive effects of lobsters on *Carcinus* (League-Pike and Shulman, 2009), is also at work: *H. americanus* → *Carcinus* → amphipods or small mussels.

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REFERENCES

- Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26: 32-46.
- . 2005. PERMANOVA: a FORTRAN computer program for permutational multivariate analysis of variance. Department of Statistics, University of Auckland, New Zealand.
- DFO. 2000a. Rock Crab (*Cancer irroratus*) Eastern Nova Scotia. DFO Science Stock Status Report C3-05 (2000).
- DFO. 2000b. Scotian Shelf (LFA 33) Jonah Crab (*Cancer borealis*) DFO Science Stock Status Report C3-09 (2000).
- Dumas, J. V., and J. D. Witman. 1993. Predation by herring gulls (*Larus argentatus* Coues(sic)) on two rocky intertidal crab species (*Carcinus maenas* (L.) and *Cancer irroratus* Say). *J Exp Mar Biol Ecol* 169: 89-101.
- El-Shaarawi, A. H., and W. W. Piegorsch. 2002. *Encyclopedia of Environometrics*, Vol. John Wiley & Sons, New York.
- Ellis, J. C., W. Chen, B. O'Keefe, M. J. Shulman, and J. D. Witman. 2005. Predation by gulls on crabs in rocky intertidal and shallow subtidal zones of the Gulf of Maine. *Journal of Experimental Marine Biology and Ecology* 324: 31-43.
- , M. J. Shulman, M. Wood, J. D. Witman, and S. Lozyniak. 2007. Regulation of intertidal food webs by avian predators on New England rocky shores. *Ecology* 88: 853-863.
- Elner, R. W. 1981. Diet of green crab *Carcinus maenas* (L.) from Port Hebert, southwestern Nova Scotia, Canada. *Journal of Shellfish Research* 1: 89-94.
- , R. N. Hughes. 1978. Energy maximization in the diet of the shore crab, *Carcinus maenas*. *Journal of Animal Ecology* 46: 103-116.
- , D. G. Raffaelli. 1980. Interactions between two marine snails, *Littorina rudis* Maton and *Littorina nigrolineata* Gray, a predator, *Carcinus maenas* (L.), and a parasite, *Microphallus similis* Jagerskiold. *Journal of Experimental Marine Biology and Ecology* 43: 151-160.
- Fredette, T. J., R. J. Diaz, J. Van Montfrans, and R. J. Orth. 1990. Secondary production within a seagrass bed (*Zostera marina* and *Ruppia maritima*) in lower Chesapeake Bay. *Estuaries* 13: 431-440.
- Good, T. P. 1992. Experimental assessment of gull predation on the Jonah Crab *Cancer borealis* (Stimpson) in New England rocky intertidal and shallow subtidal zones. *Journal of Experimental Marine Biology and Ecology* 157: 275-284.
- Gotelli, N. J., and A. M. Ellison. 2004. *A primer of ecological statistics*, Vol. Sinauer Associates.
- Grosholz, E. D., and G. M. Ruiz. 1996. Predicting the impact of introduced marine species: lessons from the multiple invasions of the European green crab *Carcinus maenas*. *Biol Conserv* 78: 59-66.
- Haefner, P. A. 1977. Aspects of biology of Jonah Crab, *Cancer borealis* Stimpson, 1859 in the Mid-Atlantic Bight. *Journal of Natural History* 11: 303-320.
- Holmes, S. J. 1905. The Amphipoda of southern New England. *Bulletin of the Bureau of Fisheries* 24: 459-529.
- Hosmer, D. W., and S. Lemeshow. 1999. *Applied survival analysis*. Wiley, New York.
- , and ———. 2004. *Applied logistic regression*. Wiley, New York.
- Jeffries, H. P. 1966. Partitioning of the estuarine environment by two species of *Cancer*. *Ecology* 47: 477-481.
- Kredeit, C. J., and M. J. Donahue. 2009. Growth-mortality trade-offs along a depth gradient in *Cancer borealis*. *Journal of Experimental Marine Biology and Ecology* 373: 133-139.
- Krouse, J. S. 1978. Effectiveness of escape vent shape in traps for catching legal-sized lobster, *Homarus americanus*, and harvestable-sized crabs, *Cancer borealis* and *Cancer irroratus*. *Fisheries Bulletin* 76: 425-432.
- League-Pike, P. E., and M. J. Shulman. 2009. Intraguild predators: behavioral changes and mortality of the green crab (*Carcinus maenas*) during interactions with the American lobster (*Homarus americanus*) and Jonah crab (*Cancer borealis*). *Journal of Crustacean Biology* 29: 350-355.
- Le Jolis, A. F. 1863. *Liste des algues marines de Cherbourg*, Vol. Baillière, Paris.
- Ledesma, M. E., and N. J. O'Connor. 2001. Habitat and diet of the non-native crab *Hemigrapsus sanguineus* in southeastern New England. *Northeastern Naturalist* 8: 63-78.
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*, ed., Vol. 10.
- Lowry, R. 2009. Concepts and applications of inferential statistics. <http://faculty.vassar.edu/lowry/webtext.html>.
- McArdle, B. H., and M. J. Anderson. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* 82: 290-297.
- McKay, K. M., and J. K. L. Heck. 2008. Presence of the Jonah crab *Cancer borealis* significantly reduces kelp consumption by the green sea urchin *Strongylocentrotus droebachiensis*. *Marine Ecology Progress Series* 356: 295-298.
- Menge, B. A. 1983. Components of predation intensity in the low zone of the New England rocky intertidal region. *Oecologia* 58: 141-155.
- Milne Edwards, H. 1837. *Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux*. 2., Vol. Librairie Encyclopédique de Roret, Paris.
- Moody, K. E., and R. S. Steneck. 1993. Mechanisms of predation among large decapod crustaceans of the Gulf of Maine coast: functional versus phylogenetic patterns. *Journal of Experimental Marine Biology and Ecology* 168: 111-124.
- Müller, O. F. 1776. *Zoologiae Danicae Prodromus, seu Animalium Daniae et Norvegiae indigenarum characteres, nomina et synonyma imprimis popularium*. M. Hallager, Havniae.
- Nair, K. K. C., and K. Anger. 1979. Life cycle of *Corophium insidiosum* (Crustacea, Amphipoda) in laboratory culture. *Helgoländ Marine Research* 32: 279-294.
- Novak, M. 2004. Diurnal activity in a group of Gulf of Maine decapods. *Crustaceana* 77: 603-620.
- Ojeda, F. P., and J. H. Dearborn. 1991. Feeding ecology of benthic mobile predators: experimental analyses of their influences in rocky Subtidal communities of the Gulf of Maine, U.S.A. *Journal of Experimental Marine Biology and Ecology* 149: 13-44.
- Pallas, P. S. 1772. *Spicilegia Zoologica, quibus novae imprimis et obscurae animalium species iconibus, descriptionibus atque commentariis illustrantur*. Berlin.
- Pontopiddan, E. 1763. *Den Danske Atlas eller Konge-Riget Dannemark*. t.1. Kisenhavn, Godiche.
- Richards, R. A., and J. S. Cobb. 1986. Competition for shelter between lobsters (*Homarus americanus*) and Jonah Crabs (*Cancer borealis*): effects of relative size. *Canadian Journal of Fisheries and Aquatic Science* 43: 2250-2255.
- Rome, M. S., and J. C. Ellis. 2004. Foraging Ecology and Interactions between Herring Gulls and Great Black-backed Gulls in New England. *Waterbirds* 27: 200-210.
- Ropes, J. W. 1968. The feeding habits of the green crab *Carcinus maenas*(L.). *US Fish and Wildlife Service Fisheries Bulletin* 67: 183-203.
- . 1988. The food habits of five crab species at Pettaquamscutt River, Rhode Island. *Fisheries Bulletin* 87: 197-204.
- Say, T. 1817. An account of the Crustacea of the United States. *Journal of the Academy of Natural Science, Philadelphia* 1: 155-169.
- Seeley, R. H. 1986. Intense natural selection caused a rapid morphological transition in a living marine snail, *Littorina obtusata*. *Proceedings of the National Academy of Sciences, U.S.A* 83: 6897-6901.
- Siddon, C. E., and J. D. Witman. 2004. Behavioral indirect interactions: multiple predator effects and prey switching in the rocky subtidal. *Ecology* 85: 2938-2945.
- Snellen, C. L., P. J. Hodum, and E. Fernandez-Juricio. 2007. Assessing western gull predation on purple sea urchins in the rocky intertidal using optimal foraging theory. *Canadian Journal of Zoology* 85: 221-231.
- Sokal, R. R., and S. R. Rohlf. 1995. *Biometry*. Freeman, New York.

- Stackhouse, J. 1801. *Nereis Britannic* ontinens species omnes *Fucorum* in *Insulis Britannicis crescentium: descriptione Latina et Anglica*. Bathoniæ and Londini, London.
- StatSoft, Inc. 2002. STATISTICA (data analysis software system), www.statsoft.com.
- Stehlik, L. L., C. L. Mackenzie, and W. W. Morse. 1991. Distribution and abundance of four brachyuran crabs on the Northwest Atlantic Shelf. *Fisheries Bulletin* 89: 473-492.
- Steimle, F. W., and R. J. Terranova. 1985. Energy equivalents of marine organisms for the continental shelf of the temperate northwest Atlantic. *Journal of Northwest Atlantic Fisheries Science* 6: 117-124.
- Stimpson, W. 1859. Notes on North American Crustacea, 1. *Annals of the Lyceum of Natural History of New York* 7: 49-93.
- Trussell, G. C. 2000. Phenotypic clines, plasticity, and morphological trade-offs in an intertidal snail. *Evolution* 54: 151-166.
- , and M. O. Nicklin. 2002. Cue sensitivity, inducible defense, and trade-offs in a marine snail. *Ecology* 83: 1635-1647.
- , and L. D. Smith. 2000. Induced defenses in response to an invading crab predator: An explanation of historical and geographic phenotypic change. *Proceedings of the National Academy of Sciences USA* 97: 2123.
- Vermeij, G. J. 1982. Environmental change and the evolutionary history of the periwinkle *Littorina littorea* in North America. *Evolution* 36: 561-580.
- Walbaum, J. J. 1792. *Genera Piscium*. Grypeswald, Rose.

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