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REGULATION OF INTERTIDAL FOOD WEBS BY AVIAN PREDATORS ON NEW ENGLAND ROCKY SHORES

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Abstract. Although there is a large body of research on food webs in rocky intertidal communities, most of the emphasis has been on the marine benthic components. Effects of avian predation on highly mobile predators such as crabs, remains practically unstudied in rocky shore ecosystems. The crab, *Cancer borealis*, is an important component of the diet of gulls (*Larus marinus*, *L. argentatus*) at the Isles of Shoals, Maine, USA. *C. borealis* prey include the predatory gastropod *Nucella lapillus* L., the herbivore *Littorina littorea*, and mussels *Mytilus edulis* L. We hypothesized that gulls reduce abundance of *C. borealis* in the low intertidal and shallow subtidal, thereby allowing *C. borealis* prey to persist in high numbers. A study of crab tidal migration showed that *C. borealis* density nearly doubled at high tide compared to low tide; thus, crabs from a large subtidal source population migrate into the intertidal zone during high tides and either emigrate or are removed by gulls during low tides. Results from a small-scale (1 m^2) predator caging experiment in the low intertidal zone indicated that enclosed crabs significantly reduced *L. littorea* abundance when protected from gull predation. In a much larger-scale gull exclusion experiment, densities of *C. borealis* increased significantly during low and high tides in exclosures relative to the controls. *C. borealis* density was inversely correlated with changes in the abundance of two mesopredators *Carcinus maenas* and *Nucella lapillus*, and with the space-occupier *M. edulis*. There was a similar negative correlation between abundance of *C. borealis* and the change in abundance of the herbivore *L. littorea*, but the trend was not significant. Mortality of tethered *L. littorea* was associated with *C. borealis* density across sites. However, preferred algae did not change in response to *L. littorea* density during the experiment. Thus, we found suggestive, but not conclusive, evidence for a three-level cascade involving gulls, crabs, and *L. littorea*. Our studies strongly suggest that gulls, as apex predators, generate three-level trophic cascades in rocky intertidal food webs by preventing the highly mobile subtidal predator, *C. borealis*, from establishing substantial populations in the low-mid intertidal zone thereby indirectly enhancing densities of two key mesopredators (*N. lapillus*, *Carcinus*) and blue mussels (*M. edulis*).

Key words: *avian predation;* Cancer borealis; Carcinus; *large-scale experiments;* Littorina littorea; *marine food webs;* Nucella lapillus; *predator exclusion; rocky intertidal and subtidal; top-down; trophic cascade*.

Introduction

The movement of predators and prey across habitat boundaries is a widespread phenomenon that can strongly influence local population fluctuations and the structure of communities (Vanni et al. 2004). A complete understanding of food web dynamics requires knowledge of such connections. Birds are important links between marine and terrestrial ecosystems along coasts throughout the world (Anderson and Polis 1999, Sanchez-Piñero and Polis 2000). These terrestrially based predators exploit intertidal species during low tide and substantially impact populations of marine invertebrates (Wootton 1997, Hori and Noda 2001, Carlton and Hodder 2003, Ellis et al. 2005). Despite this, most research on food webs in rocky intertidal communities has not addressed terrestrial predators, focusing exclusively on benthic marine organisms. A handful of studies have demonstrated that birds can reduce the abundance of herbivores (sea urchins, limpets), thereby indirectly increasing cover of macroalgae (Hockey and Branch 1984, Wootton 1992, 1995, Lindberg et al. 1998). However, the effects of avian predation on highly mobile predators such as crabs remain practically unstudied in rocky shore ecosystems.

Avian predators, particularly gulls, may play influential roles in rocky intertidal communities of New England. During the past several decades, Great

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Black-backed (*Larus marinus* L.) and Herring Gulls (*L. argentatus* Pontopiddan) have dramatically increased in abundance along rocky shores of New England and throughout the North Atlantic (Lloyd et al. 1991). A recent estimate indicates that there are ~30 000 gulls nesting on over 200 islands in Maine alone (Schauffler 1998). Both species of gull feed in intertidal habitats on crabs, sea urchins, and mussels (Dumas and Witman 1993, Pierroti and Good 1994, Good 1998). The Jonah crab, *Cancer borealis* Stimpson, is a particularly important component of the diet of gulls, comprising between 25% and 60% of prey remains found around nests in the Isles of Shoals, New Hampshire/Maine (Rome and Ellis 2004). Intense predation by gulls on *C. borealis* occurs along mainland coasts as well as offshore breeding islands throughout the Gulf of Maine (Ellis et al. 2005). Changes in numbers of predatory gulls may have significant consequences for crabs and other intertidal prey.

Gull predation on *C. borealis* may reduce the abundance of *C. borealis* in intertidal and shallow subtidal zones, thus potentially influencing densities of other invertebrates. *C. borealis* feeds on a wide variety of prey consisting of other crabs, polychaetes, sea urchins, mussels, and gastropods (Stehlik 1993, Siddon and Witman 2004) including the common periwinkle, *Littorina littorea* L. (Ojeda and Dearborn 1991). *L. littorea* is an important intertidal herbivore and is capable of substantially depleting cover of macroalgae along rocky shores (Lubchenco 1978, Bertness 1984, Trussell et al. 2002, 2003). Lubchenco (1978) suggested that gulls indirectly affect the diversity and abundance of algae in intertidal tidepools by eating *Carcinus maenas* L., which is an important predator of *L. littorea*. However, this four-level cascade was never tested experimentally.

Unlike other studies of avian predation, in which the birds consumed sessile or slow-moving invertebrates, our research focuses on bird predation on highly mobile crabs. This dynamic predator–prey system presents unique challenges for experimentation because manipulations must account for both the patchiness of avian predation and potentially high mobility of invertebrate prey (Englund 1997). Therefore, our approach consisted of measuring rates of gull predation and crab migration to provide a quantitative background for predator manipulations testing the general trophic cascade hypothesis. Because tidal migration by crabs could alter the number of crabs available to gulls and change the magnitude of crab predation on intertidal prey, we investigated migration from the subtidal into the intertidal zone by these crabs during high tide. We then experimentally tested the effect of *C. borealis* on the intertidal population of the common herbivorous snail *L. littorea*. Last, we performed a large-scale gull exclusion experiment to address critical questions related to the trophic cascade hypothesis: (1) Does gull predation limit the abundance of *C. borealis* and/or *Carcinus maenas* in intertidal and shallow subtidal zones? (2) Is there a correlation between *C. borealis* density and changes in densities of potential *C. borealis* prey (blue mussel *Mytilus edulis* L., the predatory gastropod *Nucella lapillus* L., and *L. littorea*)? (3) Do potential changes in densities of *L. littorea* alter the abundance of benthic algae?

Methods

Study area and species

The study took place in the Gulf of Maine in the Isles of Shoals, a nine-island archipelago located 10 km from the mainland coast of New Hampshire, USA. Gull exclusion and crab inclusion experiments were conducted on Appledore Island, near the Shoals Marine Laboratory (42°58′ N; 70°37′ W). The east side of the island is exposed to heavy wave action from the Atlantic Ocean, whereas the western side is relatively protected; exposed rocky headlands and boulder coves comprise the shoreline.

In the Gulf of Maine, Herring Gulls and Great Black-backed Gulls are present on offshore breeding islands from March through September. Both species forage in mainland landfills, the open ocean, and intertidal and shallow subtidal zones. Gulls capture prey in shallow subtidal areas by paddling on or flying close to the water, then plunging to a maximum depth of 1 m below the water surface (Good 1998). Gulls do not forage on the shore during high tides because they cannot access the intertidal zone during this time.

The rocky intertidal and shallow subtidal habitats where gulls forage can be divided into three distinct zones characterized by the predominant sessile species: the barnacle zone (2.1–2.7 m above mean lower low water [MLLW]), the *Ascophyllum* zone (0.6–2.1 m), and the *Chondrus* zone (0.6 m to shallow subtidal). Gulls also feed in the shallow subtidal zone adjacent to the shore. As visual predators, gulls forage in the intertidal and nearby shallow subtidal solely on diurnal low tides (J. C. Ellis, *personal observation*).

Three species of crabs (*Cancer borealis*, *C. irroratus,* and *Carcinus maenas* [henceforth referred to as *Carcinus*]) are common on rocky shores in New England. Though less abundant, the two *Cancer* crabs are consumed much more frequently by gulls than *Carcinus,* and *C. borealis* more frequently than *C. irroratus* (Ellis et al. 2005). *C. borealis* inhabits coastal and nearshore habitats from Nova Scotia to south of Tortugas, Florida (MacKay 1943, Williams 1965). In the Isles of Shoals, the vertical distribution of *C. borealis* extends from the low intertidal zone to the subtidal zone where densities can reach 1 crab/m^2 (Witman 1985, Siddon 2004). Average carapace width of *C. borealis* in the low intertidal zone, where crabs are vulnerable to gull predation, is ~75 mm ($N = 140$ crabs; J. C. Ellis, *unpublished data*). Gulls prefer medium (70–85 mm) and large (90–105 mm) crabs (Rome and Ellis 2004), and the average size of *C. borealis* consumed by gulls is ~84 mm

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($N = 195$ carapaces; J. C. Ellis, *unpublished data*). *C. borealis* feeds on a variety of invertebrate prey; mollusks (mussels and gastropods) predominate in the diet, along with sea urchins, annelids, crabs, and lobsters (Ojeda and Dearborn 1991). In this study, we focused on the potential effects of *C. borealis* on invertebrates common in the low intertidal zone. These included two gastropods, the herbivorous *Littorina littorea* and carnivorous *Nucella lapillus*, as well as the mussel *Mytilus edulis* L., and the green crab, *Carcinus*.

L. littorea inhabits rocky intertidal habitats of the North Atlantic (Reid 1996). On Appledore Island, the vertical distribution of *L. littorea* extends from the intertidal zone into the shallow subtidal zone, with a dramatic decline in density below 0 m (Carlson et al. 2006). *L. littorea* grazes on germlings of macroalgae (Lubchenco 1983), diatoms (Hunter and Russell-Hunter 1983), and ephemeral green algae (Lubchenco 1978, Bertness 1984). Due to the ecological importance and extremely high densities of *L. littorea* (>600 m^2 at some sites on Appledore Island; Carlson et al. 2006), we conducted an experiment specifically designed to determine the potential predatory impact of *C. borealis* on this species.

Estimates of tidal migration by Cancer borealis

Gulls remove 30–50% of the *C. borealis* available in the low intertidal/shallow subtidal (down to −1 m) on each diurnal low tide (Ellis et al. 2005). Tidal migration by *C. borealis*, which has previously been observed in other cancrid crabs (Robles et al. 1989), could provide the influx of crabs necessary to support this high predation rate. In turn, upward migration by *C. borealis* from a large subtidal source population could restore intertidal populations thereby maintaining a fairly constant predation rate by crabs.

Our study of tidal migration by *C. borealis* took place during a series of spring tides (12 July–27 July 2002) at two sites on each of three islands: Appledore, Smuttynose, and Duck. *C. borealis* is primarily active during the day (Novak 2004); therefore, we conducted censuses of crabs during one daytime high tide and one daytime low tide at each site. Surveys at high tide were conducted using SCUBA. Randomly selected 1-m^2 quadrats (19–30 quadrats/site/depth) were sampled along a 50-m transect at each of two depths: 0 m (±0.5 m) and −1 m (±0.5 m). These depths represent the range of overlap between gull foraging and the upper distribution of *C. borealis* in the intertidal zone. In conjunction with crab surveys, we estimated gull predation rates at the same sites. To estimate gull predation rates (in conjunction with crab censuses), we collected prey remains (e.g., decapod carapaces and appendages; sea urchin tests) from the low and mid-intertidal zones 0.5 h after low tide, when most gulls have ceased foraging (Dumas and Witman 1993, Ellis et al. 2005). Carapaces were collected after three separate diurnal low tides, and we used the three collections to calculate the average number of crabs removed by gulls per diurnal low tide for each site.

Crab densities (crabs per quadrat) were Poisson-distributed; therefore, to determine whether crab densities differed between high and low tide, we used a generalized linear mixed model ANOVA (GLIMMIX in SAS v8.2) with a Poisson distribution. Details of the statistical model are given in Appendix A.

Crab inclusion experiment: effects of C. borealis *on* L. littorea *in the low intertidal zone*

We tested for direct effects of *C. borealis* on *L. littorea* densities in the intertidal zone in a predator inclusion/exclusion experiment. The experiment was conducted at Appledore Ledges on the southeast end of Appledore Island. Experimental cages were constructed from plastic coated wire mesh (1.25-cm mesh size) and were attached to the rocky substrate by securing bolts in drill holes with plastic anchors and marine epoxy. Treatments were ordered randomly and spaced at least 1 m apart. We placed the experiment at 0 m because gulls frequently capture crabs at this tidal height (Ellis et al. 2005), and snail densities are particularly high (Carlson et al. 2006). We constructed circular cages (1 m diameter, ~0.8 m^2, 0.5 m high) with tops, sides, and enlarged holes (~3 × 3 cm) at the base that allowed *L. littorea* and small animals such as seastars, green crabs, juvenile *Cancer* crabs, and other gastropods to enter and exit, but excluded large *Cancer* crabs. The experimental design consisted of six replicates for each of four treatments: (1) crab inclusion (cage with one *C. borealis* [carapace width = 86 mm ± 0.8 mm, mean ± SE]), (2) crab exclusion (cage that excludes crabs), (3) cage control (cage with partial sides; allowing crabs to enter and exit), and (4) experimental control (open plot; allowing access by gulls, crabs and snails). Cage controls were used to account for artifacts of drilling and attaching the cages and for potential alterations in snail or crab behaviors resulting from alteration in water flow or shading. The densities of *L. littorea* in the cages and plots were censused prior to beginning the experiment (mid-August, 2001) and every 7–10 days thereafter for ~3 weeks.

To analyze the change in *L. littorea* densities over time, we log-transformed snail density data collected during the three censuses. The transformed data were used in a general linear model repeated-measures analysis (SPSS 2004). When the multivariate model showed a significant time × treatment interaction, we tested the within-subject (time) effect for each treatment separately using a Bonferroni correction for the alpha value.

Large-scale gull exclusion experiment: effects on multiple components of intertidal food webs

High predation rates by gulls on *C. borealis*, an influx of *C. borealis* into the intertidal zone, and a reduction of *L. littorea* in the presence of *C. borealis* in the crab

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inclusion treatment (see *Results*) led to the hypothesis that gulls exert top-down control on low-intertidal communities. However, earlier experiments in which gulls were excluded from 1 to 30 m^2 of low intertidal habitat showed little effect on *C. borealis* densities (J. C. Ellis and J. D. Witman, *unpublished manuscript*). One possible explanation for a lack of a gull-exclusion effect is that crabs were still exposed to predation because they frequently moved out of the exclusion cages. *C. borealis* are quite mobile, capable of moving >8 m in 15 min (M. J. Shulman, *unpublished data*). We therefore conducted a very large-scale experiment, using human presence and disturbance to prevent gulls from foraging in the intertidal during low tide. In this experiment, we tested: (1) whether predation by gulls reduces the density of *C. borealis* in low intertidal and shallow subtidal zones; (2) whether changes in densities of molluscan and crab prey of *C. borealis* were correlated with density of *C. borealis*; and (3) whether change in percent cover of preferred ephemeral algae was correlated with the density of *L. littorea*.

Three gull exclusion and three control sites were located on the protected western side of Appledore Island. Each site consisted of a 50 m length of shoreline that encompassed the *Ascophyllum*, *Chondrus,* and shallow subtidal zones. The areas of each site (estimated as the lower end of the *Ascophyllum* zone to −1.0 m) ranged from 530 to 1152 m^2 and averaged 744 m^2. All study sites were at least 100 m apart to ensure that treatments did not affect one another. Within the control plots, gulls were allowed to forage normally. In gull exclusion areas, 1–3 people prohibited gulls from foraging during low tides by scaring them away using streams of seawater from "supersoaker" water guns, thrown pebbles, and/or noise. Exclusions were typically conducted by personnel standing in the high intertidal zone, above the low intertidal zone where invertebrate and algal sampling took place. Gulls were inhibited from foraging at the exclusion sites for 2.5 h before and after every daytime low tide for a total of 174 hours over 26 days (5 July–2 August 2004). Exclusion sites were not guarded during nighttime low tides because the gulls do not feed at night (J. C. Ellis, *personal observation*).

Effects of gull exclusion on crabs

We estimated rates of gull predation on crabs by counting the number of carapaces that occurred along the shore after low tide at the six sites. At control sites, carapaces were collected every 1–3 days ~0.5 h after low tide. At the exclusion areas, gulls occasionally captured crabs before people arrived at the site or would "steal" crabs during the exclusion period. Therefore, carapaces were collected each day at the beginning of the exclusion period and the number of "stolen" crabs was recorded. Mean daily predation rates at the control sites were calculated by dividing the total number of carapaces at each site by the number of low tides during which collections were made. We estimated predation rates at exclusion areas by summing the number of carapaces and stolen crabs and dividing by the total number of low tides during which gulls were inhibited from foraging. Following the 26 days of gull exclusion, we estimated predation rate on *C. borealis* by collecting carapaces at the six sites during the three diurnal low tides following termination of the experiment.

We counted crabs during both high and low tides in order to determine whether or not crabs remained, survived, and potentially foraged during low tide, and to count the number present (and potentially foraging) during high tide. We used two methods to census crabs in the lower *Chondrus* zone (~0 m tidal height) during high tide. While on SCUBA, we counted *C. borealis* and *C. irroratus* in a 2 m wide, 50 m long band transect at each study site. These counts were made five times: just prior to the initiation of the experiment; at weeks 2, 3, and 4 of gull exclusion; and one week after the exclusion treatment was ended. A second method was used to census the more abundant green crab, *Carcinus*, at the beginning and end of the experiment. At each site, 10 1-m^2 quadrats were placed randomly every 2–6 m, and all *Carcinus* within each quadrat were counted and measured (carapace width). At low tide, we censused the number of *Cancer* crabs above the waterline in the *Chondrus* and *Ascophyllum* zones at every site. In the control areas, so as not to disturb foraging gulls, crabs were censused on the rising tide after most gulls had ceased foraging.

We compared the predation rate between exclusion and control sites using a one-way ANOVA with exclusion as a fixed factor and the number of carapaces plus stolen crabs as the response variable. Similarly, we compared the number of crabs exposed at low tide in exclusion and control sites using a one-way ANOVA with exclusion as a fixed factor and the numbers of crabs as the response variable, transformed log(crabs + 1) to meet the assumptions of ANOVA. To compare the changes in *C. borealis* and *Cancer irroratus* Say high-tide densities in the exclusion and control throughout the experiment, we used repeated-measures ANOVAs (SAS Institute 2004). Within-subject time and time × treatment effects were analyzed using univariate statistics after confirmation that the data met the assumption of sphericity. A one-way ANOVA was used to compare changes in *Carcinus* density over the course of the experiment between the control and exclusion treatments.

Effects of gull exclusion on lower trophic levels

We censused larger gastropods and the smaller invertebrate fauna in the lower *Chondrus* zone (~0 m) at the initiation and termination of the experiment. The two common snails (*L. littorea* and *N. lapillus*) were counted in 10 quadrats (50 × 60 cm) placed at randomly determined points along the 0-m contour at each site. Smaller invertebrates (e.g., mussels, sea urchins) found nestled among the algal thalli and holdfasts were

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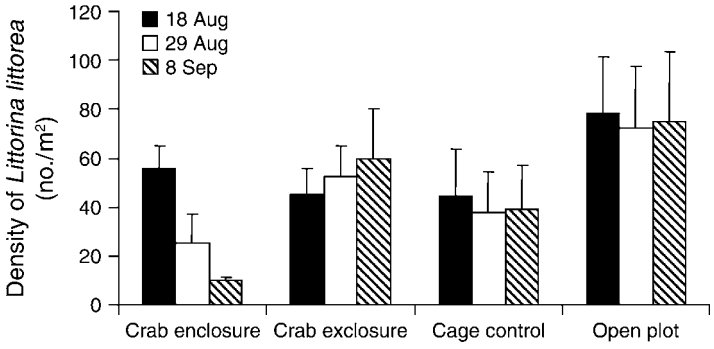

FIG. 1. Densities (mean + SE) of the herbivorous snail *Littorina littorea* in the crab inclusion/exclusion experiment that included four treatments: (1) crab inclusion (enclosure) cage with one *Cancer borealis*, (2) crab exclusion cage, (3) cage control (partial sides), and (4) experimental control (open plot). Cage controls were used to account for artifacts of drilling and attaching the cages and for potential alterations in snail behaviors and densities resulting from alteration in water flow or shading.

sampled by scraping algae and sediments from 10 20 × 20 cm quadrats. Every sample was placed in a 50% seawater solution that caused mobile invertebrates to abandon the algae; these animals and those still attached to the algae were separated, identified to species, and counted.

A possible approach to looking at the indirect effects of gull predation on *C. borealis* on lower trophic levels would be to use presence/absence of gulls as the independent variable in an ANOVA analysis. However, the gull exclusion experiment produced variable increases in the density of *C. borealis* (see *Results*), thus reducing statistical power. Additionally, we were interested in explicitly examining the effects of *C. borealis* on lower trophic levels. Therefore, to explicitly examine the effects of this crab predator on potential prey censused in quadrats and scrape samples, we examined the relationship between changes in the density of these prey species and the density of *C. borealis* across the six study sites. Data on density change for each species per site were log-transformed after first adding a constant that increased the minimum value to 1. The relationship of transformed changes in density of *Carcinus, L. littorea*, and *N. lapillus* to log-transformed *C. borealis* density were analyzed in linear regressions (SAS Institute 2004). Similar analyses were performed for other common invertebrates in the algal scrape samples. Residual plots of all these models were examined to ensure that assumptions of homogenous variances were met.

To further assess the relationship between *C. borealis* densities and predation risk for gastropods, we monitored mortality of 25 tethered medium-sized (15–20 mm in shell height) *L. littorea* in each of the study sites during the final 12 d of the experiment (see Appendix B for additional methods). The relationship between *C. borealis* densities and mortality of tethered snails across the six study sites was analyzed with a linear regression (SAS Institute 2004); examination of the residuals indicated the data met the assumptions of ANOVA.

To determine whether the trophic cascade affects benthic primary producers, we censused algae in the low *Chondrus* zone at the beginning and end of the gull exclusion experiment. Ten quadrats (50 × 60 cm) were censused at every site (see Appendix B). From these results, we calculated a mean percent cover for all algae species at each site. Algal genera were divided into "high preference" (*Porphyra, Spongomorpha, Ceramium, Cladophora*, *Ulva*), "medium preference" (*Dumontia, Rhizoclonium, Polysiphonia*), and "low preference" (e.g., *Codium*, *Ascophyllum*, *Chaetomorpha*, *Fucus*) based on Lubchenco's (1978) study on feeding preferences in *L. littorea*. All preferred algal genera are ephemeral and fast-growing and might be expected to respond quickly to changes in grazer density. We used linear regressions (SAS Institute 2004) to analyze the relationship between log-transformed mean *L. littorea* densities and changes in log-transformed percent cover of the summed high-preference and "high plus medium preference" algae.

RESULTS

Tidal migration by Cancer borealis

Cancer borealis density in the low intertidal zone nearly doubled during high tide (0.55 ± 0.05 crabs/m^2, mean ± SE) compared to low tide (0.21 ± 0.03 crabs/m^2; $P = 0.003$). Additionally, there was a trend toward higher crab densities at −1.0 m (0.50 ± 0.05 crabs/m^2) compared to 0.0 m (0.28 ± 0.04 crabs/m^2; $P = 0.067$).

Crab inclusion experiment: effects of C. borealis *on* L. littorea *in the low intertidal zone*

The general linear model repeated-measures analysis of snail densities in the crab inclusion experiment revealed a significant interaction between time and treatment ($F_{6,40} = 3.2$, $P = 0.012$; Fig. 1). We tested the within-subject (time) effect for each treatment separately and found that densities of *L. littorea* in the crab enclosures declined significantly over the three weeks of the experiment ($F_{2,10} = 12.9$, $P = 0.002$), whereas densities did not change significantly over time in the crab exclosures or controls (all $P > 0.15$). We found crushed *L. littorea* shells in all crab enclosures, providing evidence that the decrease was due at least in part to predation by *C. borealis*. Because there was no significant change in the other treatments or controls,

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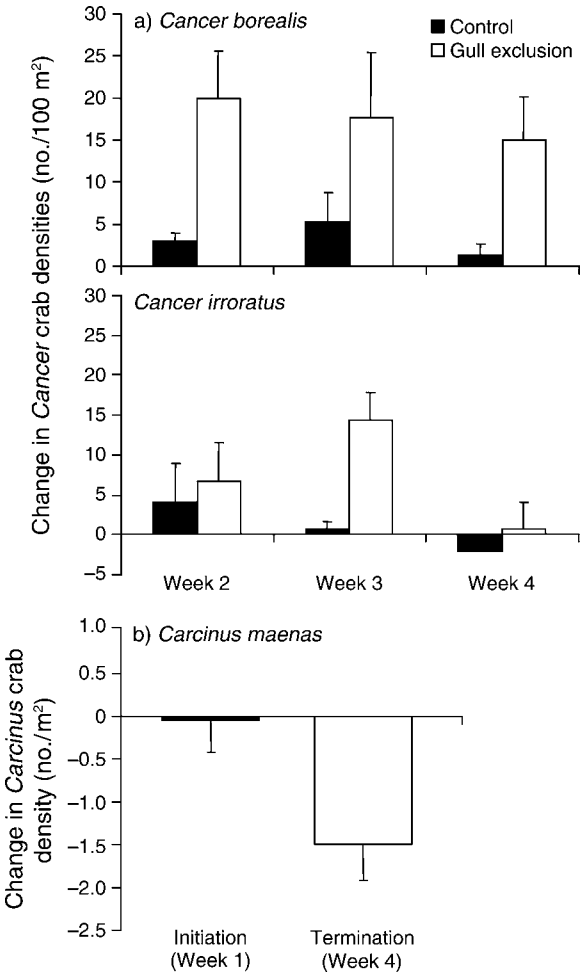

FIG. 2. Change in high-tide densities (mean and SE) of crabs in gull exclusion and control treatments (where predatory gulls had access) in the lower *Chondrus crispus* zone (mean lower low water). (a) Change in densities of *Cancer* crabs from the beginning of the experiment to weeks 2, 3, and 4. *Cancer* crabs were counted in a 2×50 m band transect five times at each site: just prior to initiation of gull exclusion, at weeks 2, 3, and 4 of exclusion, and one week after the conclusion of the experiment. (b) Change in density of *Carcinus maenas* crabs from the beginning to the end of the experiment. *Carcinus* were counted in 10 1-m^2 quadrats at each site at the initiation and termination of the experiment.

we inferred that crab predation had no detectable effect on snail densities in the presence of gull predation.

Large-scale gull exclusion experiment: effects on multiple components of intertidal food webs

Effects of gull exclusion on crabs.—The gull exclusion treatment produced a dramatic 80% reduction in predation rates on *C. borealis* (ANOVA, $F_{1,4} = 17.84$, $P = 0.013$). Control sites averaged 5.8 ± 0.8 carapaces/diurnal low tide (mean ± SE), whereas exclusion sites averaged 1.4 ± 0.6 carapaces and stolen crabs. At the exclusion sites, most of the predation (76–84%) occurred prior to the 2.5 h before low tide (when gulls were prohibited from foraging); these *C. borealis* were caught by gulls in the *Ascophyllum* (0.6–2.1 m above MLLW) or very high *Chondrus* zone (0.6 m to shallow subtidal zone). Predation rates on *Cancer irroratus* and *Carcinus* were 1–2 orders of magnitude lower than that seen for *C. borealis* and too low to test for a treatment effect.

At the initiation of the gull exclusion experiment, densities of the three species of crabs during high tide were 3.3 ± 1.4 crabs/100 m^2 (mean ± SE) for *C. borealis*, 6.0 ± 2.4 crabs/100 m^2 for *C. irroratus,* 1.8 ± 0.7 crabs/m^2 for *Carcinus*. Over the four weeks of the experiment, densities of *C. borealis* at high tide increased significantly in the exclusion areas relative to the control plots (repeated-measures ANOVA, $F_{1,4} = 17.5$, $P = 0.014$; Fig. 2). Densities of *C. irroratus* at high tide increased in the exclusion areas and decreased in the control plots during weeks 2 and 3, but densities decreased in all the plots during week 4 (time, $F_{2,3} = 26.8$, $P = 0.012$; time × treatment, $F_{2,3} = 9.8$, $P = 0.048$). Thus, there was no consistent effect of gull exclusion on densities of *C. irroratus* (treatment, $F_{1,4} = 2.5$, $P = 0.19$; Fig. 2). However, low replication and high variability within treatments means that the power to detect a treatment effect was low (power = 0.224). In marked contrast to the increases in *C. borealis* in the gull exclusion areas, densities of *Carcinus* during high tide showed a decreasing trend in the exclusion areas (ANOVA, $F_{1,4} = 6.5$, $P = 0.064$; Fig. 2).

During low tide, large numbers of *C. borealis* remained above the waterline in the *Chondrus* or *Ascophyllum* zones at the gull-exclusion sites. Mean numbers of *C. borealis* per low tide in the three exclusion sites were 14.3, 10, and 0.5, while all control sites had fewer than 0.5 (ANOVA, $F_{1,4} = 7.68$, $P = 0.0502$). *C. borealis* above the tide-line were generally found in mixed patches of *Ascophyllum nodosum*, *Fucus* spp., and *Chondrus crispus* or in shallow tidepools. Those crabs immersed in pools were often actively feeding; emergent crabs were generally facing down in the algae and not feeding. Of the 180 *C. borealis* observed above the tide-line, only nine died from exposure on a hot midday low tide. In contrast to *C. borealis*, very few *C. irroratus* were found in the intertidal zone during low tide in either the control or exclusion sites.

Following 26 days of gull exclusion, predation rates on *C. borealis* increased dramatically at two of the three exclusion sites on the first unguarded low tide, with 62 and 64 carapaces left in the intertidal zone, more than an order of magnitude greater than predation rates in the controls. Predation on *C. borealis* in the three diurnal tides following the termination of the experiment increased significantly in the exclusions relative to the controls (ANOVA, $F_{1,4} = 13.4$, $P = 0.022$).

Effects on lower trophic levels: intertidal invertebrates and algae.—Changes in density of potential *C. borealis* prey were negatively correlated with *C. borealis* abundance (Fig. 3). *C. borealis* density explained 79% and

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74%, respectively, of the variability in *Carcinus* and *Nucella lapillus* declines (*Carcinus*, $F_{1,4} = 14.9$, $P = 0.018$; *N. lapillus*, $F_{1,4} = 11.2$, $P = 0.029$). There was a negative relationship between *C. borealis* density and abundance of *L. littorea*; this trend approached but did not reach significance ($F_{1,4} = 5.6$, $P = 0.08$).

Five other taxa of invertebrates were common enough (>5 individuals/400 cm^2) to analyze: *Lacuna vincta* Montagu (small snail), juvenile *Modiolus modiolus* L. (horse mussel), *Mytilus edulis* (blue mussel), gammarid amphipods, and juvenile sea urchins (*Strongylocentrotus droebachiensis* O. F. Müller). Declines in *M. edulis* were strongly associated with *C. borealis* abundance ($F_{1,4} = 10.6$, $P = 0.031$, $R^2 = 0.73$; Fig. 3). Analyses for the other four taxa revealed no effect of *C. borealis* on changes in density.

Over the 12 days of the experiment, mortality of tethered *L. littorina* ranged from a low of 32% to a high of 100% and was positively associated with *C. borealis* density across sites; this relationship was close to, but did not reach statistical significance ($F_{1,4} = 6.4$, $P = 0.065$, $R^2 = 0.62$).

Changes in high preference and high plus medium preference algae over the 4 weeks of the experiment were not correlated with *L. littorea* density ($P = 0.84$, $P = 0.7$).

Discussion

Our studies showed that predation by gulls substantially affected species distributions and community structure in the rocky intertidal zone of New England. Foraging by gulls during low tides limited the intertidal abundance of the crab *Cancer borealis* as it migrated across the subtidal–intertidal ecotone. Higher intertidal densities of *C. borealis* were significantly correlated with reduced densities of two other important intertidal mesopredators (mid-trophic level predators), *Carcinus maenas* and *Nucella lapillus*, and the mussel *Mytilus edulis*, providing evidence for multiple cascading effects of gull predation. These effects were not detected in smaller-scale gull exclosures (J. C. Ellis, *unpublished data*); thus, it was only possible to demonstrate multiple direct and indirect effects by the use of a large-scale exclusion experiment. This finding underscores the importance of large-scale exclosures and suggests that such logistically intensive treatments may be essential to detect indirect effects in systems involving highly mobile predators and prey.

Though we found strong evidence for three-level trophic cascades precipitated by gulls, we were unable to demonstrate a four-level cascade from gulls down to intertidal primary producers. A dramatic decrease in *L. littorea* in crab enclosures, a negative (though not significant) relationship between change in *L. littorea* densities and *C. borealis* abundance, and a nearly significant positive relationship between mortality of tethered *L. littorea* and *C. borealis* density provide evidence for a three-level (gull–*C. borealis*–*L. littorea*) cascade. We did not find any effects of *L. littorea* on algal community structure, though these have been well-demonstrated in previous experimental studies. However, it is possible that the duration of the exclusion experiment was too short to detect indirect effects propagating all the way down to the producer level.

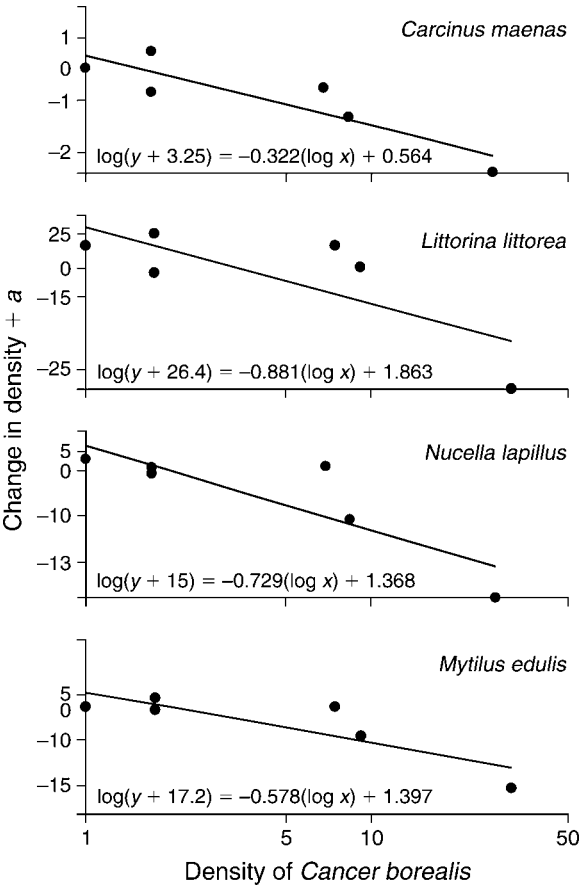

Fig. 3. Linear regressions of the change in density + *a* (plotted on a log scale) and density of *Cancer borealis* (plotted on a log scale) of: *Carcinus maenas* (green crab), *Littorina littorea* (herbivorous snail), *Nucella lapillus* (carnivorous snail), and *Mytilus edulis* (blue mussel) across the six sites. The constant, *a*, was added to density data to increase the minimum values to 1 prior to transformation.

Migration by Cancer borealis *from the subtidal into the intertidal zone*

Our censuses of crabs on low and high tides demonstrated that *C. borealis* migrates into the intertidal zone on diurnal high tides. Similarly, *Cancer productus*, the closest Pacific relative of *C. borealis* (Harrison and Crespi 1999), migrates shoreward during high tides to forage on intertidal animals (Robles et al. 1989), and may limit the lower distribution of the intertidal snail *Littorina sitkana* (Behrens-Yamada and Boulding 1996). *Cancer novaezelandiae* also migrates into the intertidal zone (Chatterton and Williams 1994). Both *C. productus* and *C. novaezelandiae* exhibit

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nocturnal activity patterns and primarily migrate into the intertidal zone during nighttime high tides. In notable contrast, *C. borealis* is much more active during the day and more abundant in the intertidal zone during diurnal high tides (Novak 2004).

Effects of gull predation on intertidal populations of crabs

When the tide recedes and the water is shallow enough for gulls to forage, they remove most of the *C. borealis* remaining in intertidal and shallow subtidal zones (Good 1992, Ellis et al. 2005). At the gull exclusion sites, densities of *C. borealis* increased sixfold during high tides and sevenfold during low tides. *C. borealis* above the tide-line were generally found in mixed patches of algae and in shallow tidepools. The crabs immersed in pools were often actively feeding on invertebrates throughout the low tide. Interestingly, of the 180 *C. borealis* observed above the tide-line, only a few died from exposure on a particularly hot midday low tide. Menge (1983) placed crabs in cages in the low-mid intertidal zone and monitored survival. These experiments showed that all *C. borealis* caged in the intertidal zone with an algal canopy survived, whereas, 18% of crabs without algal cover died. Our results, as well as those of Menge, suggest that if *C. borealis* has access to algal cover, crevices, or shallow pools of water it can survive in the intertidal zone during low tide. Thus, these findings strongly suggest that predation by gulls limits the upper distribution of *C. borealis* in the intertidal zone. However, the impact of gull predation on *C. borealis* is seasonal. *C. borealis* is most abundant in the intertidal zone during the warm summer and fall months (Krouse 1979, Stehlik et al. 1991, Leland 2002). During the winter, *C. borealis* migrates to deeper water in response to either water temperature (Jeffries 1966) or ambient light levels (Rebach 1987). Thus, the effects of gull predation on *C. borealis* are limited to summer and fall (June–September).

Effects of gull exclusion on densities of *C. irroratus* were inconclusive. Gulls eat *C. irroratus* (Ellis et al. 2005), but our results indicate that *C. irroratus* does not migrate into the intertidal zone to the same extent as *C. borealis* and thus it is probably less available to foraging gulls. Menge (1983) found that *C. irroratus* was the least tolerant of the three species of crabs to exposure during low tide; 30% of *C. irroratus* caged under algal canopy died, as did 25% caged without a canopy.

In marked contrast to the effect on *C. borealis*, exclusion of gulls from the intertidal zone resulted in a significant decrease in the intertidal density of *Carcinus maenas*. This result corroborates our previous findings that gulls eat *C. borealis* far more often, both in absolute numbers and proportionate to abundance, than *Carcinus* (Rome and Ellis 2004, Ellis et al. 2005).

Changes in densities of *Carcinus* were negatively correlated with densities of *C. borealis*. This finding suggests that there is a negative interaction (either predatory and/or competitive) between these two predator*s*. Gut content studies have shown that *C. borealis* feeds on crabs (Ojeda and Dearborn 1991). Changes in *Carcinus* shelter use and predation by *C. borealis* on *Carcinus* has been observed in sea table experiments simulating natural conditions (M. J. Shulman, *unpublished data*).

Effects of Cancer borealis *on intertidal mollusks*

Cancer borealis substantially reduced the abundance of *L. littorea* in cages in the low intertidal zone. In the presence of *C. borealis*, the snails either emigrated out of crab enclosures or were eaten by the crabs. Littorines are known to exhibit escape behavior in the presence of predators (e.g., Jacobsen and Stabell 1999, Rochette and Dill 2000); however, *C. borealis* predation was responsible for at least some losses as piles of crushed *L. littorea* shells were seen in all crab enclosures, and we observed crabs in cages eating snails. Results from this predator inclusion experiment suggested that if *C. borealis* were not removed by gulls during low tides, then crabs could have considerable effects on abundance of *L. littorea* in the low intertidal zone. Across the sites in the large-scale gull exclusion experiment, changes in *L. littorea* densities showed a nonsignificant inverse relationship with *C. borealis* densities ($P = 0.08$). Similarly, mortality of tethered *L. littorea* showed a near-significant positive relationship with densities of *C. borealis* ($P = 0.065$). Taken together, these results suggest *C. borealis* can reduce densities of *L. littorea* in the low intertidal zone; however, given the lack of statistical significance in the large-scale exclusion experiment, this hypothesis merits further investigation.

Lubchenco (1978, 1980) previously demonstrated that *L. littorea* controls the abundance of ephemeral, epiphytic algae in the mid-intertidal zone. In our experiment, we did not find a relationship between the density of *L. littorea* and changes in the abundance of preferred algae in the low intertidal zone. This negative result may be due to the much smaller differences among sites in *L. littorea* densities compared to the presence/absence treatments in Lubchenco's experiments.

Changes in the densities of the carnivorous gastropod *Nucella lapillus* were negatively correlated with *C. borealis* abundance. Laboratory experiments indicate that *C. borealis* readily feeds on *N. lapillus* and that the snails migrate away from areas where crabs are present (A. Nichols and M. J. Shulman, *unpublished data*). Abundance of the mussel *M. edulis* was also reduced significantly in the presence of higher densities of *C. borealis*. *C. borealis* is an important predator of *M. edulis* in the subtidal zone (Witman et al. 2003), and our findings indicate that in the absence of gulls, *C. borealis* is also an important predator of intertidal mussels.

Trophic Structure of the New England Rocky Intertidal Zone

Predation by gulls on *C. borealis* has far-reaching effects on intertidal and shallow subtidal food webs in

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New England (Fig. 4). Most previous studies have viewed *Carcinus* and *Nucella lapillus* as the dominant predators on wave-protected rocky intertidal shores in New England (e.g., Menge 1976, 1983, Trussell et al. 2002) with the abundance of *Carcinus* limited by gull predation (Lubchenco 1978). Our studies suggest instead that gulls are the apex predators whose foraging prevents the large, shell-breaking crab *C. borealis* from establishing substantial summer populations in the low-mid intertidal zone and that gulls indirectly enhance *Carcinus* densities.

Exclusion of *C. borealis* from the intertidal zone benefits two other mesopredators, *Carcinus* and *N. lapillus*, both of whom have diets that overlap with *C. borealis* and are potential prey of *C. borealis*. *Carcinus* is an important predator in the mid-intertidal (*Ascophyllum*/*Fucus*) zone, particularly along sheltered rocky shores where it is capable of reducing densities of *L. littorea*, *Mytilus edulis*, *Nucella lapillus*, and barnacles (*Semibalanus balanoides*) via predation and behavioral indirect interactions (Menge 1983, Leonard et al. 1998, Bertness et al. 2002, 2004, Trussell et al. 2002). *N. lapillus* is also an important predator along rocky open coasts in New England where it preys upon populations of barnacles and mussels (Menge 1976, Bertness et al. 2004). The removal of *C. borealis* from the intertidal zone by foraging gulls results in an increase in two important intertidal predators that feed on virtually all other intertidal invertebrates. The direct predatory effects of *C. borealis* on mussels (and other small invertebrate prey) may be dampened by positive indirect effects of *C. borealis* through decreases in *Carcinus* and *N. lapillus*.

Whether gull predation on *C. borealis* is an important structuring force in New England intertidal communities depends on abundances of both *C. borealis* and gulls. Densities of *Cancer* crabs (*C. borealis* and *C. irroratus*) in Maine have increased substantially during the past decade, and *C. borealis* is now considered by some to be the region's apex subtidal predator (Leland 2002, Steneck et al. 2004). Increases in *C. borealis* have probably led to its greater importance as a predator in rocky shallow subtidal and intertidal habitats (Leland 2002), and to greater reliance on this species by predatory gulls. Abundance of foraging gulls and their predatory impact is highly correlated with densities of *C. borealis* across the Gulf of Maine, at both breeding sites (offshore islands) and nonbreeding mainland sites (J. C. Ellis, *unpublished data*). Thus the impact of gulls is not a function of localized abundance but of regional population size.

Gulls were far less abundant during the 1800s due to intense hunting pressure throughout the North Atlantic (Lloyd et al. 1991). After legal protection in the early 1900s, gull populations increased dramatically due in part to food subsidies from humans. A letter written from the Isles of Shoals in the mid-1800s, when gulls were virtually absent from the archipelago, indicated

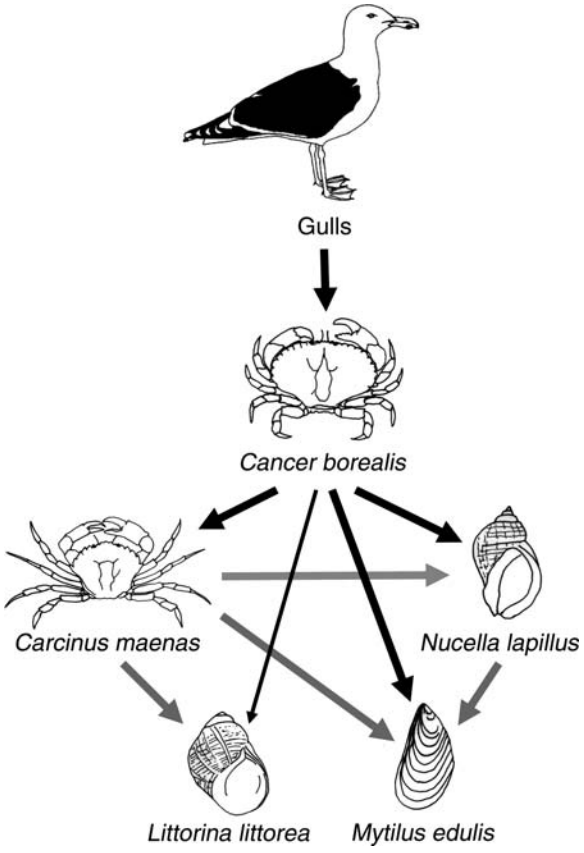

FIG. 4. Food web for moderately exposed rocky shores in the Gulf of Maine. The thick black lines represent strong interactions that were detected in our experiments, the thin black line represents an interaction that may be strong but had high variability in our experiments, and the thick gray lines represent strong interactions that were not directly measured in this study but have been demonstrated in previous studies. Predation by gulls (Herring and Great Black-backed Gulls) prevents *C. borealis*, an important generalist predator, from establishing substantial summer populations in the low-mid intertidal zone. Removal of *C. borealis* from the intertidal zone by gulls results in increased abundance of two important intertidal predators (*Carcinus maenas* and *Nucella lapillus*), the blue mussel (*Mytilus edulis*), and possibly the dominant intertidal herbivore, (*Littorina littorea*). As a consequence, gull predation indirectly benefits these intertidal invertebrates. However, the indirect benefits of gull predation on *C. borealis* for *L. littorea* and *M. edulis* may be partially offset by increased predation from greater numbers of *C. maenas* and *N. lapillus* (Menge 1976, 1983, Leonard et al. 1998, Bertness et al. 2002, 2004, Trussell et al. 2002).

that crabs occurred in such high abundance that feral cats survived on a diet composed entirely of crabs and wild birds (Laighton 1847). It is highly likely that the crabs were *Cancer* species because *Carcinus*, introduced from Europe, did not reach the northern tip of Cape Cod until the late 1800s (Audet et al. 2003). These anecdotal observations suggest that *Cancer* crabs may have been more abundant in the intertidal zone when gull numbers were low. Populations of *L. argentatus* reached a peak in the 1970s and 1980s and have since

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been declining, but *L. marinus* continue to slowly increase (Pierotti and Good 1994, Good 1998). Our results suggest that both historical and future changes in gull populations have important consequences for rocky intertidal communities.

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Literature Cited

Anderson, W. B., and G. A. Polis. 1999. Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. Oecologia 118:324–332.

Audet, D., D. S. Davis, G. Myron, M. Moriyasu, K. Benhalima, and R. Campbell. 2003. Geographical expansion of a non-indigenous crab, *Carcinus maenas* (L.), along the Nova Scotian shore into the southeastern Gulf of St. Lawrence, Canada. Journal of Shellfish Research 22:255–262.

Behrens-Yamada, S. B., and E. G. Boulding. 1996. The role of highly mobile crabpredators in the intertidal zonation of their gastropod prey. Journal of Experimental Marine Biology and Ecology 204:59–83.

Bertness, M. D. 1984. Habitat and community modification by an introduced herbivorous snail. Ecology 65:370–381.

Bertness, M. D., G. C. Trussell, P. J. Ewanchuk, and B. R. Silliman. 2002. Do alternate stable community states exist in the Gulf of Maine rocky intertidal zone? Ecology 83: 3434–3448.

Bertness, M. D., G. C. Trussell, P. J. Ewanchuk, B. R. Silliman, and C. M. Crain. 2004. Consumer-controlled community states on Gulf of Maine rocky shores. Ecology 85:1321–1331.

Carlson, R. L., M. J. Shulman, and J. C. Ellis. 2006. Factors contributing to spatial heterogeneity in the abundance of the common periwinkle *Littorina littorea* (L.) Journal of Molluscan Studies 72:149–156.

Carlton, J. T., and J. Hodder. 2003. Maritime mammals: terrestrial mammals as consumers in marine intertidal communities. Marine Ecology Progress Series 256:271–286.

Chatterton, T. D., and B. G. Williams. 1994. Activity patterns of the New Zealand cancrid crab *Cancer novaezelandiae* (Jacquinot) in the field and laboratory. Journal of Experimental Marine Biology and Ecology 178:261–274.

Dumas, J. V., and J. D. Witman. 1993. Predation by herring gulls (*Larus argentatus* Coues) on two rocky intertidal crab species [*Carcinus maenas* (L.) and *Cancer irroratus* Say]. Journal of Experimental Marine Biology and Ecology 169: 89–101.

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.

Englund, G. 1997. Importance of spatial scale and prey movements in predator caging experiments. Ecology 78: 2316–2325.

Good, T. P. 1992. Experimental assessment of gull predation on the Jonah crab *Cancer borealis* (Stimson) in New England rocky intertidal and shallow subtidal zones. Journal of Experimental Marine Biology and Ecology 157:275–284.

Good, T. P. 1998. Great Black-backed Gull (*Larus marinus*). Number 330 *in* A. Poole and F. Gill, editors. The birds of North America. American Ornithologists' Union and Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.

Harrison, M. K., and B. J. Crespi. 1999. Phylogenetics of *Cancer* crabs (Crustacean: Decapoda: Brachyura). Molecular Phylogenetics and Evolution 12:186–199.

Hockey, P. A. R., and G. M. Branch. 1984. Oystercatchers and limpets: impact and implications. a preliminary assessment. Ardea 72:199–206.

Hori, M., and T. Noda. 2001. Spatio-temporal variation of avian foraging in the rocky intertidal food web. Journal of Animal Ecology 70:122–137.

Hunter, R. D., and W. D. Russell-Hunter. 1983. Bioenergetic and community changes in intertidal aufwuchs grazed by *Littorina littorea*. Ecology 64:761–769.

Jacobsen, H. P., and O. B. Stabell. 1999. Predator-induced alarm responses in the common periwinkle *Littorina littorea*: dependence on season, light conditions, and chemical labeling of predators. Marine Biology 134:551–557.

Jeffries, H. P. 1966. Partitioning of the estuarine environment by two species of *Cancer*. Ecology 47:477–481.

Krouse, J. S. 1979. Distribution and catch composition of Jonah crab, *Cancer borealis*, and rock crab, *Cancer irroratus*, near Boothbay Harbor, Maine. Fishery Bulletin 77:685–693.

Laighton, C. 1847. Letter from Hog Island (Appledore), Isles of Shoals. New Hampshire Historical Society, Portsmouth, New Hampshire, USA. ⟨http://seacoastnh.com/Famous_People/Celia_Laighton_Thaxter/Earliest_Letter_by_Celia_Thaxter/⟩

Leland, A. V. 2002. A new apex predator in the Gulf of Maine? Large, mobile crabs (*Cancer borealis*) control benthic community structure. Thesis. University of Maine, Orono, Maine, USA.

Leonard, G. H., J. M. Levine, P. R. Schmidt, and M. D. Bertness. 1998. Flow-driven variation in intertidal community structure in a Maine estuary. Ecology 79:1395–1411.

Lindberg, D. R., J. A. Estes, and K. I. Warheit. 1998. Human influence on trophic cascades along rocky shores. Ecological Applications 8:880–890.

Lloyd, C., M. L. Tasker, and K. Partridge. 1991. The status of seabirds in Britain and Ireland. Poyser, London, UK.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preferences and algal competitive abilities. American Naturalist 112:23–39.

Lubchenco, J. 1980. Algal zonation in the New England rocky intertidal community: experimental analysis. Ecology 61: 333–344.

Lubchenco, J. 1983. *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity, and plant escapes during succession. Ecology 64:1116–1123.

MacKay, D. C. G. 1943. Temperature and world distribution of the genus *Cancer*. Ecology 24:113–115.

Menge, B. A. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. Ecological Monographs 46: 355–393.

Menge, B. A. 1983. Components of predation intensity in the low zone of the New England rocky intertidal region. Oecologia 58:141–155.

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 influence in rocky subtidal communities of the Gulf of

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Maine. Journal of Experimental Marine Biology and Ecology 149:13–44.
Pierotti, R., and T. P. Good. 1994. Herring Gull (*Larus argentatus*). Number 124 *in* A. Poole and F. Gill, editors. The birds of North America. American Ornithologists' Union and Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.
Rebach, S. 1987. Entrainment of seasonal and nonseasonal rhythms by the rock crabs *Cancer irroratus*. Journal of Crustacean Biology 7:581–594.
Reid, D. G. 1996. Systematics and evolution of *Littorina*. Rey Society, London, UK.
Robles, C., D. A. Sweetnam, and D. Dittman. 1989. Diel variation of intertidal foraging by *Cancer productus* L. in British Columbia. Journal of Natural History 23:1041–1049.
Rochette, R., and L. M. Dill. 2000. Mortality, behavior and the effects of predators on the intertidal distribution of littorinid gastropods. Journal of Experimental Marine Biology and Ecology 253:165–191.
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.
Sanchez-Piñero, F., and G. A. Polis. 2000. Bottom-up dynamics of allochthonous input: direct and indirect effects of seabirds on islands. Ecology 81:3117–3132.
Schauffler, R. P. 1998. An estimate of the number of breeding herring and great black-backed gulls on the coast of Maine and a comparison of methods used to count them. Thesis. University of Massachusetts, Amherst, Massachusetts, USA.
Siddon, C. E. 2004. Trait- and density-mediated indirect interactions in the New England rocky subtidal zone. Dissertation. Brown University, Providence, Rhode Island, USA.
Siddon, C. E., and J. D. Witman. 2004. Behavioral indirect interactions: multiple predator effects and prey switching in the rocky subtidal. Ecology 85:2938–2954.
SPSS. 2004. SPSS version 13. SPSS, Chicago, Illinois, USA.
Stehlik, L. L. 1993. Diets of the Brachyuran crabs *Cancer irroratus, C. borealis,* and *Ovalipes ocellatus* in the New York Bight. Journal of Crustacean Biology 13:723–735.
Stehlik, L. L., C. L. MacKenzie, Jr., and W. W. Morse. 1991. Distribution and abundance of four brachyuran crabs on the northwest Atlantic shelf. Fishery Bulletin 89:473–492.
Steneck, R. S., J. Vavrinec, and A. V. Leland. 2004. Accelerating trophic-level dysfunction in kelp forest ecosystems of the western North Atlantic. Ecosystems 7:323–332.
Trussell, G. C., P. J. Ewanchuk, and M. D. Bertness. 2002. Field evidence of trait mediated indirect interactions in a rocky intertidal food web. Ecology Letters 5:241–245.
Trussell, G. C., P. J. Ewanchuk, and M. D. Bertness. 2003. Trait-mediated effects in rocky intertidal food chains: predator risk cues alter prey feeding rates. Ecology 84:629–640.
Vanni, M. J., D. L. DeAngelis, D. E. Schindler, and G. R. Huxel. 2004. Overview: cross-habitat flux of nutrients and detritus. Pages 1–11 *in* G. A. Polis, M. E. Power, and G. R. Huxel, editors. Food webs at the landscape level. University of Chicago Press, Chicago, Illinois, USA.
Williams, A. B. 1965. Marine decapod crustaceans of the Carolinas. Fishery Bulletin 65:1–298.
Witman, J. D. 1985. Refuges, biological disturbance, and rocky subtidal community structure in New England. Ecological Monographs 55:421–445.
Witman, J. D., S. J. Genovese, J. F. Bruno, J. W. McLaughlin, and B. I. Pavlin. 2003. Massive prey recruitment and the control of rocky subtidal communities on large spatial scales. Ecological Monographs 73:441–462.
Wootton, J. T. 1992. Indirect effects, prey susceptibility, and habitat selection: impact of birds on limpets and algae. Ecology 73:981–991.
Wootton, J. T. 1995. Effects of birds on sea urchins and algae: a lower-intertidal trophic cascade. Ecoscience 2:321–328.
Wootton, J. T. 1997. Estimates and tests of per capita interaction strength: diet, abundance, and impact of intertidally foraging birds. Ecological Monographs 67:45–64.

APPENDIX A

Estimates of tidal migration by *Cancer borealis*: description of all main and interaction effects entered into the GLIMMIX model (*Ecological Archives* E088-053-A1).

APPENDIX B

Large-scale gull exclusion experiment: additional methods regarding (a) tethering *L. littorea* including potential tether failure and tethering artifacts; and (b) algal sampling (*Ecological Archives* E088-053-A2).

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