ELSEVIER

Journal of Experimental Marine Biology and Ecology 324 (2005) 31–43

Journal of
EXPERIMENTAL
MARINE BIOLOGY
AND ECOLOGY

www.elsevier.com/locate/jembe

Predation by gulls on crabs in rocky intertidal and shallow subtidal zones of the Gulf of Maine

Julie C. Ellis[a,*], Walter Chen[b], Brendan O'Keefe[a], Myra J. Shulman[b], Jon D. Witman[a]

[a] *Department of Ecology and Evolutionary Biology, Brown University, Providence, RI 02912, USA*
[b] *Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY 14853, USA*

Received 12 May 2004; received in revised form 14 October 2004; accepted 4 April 2005

Abstract

Most organisms in intertidal areas are marine in origin; many have distributions that extend into the subtidal zone. Terrestrial predators such as mammals and birds may exploit these animals during low tide and can have considerable effects on intertidal food webs. Several studies have shown that avian predators are capable of reducing densities of sessile and slow-moving intertidal invertebrates but very few studies have considered avian predation on mobile invertebrate predators such as crabs. In this study, we investigated predation by Great Black-backed Gulls (*Larus marinus* Linnaeus) on three species of crabs (*Cancer borealis* Stimpson, *Cancer irroratus* Say, and *Carcinus maenas* Linnaeus). The study was at Appledore Island, ME (a gull breeding island) and 8 other sites throughout the Gulf of Maine, including breeding islands and mainland sites. On Appledore Island, intertidal and subtidal zones provided over one-third of prey remains found at gull nests, and crabs were a substantial proportion (~30% to 40%) of the total remains. Similarly, collections of prey remains from intertidal areas indicated that crabs were by far the most common marine prey. *C. borealis* was eaten far more often and *C. irroratus* and *C. maenas* less often than expected at each site. Comparing numbers of carapaces to densities of crabs in low intertidal and shallow subtidal zones at each site, we estimated that gulls remove between 15% and 64% of *C. borealis* during diurnal low tides. The proportion of *C. borealis* eaten by gulls was independent of proximity to a gull colony. Approximately 97% of the outer coast of Maine is within 20 km of a breeding island. Thus, a lot of gull predation on crabs may occur throughout the Gulf of Maine during summer months. Crabs are important predators of other invertebrates; if predation by gulls reduces the number of crabs in intertidal and shallow subtidal areas, gulls may have important indirect effects on intertidal food webs.

Keywords: Avian predation; Behavioral observations; *Cancer borealis*; *Larus marinus*; New England; Rocky intertidal zones

---

1. Introduction

Nearly all organisms in intertidal areas are marine in origin; many of them also live subtidally. Terrestrial predators may exploit intertidal species during low

---

[*] Corresponding author. Present address: Shoals Marine Laboratory, Cornell University, G-14 Stimson Hall, Ithaca, NY 14853, USA. Tel.: +1 401 863 9683; fax: +1 401 863 2166.
E-mail address: jce4@cornell.edu (J.C. Ellis).

0022-0981/$ - see front matter © 2005 Elsevier B.V. All rights reserved.
doi:10.1016/j.jembe.2005.04.001

tide and can substantially affect intertidal food webs. Such opportunistic foragers include birds (e.g., gulls, shorebirds; Wootton, 1997; Hori and Noda, 2001) and mammals (e.g., raccoons, minks, bears; Carlton and Hodder, 2003). These vertebrates have fast metabolic rates, and their ability to exploit prey over large areas may be greater than that of slower-moving invertebrate predators (Feare and Summers, 1986; Marsh, 1986a; Wootton, 1997). Terrestrial vertebrate predators are generally limited to foraging in areas exposed during low tide or in very shallow water. Therefore, they have the potential to set the upper limit of vertical distributions of their prey (Edwards et al., 1982; Good, 1992a).

Avian predators, in particular, are prominent foragers in intertidal communities throughout the world (e.g., Feare and Summers, 1986; Hori and Noda, 2001). Several studies have provided evidence that birds are capable of reducing the abundance of rocky intertidal grazers (limpets: Frank, 1982; Hockey and Branch, 1984; Branch, 1985; Mercurio et al., 1985; Marsh, 1986b; Hahn and Denny, 1989; Wootton, 1992; sea urchins: Schneider, 1985; Dumas, 1996) and dominant space-occupiers such as mussels (Marsh, 1986a; Hamilton, 2000) and barnacles (Meese, 1993). In contrast, very few studies have focused on the impact of avian predation on invertebrate predators such as crabs. Understanding the effects of predation on these invertebrates is especially important because it may have significant consequences for lower trophic levels (e.g., Micheli, 1997).

Rocky intertidal habitats in New England have served as a model system for studies of several biotic interactions including competition, herbivory, and predation (e.g., Menge, 1976; Lubchenco, 1978; Lubchenco and Menge, 1978). The vast majority of these studies focused on interactions among invertebrates. The few studies on vertebrates suggest that avian predators, particularly gulls, may play an important role in this system (Good, 1992b; Dumas and Witman, 1993). During the past century, numbers of Great Black-backed Gulls (*Larus marinus* Linnaeus) and Herring Gulls (*L. argentatus* Pontopiddan) have increased dramatically in New England and throughout the North Atlantic (e.g., Lloyd et al., 1991). Both species consume intertidal mussels, crabs, lobsters, and sea urchins (Good, 1992b, 1998; Dumas and Witman, 1993; Pierotti and Good, 1994; Rome and Ellis, 2004), while Herring Gulls also eat sea stars (Dumas, 1996). Pressure on marine invertebrate prey may increase as gull populations expand.

Our initial observations indicated that crabs, especially *Cancer borealis*, are important components of the diet of gulls. *C. borealis* consume a wide variety of prey including other crabs, polychaetes, sea urchins, mussels, and gastropods (Ojeda and Dearborn, 1991; Stehlik, 1993; Siddon and Witman, 2004). *C. borealis* is a subtidal crab, but may forage in intertidal zones during high tide. *Cancer productus*, the closest Pacific relative of *C. borealis* (Harrison and Crespi, 1999), eats intertidal animals including mussels and barnacles (Robles et al., 1989), and may limit the lower distribution of the intertidal snail *Littorina sitkana* Phillipi (Yamada and Boulding, 1996). Understanding the factors that limit the abundance of *Cancer* crabs in rocky intertidal areas of New England is important. As highly mobile, large invertebrates, crabs would have strong ecological effects on intertidal prey (Menge, 1983).

In this study, we investigate predator–prey interactions between gulls and crabs in the Gulf of Maine. Of the two species of gulls, *L. marinus* appeared to be the more important predator of crabs (J.C. Ellis, personal observation; Good, 1992a). Thus, we focused on predation by Great Black-backed Gulls on three common species of crabs: *C. borealis*, *Cancer irroratus*, and *Carcinus maenas*. The main goals of the study were to determine the proportion of the crab population eaten by gulls and identify factors that modify rates of predation by gulls. Specifically, we addressed the following questions: (1) What are the rates of predation on crabs, and how do these rates vary among crab species and across tidal heights? (2) What is the impact of predation on densities of crabs in intertidal and shallow subtidal zones? (3) Are rates and impacts of predation dependent on proximity to a gull colony?

2. Materials and methods

2.1. Study sites and species

In 2000 and 2002, we conducted studies of gull diet and predation at the Shoals Marine Laboratory, Appledore Island, in the Gulf of Maine (42° 58′N; 70° 37′W; Fig. 1). Appledore Island, one of a nine-island

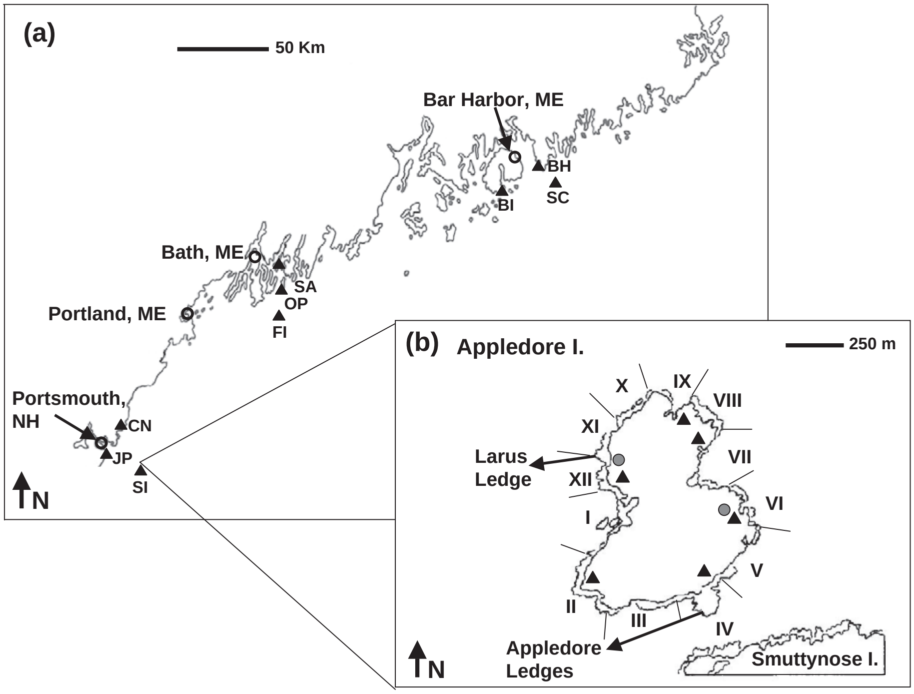

Fig. 1. (a) Map of the Gulf of Maine showing the 9 sites sampled in 2003. Three sites in each of 3 areas (southwest, central, northeast) were designated as either: an island hosting a gull breeding colony; a mainland site near (<20 km) a gull colony, or a mainland site far (>20 km) from a gull colony. The site names and designations are the following. Breeding islands: Smuttynose I. (SI), Fisherman I. (FI), Schoodic I. (SC); "Near" sites: Jaffery Point (JP), Ocean Point (OP), Blueberry Hill (BH); "Far" sites: Cape Neddick (CN), Sawyer I. (SA), Bear I. (BI). (b) Detailed studies of foraging were conducted on Appledore Island, Maine (42° 58′N–70° 37′W) located approximately 10 km from Portsmouth, New Hampshire. Each of 12 geographic regions on the island is marked with a Roman numeral. Appledore Ledges and Larus Ledge were used for behavioral observations and the tethering experiment. The locations of *L. marinus* subcolonies, where diet data were collected, are marked according to the year they were sampled: circles = 2000; triangles = 2002.

archipelago, is located ~10 km from the coast of New Hampshire, USA. The east side of the island is exposed to heavy wave action from the Atlantic Ocean, whereas the western side is relatively protected. The island interior is covered with woody and herbaceous vegetation; exposed rocky headlands and boulder coves occur along the shoreline.

To determine whether our findings from Appledore Island, the location of a large gull colony, were representative of other gull colonies and mainland sites in the Gulf of Maine, we surveyed 9 additional sites in 2003 (Fig. 1). We included 3 sites in each of 3 areas of the Gulf of Maine: the southwest, central, and northeast. The 3 areas are fairly evenly spread out over the Gulf of Maine, and were chosen to indicate whether our results from Appledore Island were representative of the region. Each site within an area was designated as either: (1) a gull colony, (2) a mainland site near a gull colony (within 20 km), or (3) a mainland or island site far (>20 km) from a gull colony. We selected sites with large, gently sloping areas of ledge or boulders, and moderate levels of wave exposure. All three species of crabs are found in similar habitats in the Isles of Shoals. One site (Sawyer Island; far from a gull colony) in the central area was later deemed unsuitable because neither gulls nor *Cancer* crabs occurred there, possibly because it had a mud bottom instead of rock. Due to logistical limitations, we were unable to sample a replacement site. Thus, Sawyer Island was excluded from our analyses leaving 3 gull colonies, 3 mainland sites near a colony, and 2 sites far from a colony.

Herring Gulls and Great Black-backed Gulls occur on offshore islands throughout the Gulf of Maine from approximately March through September. Both species forage in mainland landfills, open ocean, and intertidal and shallow subtidal zones. Gulls capture prey in open ocean and 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; J.C. Ellis, personal observation).

The rocky intertidal and shallow subtidal areas 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), the *Ascophyllum* zone (0.6–2.1 m), and the *Chondrus* zone (0.6 m to shallow subtidal). Gulls also feed in the "nearshore" zone, which is the shallow subtidal zone adjacent to the shore.

2.2. Diet of *L. marinus*

We assessed diet by collecting prey remains from around nests and from intertidal foraging areas. Previous studies indicate that prey remains accurately reflect dietary composition (Spaans, 1971; Annett and Pierotti, 1987; Pierotti and Annett, 1990). Remains were collected in multiple years in order to evaluate the generality of our results from the first year. In 2000, regurgitated pellets and whole remains were collected from 12–15 haphazardly selected nests in each of two *L. marinus* subcolonies on Appledore Island in July and August. In 2002, we increased the replication by collecting remains from around 10–12 nests selected in each of six subcolonies in July and August (Fig. 1). Prey were sorted and categorized as fish, terrestrial vertebrates, crabs, other intertidal invertebrates, or garbage. Prey were also collected from Appledore Island in 2001 and the results were published in Rome and Ellis (2004).

L. marinus leave prey remains in situ when they forage in intertidal areas. We collected remains from intertidal areas 0.5 h after low tide, after peak foraging, and before the rising tide removed remains from the shore. We could attribute remains to a single low tide because either we collected them or they were flushed away during high tide. Most of the remains were carapaces and chelipeds of the crabs *C. borealis*, *C. irroratus*, and *C. maenas*. Carapaces from crabs eaten by gulls are easily distinguished from molts because they lack an abdomen, have small remnants of flesh inside, and are often found next to detached claws and legs. Carapaces were identified to species and their widths measured to the nearest 0.1 mm. Other intertidal prey remains included sea urchin tests (*Strongylocentrotus droebachiensis* Müller), blue mussels (*Mytilus edulis* Linnaeus), and lobster (*Homarus americanus* Herrick) carapaces.

In 2000, we collected intertidal prey remains at Larus Ledge and Appledore Ledges, sites on Appledore Island where densities of foraging gulls are relatively high (J.C. Ellis, personal observation). In order to assess the generality of our results from these two sites, we collected prey remains from all regions of the shoreline of Appledore Island on 17 July 2001 (except Region IX; Fig. 1) and 11 August 2002. We further extended our sampling in 2003 by including 8 additional sites in the Gulf of Maine (Section 2.1, Fig. 1). Remains were collected during two separate diurnal low tides at each of the 8 sites; two collections enabled us to more confidently estimate predation rates. We used a χ^2 test for independence between samples to determine whether the relative abundance of crab species represented in carapace remains differed between Larus Ledge and Appledore Ledges, and between years along the shoreline of Appledore Island. We calculated the average proportion (over the two sampling dates) of each crab species in remains found at each of the 8 sites in 2003. These proportions were arcsin ($\sqrt{x+1.1}$) transformed then used in a two-way ANOVA to test for effects of proximity and crab species on relative abundance of carapaces. Carapaces collected from Appledore Island and the 8 additional sites were also used to estimate rates of predation by gulls on crabs (see Section 2.6).

2.3. Foraging behavior by gulls in intertidal and shallow subtidal zones

We assessed temporal and spatial patterns of gull foraging by conducting several behavioral studies. Foraging was observed at Larus Ledge and Appledore Ledges from June through August 2000. At Larus Ledge, we watched gulls from a vantage point on Appledore Island. Observations of gulls at Appledore Ledges were conducted from nearby Smuttynose Island (Fig. 1) because boulders and rocky terrain obscured the view from Appledore. Gulls were easily seen from the vantage point on Smuttynose Island, which was approximately 170 m from Appledore Ledges. We used binoculars and a spotting scope to facilitate observations at both sites. Instantaneous scan sampling (Altmann, 1974) was conducted every 15 min from 4 h before until 15 min after low tide and the numbers of individuals foraging were recorded. This pilot study indicated that further detailed observations should be made during peak foraging, ~1 h before to 0.5 h after low tide (see Section 3.2).

More detailed studies were done over 9 days at Appledore Ledges and 5 at Larus Ledge; due to logistical constraints, we were unable to complete 9 samples at Larus Ledge, but subsequent studies indicate that our results from this site are representative (Rome and Ellis, 2004, J.C. Ellis, unpublished data). At each site, instantaneous scan samples were taken every 30 min and focal animal samples every 10–15 min. Focal animal samples (Altmann, 1974) were observations of a single foraging bird for up to 10 min or until foraging definitively ceased. We conducted 88 focal samples at Appledore Ledges and 41 at Larus Ledge. We attempted to avoid observing the same individual more than once during a single low tide, but there were likely exceptions because individual birds were not marked. Observations were made over multiple days thereby increasing the chance of sampling multiple individuals. The following data were recorded during instantaneous scans: intertidal and shallow subtidal zone(s) in which gulls foraged (see description of zones in Section 2.1) and the number of gulls foraging per scan. During focal observations, we recorded prey types and the amount of time spent consuming each individual prey. We used data from scan samples to assess the distribution of foraging gulls. Focal observations and scan samples were used in calculations of the rates of predation (see Section 2.6).

Data on densities of foraging gulls were transformed (log $x+1.1$), which corrected heterogeneous variances, and used in a two-way ANOVA to test for effects of site and zone on density.

2.4. Depth distribution of predation by gulls

We used a tethering experiment to test whether the rate of predation by gulls varies with depth (relative to MLLW). We specifically designed our experiment to measure relative predation risk at different depths and ensured that tethered crabs had equal access to shelter sites at each depth. Tethering experiments can artificially elevate predation rates by eliminating prey escape or defense responses (e.g., Zimmer-Faust et al., 1994). However, tethered and untethered *C. borealis* remain stationary and draw in their chelipeds in response to predators (J.C. Ellis, unpublished data).

Crab tethers were constructed using a small plastic (cable tie) loop that was fastened to the posterior portion of the carapace with marine epoxy (A-788 Splash Zone Compound, Kop Coat). The epoxy was painted with pink nail polish to match carapace color. We attached a 20 cm length of fine wire to the plastic loop; the other end of the wire was tied to a metal eye-bolt. Eye bolts were placed at least 1 m apart, and fastened into cracks with marine epoxy. The wire gave tethered crabs some ability to move and hide.

C. borealis (~60–116 mm carapace width) were collected from another site on Appledore Island. Each crab was randomly assigned to one of three depths: 1.0 m, 0.0 m, and −1.0 m (relative to MLLW). At each depth, crabs were assigned to caged or uncaged treatments. Cages were used to control for mortality due to desiccation and loss due to tether failure. Cages (measuring 46 cm × 30 cm × 15 cm) were built from hardware cloth (0.4 cm^2 mesh), and attached to the substrate with wire connected to an eye-bolt anchored to the rock. One crab was tethered in each cage.

Each trial of the experiment was conducted during a single low tide cycle. We tethered crabs during evening low tides and protected them from foraging gulls until the rising tide had covered the crabs by at least 1 m of water. Approximately 30 min after the next diurnal low tide, we classified each tethered crab as either attacked (flesh damaged or consumed) or not attacked. This experiment was replicated on three different dates (3, 14, 20 August 2000) with low tides of −0.40 m, 0.34 m, 0.09 m, respectively. In each trial, sample sizes for uncaged crabs ranged from 8–13 per depth treatment. Control (caged) crabs were deployed in the first two trials with 2–3 replicates per depth.

To determine whether attack rates on tethered crabs differed among depths, we performed a contingency table analysis. Data were blocked by trial date, and therefore a Cochran–Mantel–Haenszel test (JMP version 5.0) was used in a contingency table analysis to determine whether there was an association between attack rate and depth.

2.5. Densities of crabs

We estimated crab densities in order to assess: (1) whether rates of predation by gulls varied with respect to species of crab, and (2) the proportion of the intertidal and shallow subtidal crab population eaten by gulls. In 2000, we estimated densities of crabs at Appledore Ledges and Larus Ledge. At each site, we snorkeled 1 h prior to low tide and counted crabs in 5 to 6 belt transects (5 m long × 1 m wide) placed parallel to the shoreline at a depth of -1.0 m. We identified, counted, and measured the carapace width (± 0.1 mm) of all crabs (*C. borealis*, *C. irroratus*, and *C. maenas*) occurring in each transect. *C. borealis* is slow-moving and relatively easy to count and measure while snorkeling. *C. irroratus* and *Carcinus* move more quickly and when necessary, we collected them immediately, placed them temporarily in a mesh bag, and then quickly measured each individual. All crabs were replaced after measurement.

In 2003, we estimated crab densities at 8 additional sites in the Gulf of Maine (Fig. 1) to determine whether results from Appledore Island were representative of the region. Densities were estimated by snorkeling ~3.5 h prior to low tide and counting crabs in 1 m^2 quadrats ($n=15$ per site) placed parallel to the shoreline at 0.0 m (MLLW). We identified, counted, and measured the carapace width (± 0.1 mm) of all crabs in each quadrat. Crabs were counted at 0.0 m because the tethering experiment and behavioral observations at Appledore Island indicated that this is a depth at which gulls are likely to capture crabs during most low tides. Gulls begin foraging around 2.5 h prior to low tide. We counted crabs ~3.5 h prior to low tide so we could observe foraging during low tide without disturbing the birds. Carapaces were collected (see Section 2.2) on 2 days, one when crabs were counted and the other when they were not. Numbers of carapaces were similar between days, indicating that predation by gulls was not affected by counting crabs.

Data from 2000 were log $(x+1.1)$ transformed to correct for heterogeneous variances, and then used in a two-way ANOVA to test for effects of site and species on crab density. Density data from transects were also used to generate expected frequencies of predation on each species of crab. We used a χ^2 goodness-of-fit test to compare these values to numbers of intertidal carapaces (i.e., observed frequencies).

Density data from 2003 were averaged across the 15 quadrats (1 m^2) conducted at each site, yielding a single value for each site. Data were log $(x+1.1)$ transformed to correct for heterogeneous variances, and used in a two-way ANOVA to test for effects of proximity and species on crab density. Density data from 2003 were also used to generate expected frequencies of predation on each crab species, which were then compared to intertidal carapace collections using a χ^2 goodness-of-fit test.

2.6. Rates of predation by gulls on crabs

We used two independent methods to estimate rates of gull predation on crabs. The first estimate used the number of carapaces of each crab species collected from the intertidal at the end of a low tide (see Section 2.2). By dividing the total number of carapaces by the length (km) of shoreline over which carapaces were collected, we calculated the number of crabs eaten per km of shoreline per diurnal low tide. This estimate of predation is slightly conservative because not all carapaces are left in intertidal foraging areas by the gulls. We used this method to estimate predation rates at Larus Ledge and Appledore Ledges in 2000 and at the 8 other study sites in 2003.

The second estimate of predation rate was calculated using focal animal and instantaneous scan sample data collected in 2000. From scan samples, we calculated the average number of foraging Great Black-backed Gulls over the 90 min period of peak foraging (60 min before to 30 min after low tide). By multiplying the average number of gulls feeding by 90 min, and dividing by the length of shoreline included in the scan samples, we obtained an estimate of the gull feeding-minutes per km per diurnal low tide. From the data on focal animals, we estimated the proportion of total foraging time that was spent feeding on crabs. This proportion was used to determine the gull crab-feeding-minutes per km per diurnal low tide. Focal animal data were used to calculate an average consumption time (min) per crab. The gull crab-feeding-minutes per km per diurnal low tide was divided by consumption time per crab to determine the number of crabs consumed by Great Black-backed Gulls per km per diurnal low tide.

A Mann–Whitney nonparametric test was used to determine whether the number of carapaces per km shoreline (i.e., predation rate) differed between Larus Ledge and Appledore Ledges in 2000. In order to compare rates of predation on Appledore Island between 2001 and 2002, we calculated the number of carapaces per km shoreline occurring in each region (Fig. 1) in both years. These data were then log $(x+1)$ transformed and used in a one-way ANOVA to test for differences between years. Carapace data from 2003 were averaged across the two sampling dates for each site (see Section 2.2), transformed $[\sqrt{(x+1.1)}]$ and used in a two-way ANOVA in order to determine whether the rate of predation by gulls varied with respect to proximity to a gull colony or crab species.

2.7. Impact of predation on abundance of crabs

We calculated population impact (*sensu* Wootton, 1997), the percentage of the accessible crab population eaten by gulls per diurnal low tide. Our observations and previous studies (Good, 1998) indicated that gulls can only forage in the top 1 m of water. Thus, we used the crab density data (see Section 2.5) as an estimate of the “gull-available” crabs per km of shoreline. Population impact was calculated as the predation rate (based on behavioral and/or carapace abundance data) per diurnal low tide per km divided by crabs per km of shoreline. We calculated impact at Appledore Ledges and Larus Ledge using the two estimates of predation rate. Impact was estimated for the 8 sites sampled in 2003 by using the average number of carapaces collected over the two sampling dates (see Section 2.2), and then dividing by the number of crabs per km of shoreline. The resultant proportions were $[\arcsin(\sqrt{x})]+0.5$ transformed and used in a two-way ANOVA to determine whether impact varied with respect to proximity to a gull colony and/or crab species.

3. Results

3.1. Diet of L. marinus

Prey remains collected from around *L. marinus* nests (Fig. 1b) included: garbage (especially chicken), fish (probably bait from lobster boats; Goodale, 2000), terrestrial vertebrates [including muskrats (*Ondatra zibethica*), unidentified rodents, and juvenile Herring Gulls], and intertidal and shallow subtidal prey [mussels (*M. edulis*), sea urchins (*S. droebachiensis*), lobsters (*H. americanus*), and crabs (*C. borealis*, *C. irroratus*, *C. maenas*)]. In 2000, garbage was the most abundant category, comprising nearly 40% of the prey items (Fig. 2). Marine sources (intertidal and subtidal zones) provided over one-third of prey found at nests; a substantial proportion (~30%) consisted of crabs. Similarly, in 2002, crabs and garbage were the most abundant categories, but crabs comprised a larger proportion of the total (~40%).

Prey remains collected from intertidal areas also indicated that crabs were an important part of the diet of *L. marinus*. In 2000, crabs comprised 100% ($n=24$) of remains collected at Larus Ledge and 91% ($n=435$) at Appledore Ledges; the remainder was sea urchins and lobsters. The overwhelming majority (85–96%) of all carapaces were from *C. borealis*. *C. maenas* carapaces were found at Appledore Ledges, but were absent from Larus Ledge. The relative abundance of crab species in carapace collections did not differ significantly between the two sites ($\chi_2^2=2.71$, $p=0.258$). In 2001, carapaces were found in all of regions that were sampled on Appledore Island; in 2002, carapaces were found in all but one region (Fig. 1; Region III). The vast majority of carapaces found in 2001 (98%; $n=182$) and 2002 (93%; $n=165$) were from *C. borealis*. The relative abundance of crab species in carapace collections was the same between years ($\chi_2^2=5.07$, $p=0.08$).

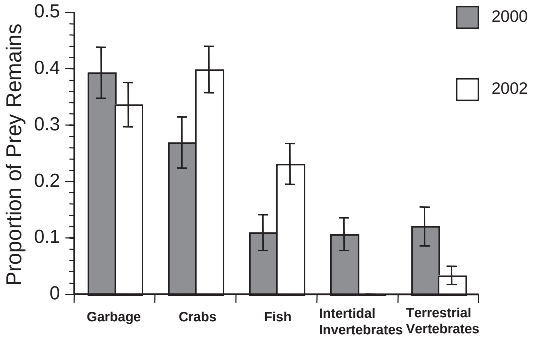

Fig. 2. Prey remains (pellets and uningested parts) collected from 4 *L. marinus* subcolonies on Appledore Island, ME in July and August 2000 and 2002. Error bars represent ± 1 S.E. $n=54$ nests in 2000 and $n=72$ nests in 2002.

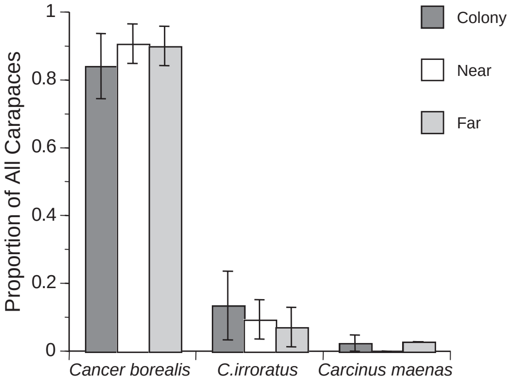

Fig. 3. Proportion (mean ± 1 S.E.) of three crab species in carapace collections from 3 types of intertidal sites: on an island hosting a gull breeding colony ($n=3$); on the mainland near (<20 km) a gull colony ($n=3$), or on the mainland or an island far (>20 km) from a gull colony ($n=2$).

Collections of prey remains from intertidal areas at the 8 additional sites in 2003 were very similar to those collected at Appledore Island. Crabs were by far the most common prey item; only 2 green sea urchins (*S. droebachiensis*) and 2 blue mussels (*M. edulis*) were found in all prey collections (2 collections per site; 139 total prey remains). *C. borealis* was the most abundant crab species found in remains at every site, ranging from 84–91% of all carapaces (Fig. 3). There was a significant effect of crab species on carapace abundance (two-way ANOVA: $F_{2,15}=59.1, p<0.0001$), but no significant proximity ($F_{2,15}=0.03$, $p=0.97$) or proximity × species effect ($F_{4,15}=0.20$, $p=0.93$). There were significantly more *C. borealis* carapaces than *C. irroratus* and *C. maenas* at all 8 sites (Tukey–Kramer HSD, $p<0.05$).

3.2. Foraging behavior of gulls in intertidal and shallow subtidal zones

In 2000, scan sampling of gulls over 4 h prior to and 15 min after low tide showed that foraging began about 135 min before low tide, increased dramatically through low tide, and declined quickly thereafter. In 2003, we observed foraging for a longer period of time after low tide (105 min) and found similar results. Foraging peaked around low tide and declined until it reached consistently low levels (1 individual foraging per scan sample) approximately 60 min after low tide.

Further scan sampling in 2000 at Appledore Ledges ($n=8$ low tides) and Larus Ledge ($n=5$) during the period 60 min before to 30 min after low tide showed that mean densities of foraging gulls were 11.6 (± 1.7 S.E.) km^{-1} and 11.0 (± 2.2 S.E.) km^{-1}, respectively. There was a significant intertidal zone effect on densities of foraging gulls (two-way ANOVA: $F_{3,44}=20.6$, $p<0.0001$), but no significant site ($F_{1,44}=0.71$, $p=0.40$) or site × zone interaction ($F_{3,44}=1.62$, $p=0.20$). Densities were significantly higher in the *Chondrus* and *Ascophyllum* zones compared to nearshore and barnacle zones (Tukey HSD post hoc test: $p<0.05$; Fig. 4).

Focal animal samples showed that gulls generally consumed crabs in intertidal zones (i.e., *Ascophyllum*, *Chondrus* zones), but caught them in shallow subtidal areas (i.e., nearshore zone). Thus, scan samples indicated where gulls were located while consuming prey, but did not necessarily represent the locations where prey were originally captured.

Data from 129 focal animal observations (41 at Larus Ledge, 88 at Appledore Ledges) showed that 32.1% and 28.9% of gull foraging time was spent consuming crabs at each site, respectively, with a mean consumption time of 3.5 (± 0.5 S.E.) min per crab.

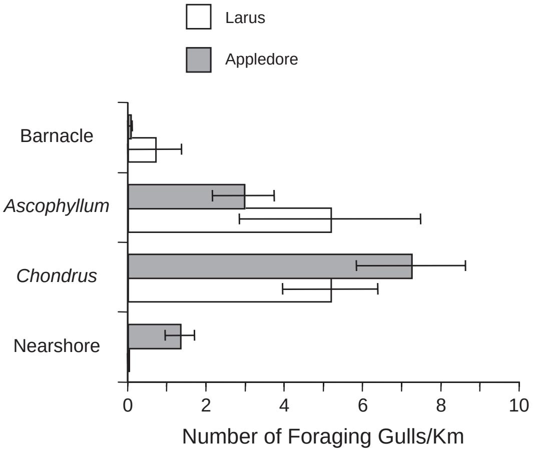

Fig. 4. Mean (± 1 S.E.) number of foraging *L. marinus* (km^{-1}) at two sites in three intertidal zones (barnacle, *Ascophyllum*, *Chondrus*) and nearshore. Instantaneous scan samples were conducted every 30 min from 1 h before to 0.5 h after a single low tide. $n=8$ sampling dates at Appledore Ledges and $n=5$ at Larus Ledge.

3.3. Depth distribution of predation by gulls

In the tethering experiment, all but one of the caged crabs was found alive and attached to tethers at the end of the experiment. The single exception occurred when a cage was dislodged by waves and no longer covered the tethered crab. Predation on tethered crabs varied significantly across depths (Cochran–Mantel–Haenszel test: $\chi_2^2=57.1$, $p<0.0001$). In all three trials of the experiment, 100% of crabs were attacked at 1.0 m (*Ascophyllum* zone) and 0.0 m (*Chondrus* zone), whereas 20–40% were attacked at −1.0 m (shallow subtidal zone).

3.4. Densities of crabs

Crab densities at 1 m below MLLW in 2000 were 8× higher at Appledore Ledges than Larus Ledge; the two sites also differed in relative abundance of the 3 crab species (Fig. 5). The two-way ANOVA showed significant site ($F_{1,27}=28.93$, $p<0.0001$), species ($F_{2,27}=4.17$, $p=0.026$), and site × species interaction effects ($F_{2,27}=10.86$, $p=0.0003$) on densities. The site × species interaction indicated that the relative abundances of crab species did not differ significantly at Larus Ledge, whereas at Appledore Ledges densities of *C. maenas* were significantly greater than those of *C. borealis* and *C. irroratus* (Tukey–Kramer HSD: $p<0.05$).

Crab density data were also used to generate expected proportions of each crab species in intertidal carapace collections. A χ^2 goodness-of-fit test showed that the carapace species proportions differed from those found in shallow subtidal populations, with *C. borealis* preyed upon far more often and *C. maenas* less often than expected at both sites (Appledore Ledges: $\chi_2^2=2632.6$, $p<0.0001$; Larus Ledge: $\chi_2^2=11.43$, $p=0.003$).

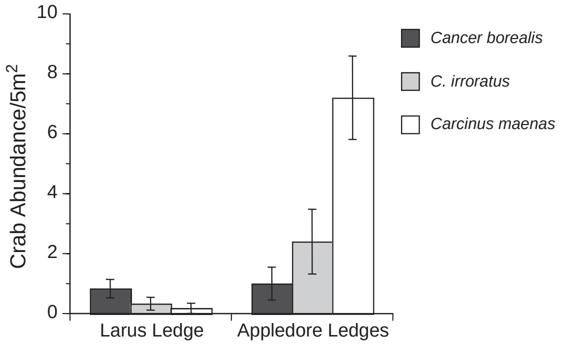

Fig. 5. Mean (± 1 S.E.) abundances of the 3crab species at −1.0 m (relative to MLLW) within 5 m^2 belt transects. Error bars represent ± 1 S.E. $n=5$ transects at Appledore Ledges $n=6$ at Larus Ledge.

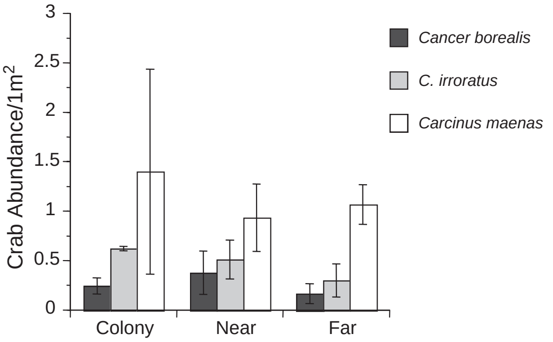

Fig. 6. Mean (± 1 S.E.) abundances of the 3 crab species at 0.0 m (relative to MLLW) within 1 m^2 quadrats from 3 types of intertidal sites: on an island hosting a gull breeding colony ($n=3$); on the mainland near (<20 km) a gull colony ($n=3$), or on the mainland or an island far (>20 km) from a gull colony ($n=2$). Fifteen quadrats were sampled at each of the 8 sites.

In 2003, average density of all species of crabs in quadrats (at 0.0 m) ranged from 0.87–4.5 m^{-2} among the 8 sites. Densities were similar among sites regardless of proximity to a gull colony (Fig. 6). There was a significant species effect on densities (two-way ANOVA: $F_{2,15}=4.24$, $p=0.035$), but no effect of proximity ($F_{2,15}=0.15$, $p=0.86$) and no species × proximity effect ($F_{4,15}=0.17$, $p=0.95$). Densities of *C. maenas* were significantly greater than those of *C. borealis*, but did not differ significantly from *C. irroratus* (Tukey–Kramer HSD, $p<0.05$).

Densities of crabs in quadrats were also used to generate expected proportions of each species in carapace collections (all sites combined). A χ^2 goodness-of-fit test showed a similar pattern to that found on Appledore Island: *C. borealis* was preyed upon far more often and *C. maenas* and *C. irroratus* less often than expected ($\chi_2^2=1759.4$, $p<0.0001$).

3.5. Rates of predation by gulls on crabs

In 2000, the average number of crab carapaces per km of shoreline per diurnal tidal cycle (i.e., predation rate) was 58.9 ± 9.2 (± 1 S.E., $n=10$ tidal cycles) at Appledore Ledges and 60.1 ± 13.0 ($n=3$ tidal cycles) at Larus Ledge. Rates of predation on crabs (all species combined) did not differ significantly between Appledore Ledges and Larus Ledge (Mann–Whitney test, $p = 0.866$).

Among regions on Appledore Island, predation rates ranged from 6.8 to 97.5 per km in 2001 and from 0 to 64.1 per km in 2002. The average (± 1 S.E.) rate of predation per km in 2001 was 35.3 ± 8.9, while in 2002 the average for the entire island was 26.6 ± 5.3 per km. Predation rates did not differ significantly between the 2 years (one-way ANOVA, $F_{1,21} = 0.53$, $p = 0.47$).

The average (± 1 S.E.) predation rate in 2003 was 87.6 ± 31.5 at the three breeding islands, 108.0 ± 49.2 at the 3 mainland sites <20 km from a breeding island, and 67.5 ± 53.2 at the two sites >20 km from a breeding island. The rate of predation did not vary significantly with distance from a colony (two-way ANOVA: $F_{2,15} = 0.21$, $p = 0.81$), nor was there a significant proximity × crab species interaction ($F_{4,15} = 0.34$, $p = 0.85$). However, rates of predation varied significantly with respect to crab species ($F_{2,15} = 9.30$, $p = 0.002$); predation on *C. borealis* was significantly greater than on *C. irroratus* and *C. maenas* (Tukey–Kramer HSD, $p < 0.05$).

3.6. Impact of predation on abundance of crabs

The rate of predation on *C. borealis* (as determined through behavioral observations in 2000) during a single diurnal tidal cycle was 83 crabs removed per km of shoreline at Larus Ledge and 73 at Appledore Ledges. Comparing these numbers with densities of crabs in −1.0 transects, we estimated that gulls eat 50% and 36% of *C. borealis* in shallow subtidal areas at Larus Ledge and Appledore Ledges, respectively. Estimates of predation impact from intertidal carapace collections in 2000 were 35% at Larus Ledge and 25% at Appledore Ledges.

Similar calculations for the 8 additional sites in the Gulf of Maine indicated that gulls ate 15.3–64.4% of *C. borealis*, 0–12.9% of *C. irroratus*, and 0–0.8% of *C. maenas* occurring in the low intertidal zone (around 0.0 m) at each site (Fig. 7). Gulls removed a mean of 30.6% ± 5.56 S.E. of *C. borealis* occurring in the low intertidal zone across the 8 sites. Proximity to a gull colony did not affect population impact (two-way ANOVA: $F_{2,15} = 0.13$, $p = 0.88$). There was no significant proximity × crab species interaction ($F_{4,15} = 0.11$, $p = 0.98$), but population impact was dependent on crab species ($F_{2,15} = 28.6$, $p < 0.0001$). Impact was significantly greater on *C. borealis* than on *C. irroratus* and *C. maenas* (Tukey–Kramer HSD, $p < 0.05$).

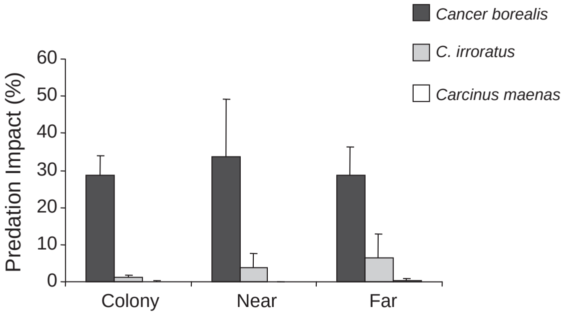

Fig. 7. Impact of gull predation on intertidal/shallow-subtidal populations of 3 crab species from 3 types of intertidal sites: on an island hosting a gull breeding colony ($n = 3$); on the mainland near (<20 km) a gull colony ($n = 3$), or on the mainland or an island far (>20 km) from a gull colony ($n = 2$). Impact was calculated by dividing the mean number of crab remains (carapaces) per linear distance of shore by the mean density of crabs found in 1 m^2 quadrats at 0 m (relative to MLLW). Results are expressed as mean (± 1 S.E.) percentages of crabs consumed per diurnal low tide.

4. Discussion

Our results from multiple years and sites throughout the Gulf of Maine indicate that crabs are a significant component of Great Black-backed Gull diet. Rates of predation on crabs varied among sites, but were quite high at some. Crabs comprised a large portion of the diet of gulls on Appledore Island in both 2000 and 2002. Similarly, in a related study conducted on Appledore in 2001, crabs comprised between ~20% and ~50% of prey remains collected from June through September (Rome and Ellis, 2004). Collections of intertidal prey remains further demonstrated that crabs, especially *C. borealis*, were a significant component of gull diet at all sites.

When extrapolated over a breeding season, predation on *C. borealis* in intertidal and shallow subtidal areas is considerable. Based on carapace collections from the entire coast of Appledore Island in 2001 and 2002, gulls can remove an average of 165.5 crabs per diurnal spring tide (low tide height of 0.0 m or less).

In 2001 and 2002, there were approximately 36–37 diurnal spring tides from June through August (Harbor Master 5.2.0). Thus, gulls potentially removed 5958–6123.5 *C. borealis* during the summer season each year. If gulls removed only half the number of crabs (165.5/2 = 82.7) during daylight low tides greater than 0.0 m in height, an additional 6203–6533 *C. borealis* were eaten. In total, an estimated 12,161 *C. borealis* were removed during 2001 and 12,656 in 2002 during the period of maximal gull foraging on crabs. These estimates are conservative because gulls begin foraging on crabs in late May and continue through September (J.C. Ellis, personal observation; Rome and Ellis, 2004). Carapace collections from other colonies and mainland sites indicated that predation rates occurring on Appledore Island, a gull colony, are similar to those found at a variety of locations throughout the Gulf of Maine.

Several lines of evidence demonstrate that gull predation reduces densities of *C. borealis* in intertidal and shallow subtidal areas during low tide. Estimates from behavioral observations on Appledore Island indicated that 36% to 50% of available *C. borealis* were removed on each diurnal low tide cycle; calculations from carapace collections yielded more conservative estimates of 25% to 35%. Similarly, in the crab tethering experiment, 20–40% of *C. borealis* at −1.0 m were attacked by gulls; all crabs tethered at 1.0 m and 0.0 m were attacked. Finally, gulls consumed an average of 31% of the *C. borealis* available at eight additional sites throughout the Gulf of Maine. These estimates are remarkably similar and suggest that the impact of predation on *C. borealis* on Appledore is representative of many areas in the Gulf of Maine where gulls and *C. borealis* co-occur.

The total number of gulls in intertidal areas during low tide can be much greater on breeding islands than mainland sites. However, the majority of these individuals are often resting or preening rather than foraging (O'Keefe and Ellis, unpublished data; see also Wootton, 1997). Therefore, high densities of gulls do not necessarily predict high predation rates. Behavioral observations at the 8 sites sampled in 2003 indicated that a small number of individuals were capable of removing numerous crabs during a single low tide. In fact, predation rates at the 3 sites within 20 km of a breeding island were as high as, or higher than, those occurring on the 3 breeding islands. There are over 320 islands in the Gulf of Maine on which gulls breed (R. Houston, unpublished data) and approximately 97% of the outer coast of Maine (~1854 km in total length) is within 20 km of a breeding island (O'Keefe and Ellis, unpublished data). Given that gulls can forage at least 40 km from a colony (Kubetzki and Garthe, 2003), rates of predation on crabs may be significant throughout much of coastal Gulf of Maine during the summer.

High removal rates of shallow-subtidal/intertidal *C. borealis* by gulls can only be maintained through immigration from a large subtidal population. One possibility is that, like its Pacific relative *C. productus*, *C. borealis* migrates into the intertidal during nocturnal high tides (Robles et al., 1989). However, previous work in the Isles of Shoals showed that active *C. borealis* were 20× more abundant during the day than at night, possibly due to avoidance of predation by nocturnal lobsters (*H. americanus*; Novak, 2004). Thus, *C. borealis* probably move into intertidal/shallow-subtidal areas on crepuscular or diurnal high-tides, with at least some remaining there during the following low tide.

The impact of gull predation on crabs is limited to the area of overlap between gull foraging habitat and crab habitat. The vast majority of *C. borealis* and *C. irroratus* occur deeper than the foraging depth of gulls (e.g., Rathbun, 1930; MacKay, 1943; Williams, 1965; Witman et al., 2003; Siddon and Witman, 2004). In the Isles of Shoals, Novak (2004) found that at depths of −9.0 to −11.0 m, population densities of *C. borealis* were at least 2× the densities in the shallow subtidal (−1.0 to −3.0 m). Despite the fact that gulls can consume over 60% of the standing crop of shallow subtidal (0 m to −1.0 m) *C. borealis* per diurnal low tide, this probably represents only a tiny fraction of the entire subtidal population. Predation may be very important in limiting the abundance and distribution of *C. borealis* in intertidal and shallow-subtidal habitats, but have little effect on overall population size.

Surprisingly, predation rates on the two other common species of crabs, *C. irroratus* and *C. maenas*, are much lower than predicted by their relative abundances in the field. It is particularly striking that *C. maenas*, which has its major population densities within the range of gulls, is rarely eaten by Great Black-backed Gulls. Hypotheses explaining this phenomenon are currently under investigation, and include differential: (1) crypticity; (2) chemical or structural defenses; (3) behavioral defenses; (4) microhabitat use; and/or (5) profitability. Dumas and Witman (1993) studied Herring Gulls feeding in mid-intertidal pools and found that *C. maenas* was eaten less often than *C. irroratus*. The pink carapace of *C. irroratus* may have been more conspicuous than the dark-colored carapace of *C. maenas* against the dark background of the intertidal mussel bed.

Our study indicated that foraging peaks around low tide, and that crabs are most vulnerable to predation by gulls during this period. Behavioral observations conducted during a single low tide indicated that foraging begins at least 2.5 h prior to low tide, and can continue up to approximately 1.5–2.0 h afterward. This period also corresponded to initial emergence and final submergence of the *Chondrus* zone. Thus, gulls appear to capture crabs primarily while the *Chondrus* zone (0.6 m to shallow subtidal) is exposed. Depending on the height of the low tide, crabs may be vulnerable to predation for as much as 4–5 h/day during diurnal low tides. Gull predation appears to reduce the abundance of crabs in intertidal and shallow subtidal zones, either via escape response and emigration of crabs or through direct mortality. Thus, gulls may indirectly affect prey of crabs including other crabs, polychaetes, sea urchins, mussels, and gastropods (Ojeda and Dearborn, 1991; Stehlik, 1993; Siddon and Witman, 2004).

Our results indicate that gulls are important predators of crabs in rocky intertidal and shallow subtidal habitats in the Gulf of Maine. Gulls have the potential to limit the abundance of crabs in rocky intertidal zones. Several studies have shown that birds are capable of reducing densities of rocky intertidal grazers and dominant space-occupiers. However, ours is one of very few studies to demonstrate impacts of avian predators on densities of mobile invertebrate predators. Invertebrate predators, in turn, have the potential to strongly impact a variety of invertebrate prey. Thus, predation by gulls should be included in models of New England rocky intertidal food webs.

Acknowledgements

The authors are indebted to the staff of Shoals Marine Laboratory for logistical and moral support during this project. We also thank K. Sargianis, M. Novak, P. Wallem, and several REU's for field assistance and B. Tuttle for use of his boat. This work was funded in part by a grant from Project A.W.A.R.E. Foundation (PADI), the Patty McGill Fellowship (Shoals Marine Laboratory, Cornell University and University of New Hampshire), and a Doctoral Dissertation Improvement Award (National Science Foundation DEB-0206609) to J.C. Ellis. The National Science Foundation's Research Experience for Undergraduates Program at the Shoals Marine Laboratory provided support for W. Chen and B. O'Keefe. The Royce Fellowship at Brown University provided additional funding for B. O'Keefe. This paper is contribution number 120 to the Shoals Marine Laboratory. **[AU]**

References

Altmann, J., 1974. Observational study of behavior: sampling methods. Behaviour 49, 227–265.

Annett, C.A., Pierotti, R., 1987. Chick hatching as a trigger for dietary switching in the western gull. Colon. Waterbirds 12, 4–11.

Branch, G.M., 1985. The impact of predation by kelp gulls *Larus dominicanus* on the sub Antarctic limpet *Nacella delesserti*. Polar Biol. 4, 171–177.

Carlton, J.T., Hodder, J., 2003. Maritime mammals: terrestrial mammals as consumers in marine intertidal communities. Mar. Ecol. Prog. Ser. 256, 271–286.

Dumas, J.V., 1996. Factors affecting the abundance and distribution of the green sea urchin (*Strongylocentrotus droebachiensis*) in rocky intertidal pools in New England. Unpublished PhD thesis, Drexel University.

Dumas, J.V., Witman, J.D., 1993. Predation by Herring Gulls (*Larus argentatus* Coues) on two rocky intertidal crab species [*Carcinus maenas* (L.) and *Cancer irroratus* Say]. J. Exp. Mar. Biol. Ecol. 169, 89–101.

Edwards, D.C., Conover, D.O., Sutter, F., 1982. Mobile predators and the structure of marine intertidal communities. Ecology 63, 1175–1180.

Feare, C.J., Summers, R.W., 1986. Birds as predators on rocky shores. In: Moore, P.G., Seed, R. (Eds.), The Ecology of Rocky Coasts. Columbia University Press, New York, pp. 249–264.

Frank, P.W., 1982. Effects of winter feeding on limpets by Black Oystercatchers, *Haematopus bachmani*. Ecology 63, 1352–1362.

Good, T.P., 1992a. Experimental assessment of gull predation on the Jonah crab *Cancer borealis* (Stimpson) in New England rocky intertidal and shallow subtidal zones. J. Exp. Mar. Biol. Ecol. 157, 275–284.

Good, T.P., 1992b. Herring Gulls *Larus argentatus* and Great Black-backed Gulls *Larus marinus* as rocky shore predators:

patterns and implications for intertidal communities. Master's thesis, University of New Hampshire.

Good, T.P., 1998. Great black-backed gull (*Larus marinus*). In: Poole, A., Gill, F. (Eds.), The Birds of North America, No. 330. The Birds of North America, Inc., Philadelphia, PA.

Goodale, M.W., 2000. Herring Gulls' use of lobsterbait during the breeding season in Penobscot Bay, Maine. Unpublished Masters thesis, College of the Atlantic, Bar Harbor, Maine.

Hahn, T., Denny, M., 1989. Tenacity-mediated selective predation by oystercatchers on intertidal limpets and its role in maintaining habitat partitioning by *Collisella scabra* and *Lottia digitalis*. Mar. Ecol. Prog. Ser. 53, 1–10.

Hamilton, D.J., 2000. Direct and indirect effects of predation caused by common eiders and abiotic disturbance in an intertidal community. Ecol. Monogr. 70, 21–43.

Harrison, M.K., Crespi, B.J., 1999. A phylogenetic test of the ecomorphological adaptation of *cancer* crabs. Evolution 53, 961–965.

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

Hori, M., Noda, T., 2001. Spatio-temporal variation of avian foraging in the rocky intertidal food web. J. Anim. Ecol. 70, 122–137.

Kubetzki, U., Garthe, S., 2003. Distribution, diet and habitat selection by four sympatrically breeding gull species in the south-eastern North Sea. Mar. Biol. 143, 199–207.

Lloyd, C., Tasker, M.L., Partridge, K., 1991. The Status of Seabirds in Britain and Ireland. Poyser, London.

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

Lubchenco, J., Menge, B.A., 1978. Community development and persistence in a low rocky intertidal zone. Ecol. Monogr. 48, 67–94.

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

Marsh, C.R., 1986a. Rocky intertidal community organization: the impact of avian predators on mussel recruitment. Ecology 67, 771–784.

Marsh, C.R., 1986b. Impact of avian predators on high intertidal limpet populations. J. Exp. Mar. Biol. Ecol. 104, 185–201.

Meese, R.J., 1993. Effects of predation by birds on gooseneck barnacle *Pollicipes polymerus* Sowerby distribution and abundance. J. Exp. Mar. Biol. Ecol. 166, 47–64.

Menge, B.A., 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. Ecol. Monogr. 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.

Mercurio, K.S., Palmer, A.R., Lowell, R.B., 1985. Predator-mediated microhabitat partitioning by two species of visually cryptic, intertidal limpets. Ecology 66, 1417–1425.

Micheli, F., 1997. Effects of predator foraging behavior on patterns of prey mortality in marine soft bottoms. Ecol. Monogr. 67, 203–224.

Novak, M., 2004. Diurnal activity in a group of Gulf of Maine decapods. Crustaceana 77, 603–620.

Ojeda, F.P., Dearborn, J.H., 1991. Diversity, abundance, and spatial distribution of fishes and crustaceans in the rocky subtidal zone of the Gulf of Maine. Fish. Bull. 88, 403–410.

Pierotti, R., Annett, C.A., 1990. Diet and reproductive output in seabirds. Bioscience 40, 568–574.

Pierotti, R., Good, T.P., 1994. Herring Gull (*Larus argentatus*). In: Poole, A., Gill, F. (Eds.), The Birds of North America, No. 124. The Birds of North America, Inc., Philadelphia, PA.

Rathbun, M.J., 1930. The cancroid crabs of America and of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae, and Xanthidae. Bull.-U.S. Natl. Mus., 152.

Robles, C., Sweetham, D., Dittman, D., 1989. Diel variation of intertidal foraging by *Cancer productus* in British Columbia. J. Nat. Hist. 23, 1041–1049.

Rome, M.S., Ellis, J.C., 2004. Foraging ecology and interactions between Herring Gulls (*Larus argentatus*) and Great Black-backed Gulls (*L. marinus*) in New England. Waterbirds 27, 200–210.

Schneider, D.C., 1985. Predation rate on the urchin *Echinometra lucunter* (Linnaeus) by migratory shorebirds on a tropical reef flat. J. Exp. Mar. Biol. Ecol. 92, 19–27.

Siddon, C., Witman, J.D., 2004. Behavioral indirect interactions: multiple predator effects and prey switching in the rocky subtidal. Ecology 85, 2938–2945.

Spaans, A.L., 1971. On the feeding ecology of the herring gull *Larus argentatus* Pont. in the northern part of the Netherlands. Ardea 59, 73–188.

Stehlik, L.L., 1993. Diets of the brachyuran crabs *Cancer irroratus*, *C. borealis*, and *Ovalipes ocellatus* in the New York Bight. J. Crust. Biol. 13, 723–735.

Williams, A.B., 1965. Marine decapod crustaceans of the Carolinas. Fish. Bull. 65, 1–298.

Witman, J.D., Genovese, S.J., Bruno, J.F., McLaughlin, J.W., Pavlin, B.I., 2003. Massive prey recruitment and the control of rocky subtidal communities on large spatial scales. Ecol. Monogr. 73, 441–462.

Wootton, J.T., 1992. Indirect effects, prey susceptibility, and habitat selection: impacts of birds on limpets and algae. Ecology 73, 981–991.

Wootton, J.T., 1997. Estimates and tests of per capita interaction strength: diet, abundance, and impact of intertidally foraging birds. Ecol. Monogr. 67, 45–64.

Yamada, S.B., Boulding, E.G., 1996. The role of highly mobile crab predators in the intertidal zonation of their gastropod prey. J. Exp. Mar. Biol. Ecol. 204, 59–83.

Zimmer-Faust, R.K., Fielder, D.R., Heck, K.L., Coen, L.D., Morgan, S.G., 1994. Effects of tethering on predatory escape by juvenile blue crabs. Mar. Ecol. Prog. Ser. 111, 299–303.