Terrestrially-based Predators in the Intertidal Zone:

The Impact of Gull Predation on Crabs throughout the Gulf of Maine

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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 of intertidal webs. The effects of avian predation on highly mobile predators such as crabs, remains practically unstudied in rocky shore ecosystems. Previous studies at the Isles of Shoals, Maine USA (Rome and Ellis 2004) found that crabs comprise a substantial proportion of the diet of gulls (*Larus marinus*, *Larus argentatus*) on Appledore Island, the site of a large breeding colony. The study also indicated that gulls prefer one species of crab, *Cancer borealis*, and that predation rates on this crab were high. In this study we investigated whether high rates of predation on *C. borealis* are restricted to breeding islands, or are generalizeable to non-breeding sites. We sampled nine sites along the Maine coast from three regions (Southwest, Central and Northeast). Each region had three sites; a breeding island, a site near a breeding island, and a site far from a breeding island. We addressed the following questions: 1) Are the number of foraging gulls proportional to the total number of gulls at a site? 2) Does gull preference for *Cancer borealis* remain consistent at multiple sites throughout the Gulf of Maine?
3) Does gull predation on crabs vary with a) proximity to breeding colony, b) geographic differences? We found that gull density did not determine predation. . Although total density of gulls was higher on breeding islands, the impact was almost the same as at mainland sites. Predation rates were dependent on the abundance of crabs in the intertidal. Of the three species of crab we studied (*Carcinus maenas, Cancer borealis, Cancer irroratus*) *C. maenas* the most abundant at all sites in quadrats, but predation rates on *C. borealis* were much higher; disproportionate to the relative abundance of the

three species. We found between 15-64%, with a mean of 30.6$\pm$ 5.6 of the available *C. borealis* were consumed by gulls at each low tide. Predation impact found at the 9 sites was very similar to results found on Appledore Island, suggesting the impact of gull predation on *C. borealis* is high throughout the Gulf of Maine. Because C. borealis is an important invertebrate predator, high gull predation rates may have implications for other components of intertidal food webs. These interactions appear to be dynamic and may be shifting with changing abundance of prey species in the intertidal.

INTRODUCTION

Terrestrial and marine organisms are physiologically designed for very different modes of living, but in a few unique environments the ranges of these organisms overlap and they can substantially influence one another's survival and distribution. The intertidal zone acts as a meeting ground for terrestrial and marine ecosystems. Despite the fact that the vast majority of intertidal inhabitants are marine in origin, terrestrial consumers may exploit the intertidal during low tides and play vital roles in intertidal food webs (e.g., Hori & Noda 2001, Wootton 1992, 1997, Levin et al. 1992). Such opportunistic foragers include mammals (e.g., bears, lemmings, raccoons) and birds (e.g., gulls, shorebirds, crows). The abundance of these terrestrial consumers in the intertidal is small and patchy in comparison to that of marine predators, yet their high metabolic rates and ability to exploit prey over a large area results in an influence disproportionate to their density and biomass. Thus, birds and mammals may be keystone predators, limiting the abundance and distribution of their marine prey in the intertidal (Feare & Summers 1986, Marsh 1986a, Wooton 1997).

The classical paradigm of intertidal zonation for temperate rocky shores was generated from many studies that focused on sessile organisms such as mussels (*Mytilus edulis*) barnacles (*Balanus balanoides*), and specialized intertidal consumers such as the periwinkle (*Littorina litorea*), the whelk (*Nucella lapillus*) and the green crab (*Carcinus meanas*). These studies indicate that the upper limit of species distributions in the intertidal is set by physical factors (wave shock and tolerance to desiccation) and the lower limit is set by biological interactions (competition and predation) (Connel 1961, 1970, 1983; Menge 1983; Menge & Lubchenco 1981; Paine 1974; Petraitis 1990;

Schoener 1983). Absent from most of these studies are highly mobile subtidal species such as Cancer crabs as well as the terrestrially-based consumers. Both types of organisms may play a vital role in shaping the structure of intertidal communities. Vertebrate terrestrial predators are generally limited to foraging in areas that are exposed at low tide or in very shallow water. Therefore they have the potential to set the limit on the upper distribution of their marine prey, adding a new type of biological interaction to classic intertidal models (e.g Hockey & Branch 1984, Feare & Summers 1986, Wootton 1997).

Avian predators, in particular, are prominent foragers in intertidal communities throughout the world (e.g. Hockey & Branch 1984, Feare & Summers 1986, Wootton 1997). Several studies have provided evidence that birds reduce densities of dominant space occupiers such as mussels (Marsh 1986a, Hamilton 2000) as well as intertidal gastropods (limpets: Frank 1982, Hockey & Branch 1984, Branch 1985, Mercurio et al. 1985, Hahn & Denny 1989, Wooton 1992, Marsh 1986b) and sea urchins (Schneider 1985, Dumas 1996). Few studies however have focused on the impact of avian predation on highly mobile invertebrate predators such as crabs (Good 1992b, Dumas and Witman 1993). It is especially important to understand the effect of avian predation on these consumers because they are key predators of a variety of other invertebrates, such as snails and mussels. Therefore, predation on crabs may have important consequences for lower trophic levels (e.g Micheli 1997).

In the New England rocky intertidal, the role of avian predators is virtually unknown. The few avian predation studies conducted in New England focused on interactions among space occupiers, algae and slow moving intertidal invertebrate predators. Noticeably absent are the mobile subtidal predators (cancer crabs). On the Pacific coast *Cancer productus* forages in the rocky intertidal and has been found to be ecologically very important in determining the abundance and vertical distribution of gastropod prey (Robles et al 1989, Yamada & Boulding 1996).   The role of the two predominant New England species, the Jonah crab (*Cancer borealis)* and the Rock crab (*Cancer irroratus)*, in the intertidal has not been documented to the same extent. However, both species are abundant subtidally in the Gulf of Maine and move into the intertidal in large numbers during the spring and summer, preying heavily on gastropods and mussels (DFO, 2000). As these large meaty predators climb into the shallow water they become vulnerable to the avian predators descending from above. The interaction of these two important consumers is inevitable, yet the impact of avian predation on crabs throughout the Gulf of Maine has not been documented.

During the past century along the east coast of North America, dramatic increases in two species of gull, the Herring Gull (*Larus argentatus*) and Great Black-backed Gull (*L. marinus*) have lead to greater overlap of the two species and exclusion of smaller less aggressive species (Drury 1973; Erwins et al. 1992; Good 1998). Great Black-backed and Herring Gulls breed on many offshore islands throughout New England. The closing of landfills and improved sanitation practices in recent years may have increased the reliance of these species on natural foraging habitats, such as the intertidal zone (Good 1992, 1998, Pierotti and Good 1994). Increased reliance on natural foraging habitats combined with the significant population increase has likely lead to an increased impact on marine sources of prey (Rome and Ellis *in press*).

Both gull species feed in the intertidal on mussels, sea urchins, sea stars and the three most abundant species of crabs in the northeast *C. maenas*, *C. irroratus* and *C. borealis* (Good 1992a, 1998, Dumas & Witman 1993, Pierroti & Good 1994). Gull predation on crabs could be of particular importance because it may set the upper distribution of crabs in the intertidal, reduce their intertidal abundance and cause trophic cascades. Previous studies in the Isles of Shoals have investigated the interactions between gulls and crabs and found that gulls prefer *C. borealis*, despite the greater availability of *C. irroratus* and *C. maenas* (Rome and Ellis *in press*). Additional studies have shown that gulls remove as many as 25 -50% of the available *C. borealis* during a single low tide (Ellis et al., *in prep*). Such high predation rates suggest that gulls in the Isles of Shoals have a large impact on crab populations. However, the Isles of Shoals are the site of some of the largest breeding islands in the Gulf of Maine. Therefore, these high predation rates may simply be a function of the relatively high abundance of gulls present on these breeding islands. In this study we set out to test if the high predation rates are unique to gull breeding islands, or if the interaction is representative of the Gulf of Maine in general.

In this study we addressed the following questions: 1) Are the number of foraging gulls proportional to the total number of gulls at a site? 2) Does gull preference for *Cancer borealis* remain consistent at multiple sites throughout the Gulf of Maine? 3) Does gull predation on crabs vary with a) proximity to breeding colony, b) geographic differences?

MATERIALS AND METHODS

Description of study sites

We surveyed nine rocky intertidal sites extending from the Southwest to the Northeast coast of Maine (Figure 1). There were three sites in each of 3 regions: Southwest, Central, and Northeast. Each site within a region was designated as either a: 1) gull colony, 2) mainland site near a gull colony, or 3) mainland site far from a gull colony. We chose the sites based on particular geological features (exposure, terrain, slope) that typically yielded moderate to high abundance of the three focal species of crab (*Cancer borealis*, *Cancer irroratus*, and *Carcinus maenas*) at the Isles of Shoals. In particular, we looked for sites with large, gently sloping areas of ledge or boulders, with medium to high levels of wave exposure. We avoided areas with steep vertical ledges. Abundance and vertical zonation of sessile intertidal organisms such as mussels, barnacles and algae (*Ascophylum nadosum*, *Chondrus crispus*) can be used to determine the magnitude of continual exposure at a site. The preferred moderate exposure level generally contains an abundant population of mussels and *C. crispus*, with *A. nadosum* and the ephemeral algae is less dominant then in sheltered areas. We avoided areas of highest exposure, where mobile predators are inhibited by intense wave action (Menge 1983; Menge & Lubchenco 1981).

We determined the length of shore for each site, by choosing a portion of shoreline that could be easily observed from a single location. Shore lengths ranged from 70 to 140 meters among sites.

Description of specific sites (Fig. 1)

Southwest Region:

(1) Smuttynose Island (SI), Isles of Shoals, ME. (42 98’N, 70 61’W; mean tidal range = 2.6m, sampled 6/30/03 & 7/01/03) Designation: gull colony

(2) Jaffery Point (JP), New Castle, NH. (43 03’N, 70 42’W; mean tidal range 2.7m, sampled 7/03/03 & 7/05/03) Designation: near gull colony

(3) Cape Neddick (CN), York, ME. (43 09’N, 70 35’W; mean tidal range = 2.7, sampled 7/06/03 & 7/07/03) Designation: far from gull colony

Central Region:

(1) Fishermen Island (FI), 1.5 miles off Ocean Point, ME. (43 46’N, 69 38’W; mean tidal range = 3.0 m, sampled 8/05/03 & 8/06/03) Designation: gull colony

(2) Ocean Point (OP), off Boothbay Harbor (43 48’N, 69 35’W; mean tidal range = 3.0 m, sampled 8/03/03 & 8/04/03) Designation: near gull colony

(3) Sawyer Island (SA), Sheepscot Bay, ME. (43 52’N & 69 40’W; mean tidal range = 3.0m, sampled 8/07/03 & 8/08/03) Designation: far from gull colony

Northeast Region:

(1) Schoodic Island (SI), ~1 mile off the coast of Blueberry Hill, ME. (44 19’N, 68 02’W; mean tidal range = 3.1 m, sampled 7/17/03 & 7/18/03). Designation: gull colony

(2) Blueberry Hill (BH), Schoodic Peninsula, ME. (44 20’N, 68 02’W; mean tidal range = 3.1 m, sampled 7/14/03 & 7/14/03). Designation: near gull colony

(3) Bear Island (BI), off the coast of Mt Desert Island, ME. (44 16'N, 68 16'W; mean tidal range = 3.5m, sampled 7/16/03 & 7/18/03) Designation: far from gull colony

Study organisms

Herring Gulls and Great Black-backed Gulls in the Gulf of Maine breed on offshore islands from March until late September. Both species forage in mainland landfills, open ocean (i.e., on lobster fisheries refuse), intertidal, and shallow subtidal (Good 1998, Pierotti and Good 1994). Gulls forage in low intertidal and shallow subtidal zones by swimming or flying above the surface and plunging to a maximum depth of 1 m (Good 1998; J.C. Ellis personal observation).

The rocky intertidal and shallow subtidal, can be divided into three distinct zones characterized by the predominant sessile species: the barnacle zone (+2.1-2.7 m relative to Mean Lower Low Water), the *Ascophyllum* zone (0.6-2.1 m) and the *Chondrus* zone (0.6 m to shallow subtidal). Gulls also foraged in the "nearshore" zone, the shallow subtidal zone adjacent to the shore.

Cancer borealis, *Cancer irroratus* and *Carcinus maenas* are the predominant species of crab in the Gulf of Maine. These three species are influential predators and play an important role in the rocky intertidal food web.

The Green crab, *Carcinus maenas* is a well-known predator of ecologically important consumers such as *Littorina littorea* and is very abundant in the intertidal. An introduced species, *C. maenas* was only found from New Jersey to Cape Cod in North America before 1900, since then its population has spread as far east as Halifax, Nova Scotia. Throughout its North American range, *C. maenas* is subject to large population fluctuations and is particularly sensitive to the cold (Vermeij, 1981). The Rock crab *Cancer irroratus*, and the Jonah crab *Cancer borealis*, two large-bodied benthic invertebrates, are economically and ecologically very important in the Gulf of Maine (Palma et al., 1999). The two crab species resemble each other in appearance, but *C. borealis* is generally larger with a jagged anterior carapace. The Jonah crab is found from Nova Scotia to South Carolina and the Bermudas at depths ranging from intertidal to 800m. Their substrate of preference ranges from rocky to sand, clay to mud (DFO, 2000). The Rock crab ranges from Labrador to South Carolina, but is found generally in more shallow water than *C. borealis.* Both species enter the intertidal and shallow subtidal to feed on mussels and gastropods and hide in the structurally complex substrate. It is typically the smaller individuals that move into the intertidal to hide beneath rocks and in crevices because they are more vulnerable to the large subtidal predators than a full sized adult (Harrison and Crespi, 1999). Subtidal populations of *C. borealis* have increased dramatically in the coastal Gulf of Maine, likely due to long term effects of overfishing of crab predators (Witman and Sebens 1992) and bottom-up effects of massive prey recruitment (mussels, Witman et al. 2003).

Gull abundance and behavior

Studies of gull foraging behavior were conducted twice (over two low tides) at every site. All behavioral observations were conducted from a boat approximately 50m from shore (so as not to disturb foraging gulls). Instantaneous scan samples were taken every 15 minutes, during each low tide cycle, beginning an hour and a half before low tide, and ending 15 minutes afterward, for a total of 8 scans per low tide. During each scan, I recorded species and age (adult or juvenile) of each individual and the following behaviors: aggression, eating, loafing, preening, flying, walking, searching, and swimming. I also recorded the location of each gull in each of four zones: Barnacle, *Ascophyllum*, *Chondrus*, and Nearshore.

During each period of behavioral observations, I also conducted focal animal samples every 10-15 min. Focal animal samples (Altmann 1974) were observations of a single randomly chosen bird for 5-8 min., or until the gull vacated the study site. The following data were recorded: intertidal zone(s) in which the gull was located or moved into, activity of the gull, the prey type and duration of the particular activity.

The total gull abundances were averaged across the 16 scans conducted during two low tides at each site and log (x + 1.1) transformed to correct for heterogeneous variances. The data were then used in a two-way ANOVA with gull species and proximity to a gull colony as factors. A separate two-way ANOVA testing the effects of gull species and region on gull density was also conducted.

In addition to overall abundance of gulls the number of gulls foraging at each site was also calculated. The number of gulls consuming a prey item was tallied and averaged across the 16 scans for each site. Data were then log (x + 1.1) transformed and used in two separate two-way ANOVA's, one with gull species and proximity to a gull colony as factors and one with gull species and region as factors. All posthoc comparisons were made using the linear contrast function in JMP.

I used data from my focal samples to look at the percent of time spent in various activities during a diurnal low tide for both species of gull. All focal observations were totaled and the amount of time spent at each of the eight activities (aggression, eating, flying, loafing, preening, searching, swimming, walking.) was summed. The time spent at each activity was divided by total time to acquire a proportion.

Estimate of crab abundance

I measured crab densities in order to assess: 1) whether rates of gull predation differed among sites and among species of crab, and 2) the proportion of the crab population preyed upon by gulls. I measured crab densities at 0m (relative to MLLW) because this is a depth at which gulls are most likely to capture crabs at low tide (Ellis et al. in review). I snorkeled at each site between 3.5 and 4 hours before low tide. The snorkel concluded within 1 hour and 15 minutes, well before the gulls began to forage. At all sites, I randomly placed $1m^2$ quadrats (n=15 per site) parallel to the shoreline at 0 m (relative to MLLW). While snorkeling, I identified, counted, and measured carapace width ($\pm$ 0.1 mm) of *Cancer borealis* and *Cancer irroratus* in each quadrat. *Carcinus maenas* were counted and categorized into small (< 25 mm), medium (25-50 mm), and large (> 50 mm) carapaces.

The crab density data were averaged across quadrats to generate a single density value for each site and then log (x + 1.1) transformed to correct for heterogeneous variances. The transformed data were then used in two separate 2- way ANOVA's: one with crab species and proximity to a gull colony as factors and the other with crab species and geographic region as factors. We used the linear contrasts function in JMP (version 3.2.6) to make posthoc comparisons.

Estimate of gull predation rates

Gulls foraging in the intertidal leave prey remains *in situ* (Ellis et al. in review). Therefore, I collected prey remains from the intertidal one half-hour after low tide, after peak foraging. Prey remains consisted primarily of the carapaces and chelipeds of the crabs' *C. borealis*, *C. irroratus*, and *C. maenas*. Carapaces from crabs eaten by gulls lack an abdomen, have small remnants of flesh inside, and are often found next to detached claws and legs; thus, I could easily distinguish them from molts. Gulls leave carapaces in the low and mid-intertidal zones where they are flushed away from shore on the subsequent high tide, thus enabling me to attribute carapaces to a single low tide cycle.

Carapaces were collected over two diurnal low tides at each site in order to assess temporal variability and to generate a mean predation rate for every site. I estimated predation rates by dividing the number of carapaces collected by the length (m) of shoreline over which carapaces were collected. This results in the number of crabs removed by gulls per linear meter of shoreline.

Crab carapace data were averaged across the two days, yielding a single value for each site. These values were then log (x + 1.1) transformed to correct for heterogeneous variances and used in a 2-way ANOVA with crab species and proximity to a breeding island as factors. A separate 2-way ANOVA was also used with crab species and region as factors. Posthoc comparisons were made using the linear contrast function in JMP.

Estimate of crab population impact

In addition to estimating predation rates, we calculated population impact (*sensu* Wootton 1997), the percentage of the available crab population consumed by gulls per diurnal low tide. The crab carapaces collected over two separated low tides at each site were averaged and then divided by densities per m^2 averaged among the 15 quadrates conducted at each site. The resultant proportion of available crabs eaten by gulls (i.e. population impact) for each site was then used to determine whether predation impact varied with proximity to a gull colony as well as region through the use of two separate 2-way ANOVA's. The linear contrast function was used for posthoc comparisons

Gull predation range

A GIS (Geographic Information Systems) mapping analysis was used in order to determine what proportion of the coastline in the Gulf of Maine is within 20km of a gull breeding island. We obtained a map of the Maine coastline and linked it to a map of primary breeding islands in Maine (approximately 320 islands total). Preliminary analyses and results from other studies indicated that foraging gulls are present at mainland areas within 20km of a breeding island. We used this figure and created a 20km buffer around each of the breeding islands. The map of Maine was converted from a polygon to a line file, then the coastline was clipped using a geometry feature on Arcview and the length of the line file was calculated (i.e. the coast of Maine). We then overlay the line file with the buffered region, clipped the parts of the coastline outside the buffer and calculated the remaining portions. Dividing the length of shore within the buffered region by the total length of coastline yields the proportion of the Maine coast within 20 km of a breeding island.

RESULTS

Estimate of gull densities

The two species of gull did not differ significantly in overall abundance, but showed numbers approaching significance among site types (2-way ANOVA; species: $F_{1,17}$=0.1309, p=.7238, proximity: $F_{2,17}$=3.06, p=0.0843). Great Black-backed gull density was significantly higher on the shores of breeding islands then near or far from colony's on the mainland (LS mean contrast $F_{1,17}$=8.94, p=0.011) (Fig. 2.). Herring gull density was highest on breeding islands, but there was no significant difference. (Fig. 3.).

The abundance of both gull species did not differ significantly and showed no significant difference among regions. (2-way ANOVA; species: $F_{1,17}$=0.0795, p=0.78, region $F_{2,17}$=0.95, p=0.41).

Densities of gulls foraging in the intertidal did not differ with respect to species or proximity to a gull colony (2-way ANOVA; species: $F_{1,17}$=0.97, p=0.34, proximity F=$_{2,17}$=1.23, p=0.3256). (Fig. 4 & 5.) In addition there was no significant difference between species for the regional analysis (2-way ANOVA; species: $F_{1,17}$=1.3, p=0.27). There was, however a significant difference among regions (region: $F_{2,17}$=4.4226, p=0.0364). The number of gulls foraging in the intertidal decreased from south to north for both species (Fig. 6.). The abundance of foraging gulls in the southwest was significantly greater than both other regions (LS mean contrast; $F_{1,17}$=7.44, p=0.018).

Results from the focal sample analysis of activity patterns showed Great Black-backed gulls spent 27% of their time eating in the intertidal, while the Herring gulls only spent 16% of their time eating. Great Black-backed gulls also spent 5% of their time in aggressive attacks on Herring gulls. These attacks typically ended in the Great Black-back stealing a prey item from the Herring gull. Herring gulls however spent considerably more time searching, which we categorized as walking with head down, picking at the algae (Fig. 7 & 8).

Estimate of crab abundance

The mean density of all species of crab in quadrats (at MLLW) combined ranged from 0.67 m^2 to 4.5 m^2 among sites. The relative abundance of the three crab species differed significantly, but did not differ with proximity to breeding colony (2-way ANOVA; species: $F_{2,26}$= 5.49, p=0.0137) *Carcinus maenas* was significantly more abundant than *Cancer borealis* and *C. irroratus* at all three site types (LS mean contrast; $F_{1,26}$= 9.94, p=0.0054)

Density of crabs depended on both the species of crab and the region (2-way ANOVA; species: $F_{2,26}$=9.43, p=0.0016; region: $F_{2,26}$=5.1, p=0.0176). *C. borealis* had significantly lower overall densities than the other two species (LS mean contrast; $F_{1,26}$=10.38, p=0.0047; Fig. 9.). *C. borealis* abundance decreased from south to north, though not significantly (Fig. 10.). *C. irroratus* densities were highest and significantly greater then *C. borealis* in the northeast (LS mean contrast; $F_{1,26}$=4.377, p=0.05). *C. maenas* abundances were significantly greater than the other two species in the southwest ($F_{1,26}$=16.47, p=0.0007).

Estimate of gull predation rates

Prey remains collected from the intertidal at the 9 sites throughout the Gulf of Maine showed patterns similar to those found in the Isles of Shoals. Crabs were by far the most common prey item: only 2 blue mussels (*Mytilus edulis*) and 2 green sea urchins

(*Strongylocentrotus droebachiensis*) were found in all prey collections (2 collections per site: 139 total prey remains). *Cancer borealis* was the most abundant crab species found in remains at every site, ranging from 66.7% to 100% of all crab remains (except at Sawyer I. where no remains were found:). Mean ($\pm$ 1SE) numbers of crab carapaces per km of shoreline per diurnal tidal cycle were 75.9 $\pm$ 31.9 at the three colonies, 102.7 $\pm$ 46.7 at the near sites, and 36.9 $\pm$ 30.1 at the far sites.

Gull predation rate (number of carapaces per km shoreline) varied with respect to crab species, but did not differ with proximity to breeding colony (Two-way ANOVA; species: $F_{2,26}=10.1$, $p=0.0011$, proximity: $F_{2,26}=0.7506$, $p=0.4863$). Predation rates on *C. borealis* were significantly higher than on either of the other two species (LS mean contrast: $F_{1,26}=20.144$, $p=0.00028$) (Fig 11). Predation rates on *C. borealis* were consistently high among the sites, but were highest at mainland sites near breeding and lowest at sites far from breeding islands, although the difference was only marginally significant (LS mean contrast $F_{1,26}=4.57$, $p=0.046$).

The predation rate on the three species of crab differed significantly in abundance and showed a marginally significant difference among regions (2-way ANOVA: species; $F_{2,26}=15.85$, $p=0.0001$, region: $F_{2,26}=3.51$, $p=0.0516$). Predation rates on *C. borealis* were significantly higher than on both other species at all three regions (LS mean contrast; $F_{1,26}=31.58$, $p=0.000025$; Fig. 12.). Predation rates on *C. borealis* were highest in the Southwest and lowest in the Northeast where they were significantly lower than both Central and Southwest regions (LS mean contrast; $F_{1,26}=14.79$, $p=0.0011$; Fig 13).

Data from the 1.0 m quadrats were used to generate expected proportions of each crab species in carapace collections. A X2 goodness-of-fit test on the total number (averaged across sites) of each species of crab found in quadrats and carapace remains showed similar patterns to the Isle of Shoals: *C. borealis* was preyed upon more often and *C. maenas* and *C. irroratus* less often then expected (X2 = 1638.0, p<0.0001).

Estimate of the impact of gull predation on crab populations

The percent of *Cancer borealis* removed at each diurnal low tide remained high at every site, ranging from 15.29% to 64.36%, with a mean of 30.64%. In comparison, the abundant *Carcinus maenas* was preyed upon far less, with the percent removal ranging from 0 to 0.79%.

The percent of crabs removed at each low tide differed significantly among the three species of crab, but did not differ with proximity to breeding colony (2-way ANOVA; species: $F_{2,24}$=39.26, p=<.0001, proximity: $F_{2,24}$=0.20, p=0.819). *Cancer borealis* were removed from the intertidal significantly more than the other two species of crab at all three site types (LS mean contrast; $F_{1,24}$=71.13, p=<0.0001) (Fig. 14 & 15)

The predation impact on the three species of crab differed significantly, but showed no difference between regions (2-way ANOVA; species: $F_{2,24}$=48.126, p=<0.0001, region: $F^{2,24}$=1.267). The percent of *Cancer borealis* consumed at each low tide was significantly greater than the other two species of crab at all three regions (LS mean contrast; $F_{1,24}$=87.617, p=<0.0001; Fig. 16.). *Carcinus maenas* was not consumed in the central and northeast regions.

We calculated the length of the Maine coastline to be 1854 km using GIS. The analysis of gull distribution, showed that 97.02% of the Maine coast was within 20 km of a gull breeding island.

DISCUSSION

Studies on the Isle of Shoals found that gulls strongly preferred *Cancer borealis* over the other species of crab in New England and as many as 25-50 % of the *C. borealis* available in the intertidal were being removed each low tide (Ellis et al. *in prep.*). A rate this high indicates that gulls may influence the abundance of *C. borealis* in the intertidal, changing the dynamics of intertidal communities. However, with the inflated number of gulls on the Isles of Shoals (roughly 2000 gulls in the spring and summer months), predation rates may also be abnormally large. The primary goal of my study was to test if these high predation rates were generalizeble to the Gulf of Maine or simply a breeding island phenomenon; where competition for food forces a larger number of gulls into the intertidal to forage. We found concrete evidence that a considerable number of crabs are consumed all along the Maine coastline regardless of the number of gulls present at a site.

From the southern tip of Maine to the Northeast coast, wherever cancer crabs were found, gulls were consuming them. At every site at which predation occurred, *Cancer borealis* was preferred regardless of the relative abundance of the three species. The vast majority of carapaces found were C. *borealis*. Whether it is their unique defense strategy, lack of crypticity in shallow water or greater profitability (Rome and Ellis *in press*), gull preference for this species is consistent throughout the Gulf of Maine. In some areas you cannot step in the intertidal without scattering dozens of green crabs, yet few are consumed (personal observation). Gull impact on C. *borealis* is much greater than on any other species, and predation on this species appears to be more than an irregular occurrence found only were gulls are extremely abundant.

Whether there were one hundred gulls at a site or five, whether *C. borealis* were abundant or scarce, a very consistent proportion of crabs were being pulled from the intertidal at all sites. On average 30% of the available *C. borealis* were removed by gulls each low tide. Thus, it appears that the predation rate is limited not by gull abundance but by the number of crabs available.

Our results indicate that gulls are very effective predators on crabs. Throughout the gulf of Maine gulls are pulling out 30% of the available *C. borealis* with each low tide. This is a huge impact but it is even more impressive when one considers that 'available' refers to all the crabs I could find by digging through algae and reaching deep into crevices. Gulls scan the water from above, they can only pull out the crabs at their depth range and those that are visible (Good 1998). I found, on average, that less than 50% of the crabs found in a quadrate were initially visible from above. The gulls are likely removing as many crabs as they can find. On the crowded breeding islands there are not enough *C. borealis* for the hundreds of gulls to be feeding at one particular site. However the gulls appear to dissipate in order to make the greatest use of this profitable food source. I would arrive at a site with no gulls visible, yet as the lower levels of the intertidal were exposed a Great Black-back would appear in the distance tracing the shoreline, diving periodically. Soon others would arrive flying 15 to 20 feet above the water with their head down, if a crab was spotted they would dive immediately, most dives were successful. There were never more than three gulls on the site at one time, yet by the end of the low tide enough crabs had been removed that the predation levels were equal to the breeding islands where 50 or more gulls loafed on the shoreline.

Of the nine study sites I studied, the three breeding islands had the largest abundance of gulls along the shoreline. One site in particular, Smuttynose, a loafing ground for the gulls on the largest of the breeding islands, had a very high overall abundance of gulls on the shore. This island was an outlier and was the cause of a large amount of variance in the Analysis. Despite the fact that this island had a significantly higher number of gulls than any site, it was not among the 3 highest sites for number of foraging gulls.

C. borealis abundance appears to be the factor limiting gull predation. Therefore the range of *C. borealis* and the scope of gull colonies are important pieces of information to obtain when looking for gull predation. There are over 320 major breeding islands along the coast of Maine (Houston, 2000). Our criterion for sites far from a gull colony was that they be greater than 20km from any breeding island. With such a large number of breeding islands it was difficult to find sites on the coast the preferred distance from a gull colony that also fit the criteria for a typical rocky intertidal site. One site far from a gull colony, Sawyer island, was in a bay and the physical features of the intertidal zone at this site where much different than the other eight sights. *Ascophyllum* and kelp were the dominant algae types, there was very little *Chondrus*, the bottom was muddy, the water was murky and the wind and wave exposure was very low. I found neither of the two cancer crabs while snorkeling and thus was not surprised to find zero predation. The cancer crabs, *C. borealis* and *C. irroratus* move into the rocky intertidal to hide in the complex environment, and feed on organisms such as mussels and gastropods (Harrison and Crespi, 1999). The intertidal environment at Sawyer Island showed neither of these advantages for the gulls, thus the crabs have no reason to leave the subtidal environment in areas such as this. Upon arriving at the site there were a few gulls, but contrary to the other sites as the low tide arrived, the gulls left, most likely flying to sites where prey could be found. Although this site added inconsistency to the analysis it also proved very informative. With such a large number of breeding islands on the Maine coast if would prove difficult if not impossible to find a site with *C. borealis* present that was out of reach of the gulls. This suggests a large impact on the intertidal population of *Cancer borealis* throughout the gulf of Maine.

Our findings indicate that prey abundance rather than predator abundance predicts the magnitude of predation. This is important to keep in mind when determining predation hot spots. In many studies looking at predator-prey interactions, sites are chosen based on areas where the predator is abundant. If the prey are not overly plentiful, and the predator is limited by the prey, than these sites may be no better than average (Baalan and Sabelis, 1992). In my study many mainland sites had higher predation rates than breeding islands. In addition, areas on the breeding islands with the most gulls could be the most difficult for observation. At these sites there were many gulls doing any number of activities that could distract the observer from the focal predation observations.

I found a significant difference from the Southwest to the Northeast in the total number of *Cancer borealis* removed at each low tide. Initially I hypothesized that perhaps a greater density of kelp in the Northeast or larger amount of fishing refuse could account for these lower predation rates. However, when I compared gull predation rates to the abundance of *C. borealis* in the intertidal at each region, there was a perfect correlation. In the Northeast I found very few *C. borealis* in my snorkels and found few carapaces on the shore, yet the proportion of C. *borealis* consumed were essentially the same as the Southwest where both were higher. So the question now is; why is C. *borealis* abundance so much lower in the Northeast? What factors contribute to a lower abundance? One possible explanation for this could be the temperature of the water. *C. Borealis* move into the intertidal during the late spring. The waters in the Northeast are cooler and it may take until early summer before temperatures in the shallow water are suitable for *C. borealis* (DFO, 2000). I sampled in the Northeast during the month of July. It is possible that there is still movement into the intertidal during this time and the population may not have reached its peak as it had in the Southwest. Another explanation could be the Cancer borealis fishery in Nova Scotia. Since the mid 1960's borealis have been exploited to a lesser degree through lobster fishery by-catch. This occurs all along the Maine coast, but each crab is only worth a nickel few fishermen bother to collect the crabs. There is however a *Cancer borealis* fishery in Nova Scotia that was reintroduced in 1997 after an experimental period from 1980 to 1984 (DFO, 2000). This fisheries landings are much larger than the lobster by-catch and its location in the North could possibly effect the population of *C. borealis* along the Northeast coast.

Another interesting observation I came across at almost all the sites was the apparent prey specialization by the gulls. It was most noticeable at the breeding sites where there was an abundance of gulls but only a few foraged. The same few appeared to spend most of the low tide in the intertidal foraging while others sat on the shore, never entering the water unless a lobster boat came by throwing out bait. At one site an individual pulled 7 large crabs from the intertidal, over half of the total removed. It appeared more skilled than most, diving from heights of 30 ft, almost always successful.

Juveniles rarely caught crabs, though they would pick at the remains once the adults had left. Diving for crabs appeared an acquired skill, one that perhaps some individual gulls become particularly efficient at, utilizing the intertidal to a greater extent than others**.** This sort of prey specialization has been documented in a number of sea birds (Ens B.J., D. Alting; Good, 1992)

I found through my observations that Great Blacked-back gulls were consuming more crabs in the intertidal than Herring gulls. The intertidal is an intense site of competition for these two abundant species of gull. For a century the Herring gull has been the more abundant of the two species, found everywhere from; lakes to fast-food parking lots, to the coastline, to open landfills. Both species of gull utilized the dumps as a picking ground. With food prevalent, scattered about and easily obtained, competition is not fierce. Gulls obtained the majority of their diet from food scraps in these dumps (Chicken composes a large part of their diet), bait discarded by fisherman and prey removed from the intertidal zone (Good, 1998). Two decades ago the open landfills began to shut down, removing a key portion of the gull's diet. Thus, the gulls had to turn to other sources, relying more on areas such as the intertidal. Since the closing of the dumps, the abundance of the Great Black-back relative to the Herring gull has increased dramatically (Good, 1992). The larger more aggressive Great Black-back appears to out-compete the Herring gull for the discarded bait of lobsterman as well as prey items removed from the intertidal (Rome and Ellis, *in review* and personal observation). It was clear at every site I visited that the Herring gull has difficulty catching and keeping hold of crabs or other large prey items in the presence of the Great Black-backed gull. When a Herring gull obtains a crab it begins consuming it immediately. If a Great Black-backed gull is nearby it will chase the Herring gull until the carapace is dropped, or if the prey has been swallowed it may harass the gull until it regurgitates the food item (personal observation).

Through my focal observations I found that Herring gulls and Great Black-backs consistently had different patterns of feeding when consuming prey. The Great Black-backs would stab and pick at the carapace for 12-15 seconds then look up for a second or two, repeating this pattern until there was little meat left in the crab. All the Herring gulls picked at the crab for only 2 or 3 seconds before looking up; if a Great Black-back was spotted they would grab the carapace and fly off. The only two Great Black-backs that consumed their crabs in a pattern similar to Herring gulls had their prey stolen by larger Great Black-backs (personal observation). Perhaps the typical Great Black-back method of feeding is more efficient, yet if the gull is smaller and likely to lose its prey to a larger individual, it must spend more time looking up, viewing its surroundings and the potential dangers.

High predation rates on crabs may be a relatively recent phenomenon resulting from recent changes in prey availability. A study, by Dumas et al 1996, conducted between 1992 & 1995, looked at gull predation along the coast of Maine, specifically its impact on the green urchins (*Strongylocentrotus droebachiensis*) population. Dumas conducted her study at two sites close to those that I observed. She made observations during July and August, used the same scan sampling method as I did and collected the remains of prey following the low tide. She observed the same behaviors used for the capture of prey, such as surface plunging. She found that gulls never foraged in the upper intertidal and the greatest number of gulls foraged during the low tide. Despite these methodological similarities, the results of her predation analysis were remarkably different. At Swans Island, a site within miles of one of my sites, she found that Herring gulls consumed mainly green sea urchins, comprising 66% of their diet. At all my sites I found that urchins comprised less than 1% of the gull's diet. She found that less than 10-15% of the Herring gull's diet was cancer crabs. Recent studies on the Isle of Shoals showed that greater than 90 % of the species gulls pull out of the intertidal are crabs. I found similar results at all the sites I visited, for both species of gull. She did find that Great Black-backed gulls ate mostly cancer crabs (65% diet). However she found at this time that Great Black-backs represented a very small fraction of gulls present. I found during my study that Great Black-backs were actually a lot more common along the shore than Herring gulls, representing 72.2% of species present. The reduction in urchin numbers could be another contributing factor to the population increase of the Great Black-back at the expense of the Herring gull. Urchins were a more abundant and easily obtained food source than *C. borealis*, therefore there was likely less competitive interaction between the two species. The Herring gulls had an alternative to the Black-backs preferred prey. Now both species are feeding heavily on cancer crabs, the impact on *C. borealis* is large, the competition is intense, and the larger of the two species is winning out. It should also be noted that Great Black-backs feed on ducks and Herring gull chicks and so may have more alternative food sources than the Herring gull.

The results of Dumas study and my own are vastly different for such as short period of time. There is however a likely explanation. A small urchin fishery existed in Maine for many years, but prior to 1986 the urchin harvest was limited to about 45 metric tons, which supplied ethnic markets in Boston and New York. Urchin roe is a delicacy in parts of Europe and Japan. The Japanese, who had overfished urchins in their waters, opened a market in Maine beginning in 1987. Landings began to rise dramatically; by 1992 they reached almost 12000 metric tons (over 26 million pounds). They continued to rise through the next couple years, peaking in the mid nineties, before a striking decline at the end of the decade. By 2000 urchins were overfished, and the industry crashed (Leland et al., 2002).

Intense fishing of cod and other predatory groundfish in the Gulf of Maine allowed sea urchins to become one of the most abundant species of shallow subtidal and intertdal environments in the 1970s and 1980s (Steneck et al. 1994, Vadas and Steneck 1995, Steneck 1997). The urchin is the dominant benthic grazer in the shallow subtidal and has the ability to completely strip fleshy algae, leaving vast urchin barrens. Since the crash of the urchin populations, these thick beds of algae have become reestablished and continue to thrive because they harbor predators (amphipods and newly settled Cancer crabs) of juvenile sea urchins. Despite an abundant larval supply the, sea urchin recruitment is prevented and the population continues to flounder (Leland et al., 2002). The drastic decline of the urchin population in just over a decade is sure to largely affect many predators of the intertidal and shallow subtidal including the gull. Concomitant with the urchin decline is the dramatic increase in Cancer crabs because of the overfishing of cod, which were also top predators on crabs (Whitman et al. 2003)

The reduction in urchin numbers, increase in Cancer crabs and the altered diet of Herring gulls (the more populous of the two species) along with the closing of landfills and greater dependence on the intertidal, has likely led to an increased impact on the intertidal population of *Cancer borealis*. C. *borealis* is an important consumer in the intertidal feeding on *Littorina litorea*, a dominant consumer which feeds heavily on ephemeral algae. A number of studies have shown that predation by birds can initiate trophic cascades in rocky intertidal communities. These studies demonstrated that birds reduce herbivore (ie. limpets and sea urchins) abundance, thus increasing abundance of primary producers (Lindberg et al 1998, Wootton 1992). It would seem likely that a reduction of *C. borealis* numbers by gulls could lead to an increase in snail densities and a decrease in ephemeral algae; a top down trophic cascade affecting a variety of organisms. A recent study by Ellis et al, has shown that gull predation does not significantly reduce snail populations. Thus, at least in the short term, gull predation on crabs does not appear to severely alter the abundances of many lower trophic organisms in the New England intertidal. It is however a distinct phenomenon all along the coast of Maine, and should be taken into account in any evaluation of species interactions and predator prey relationships in the New England intertidal.

FIGURES

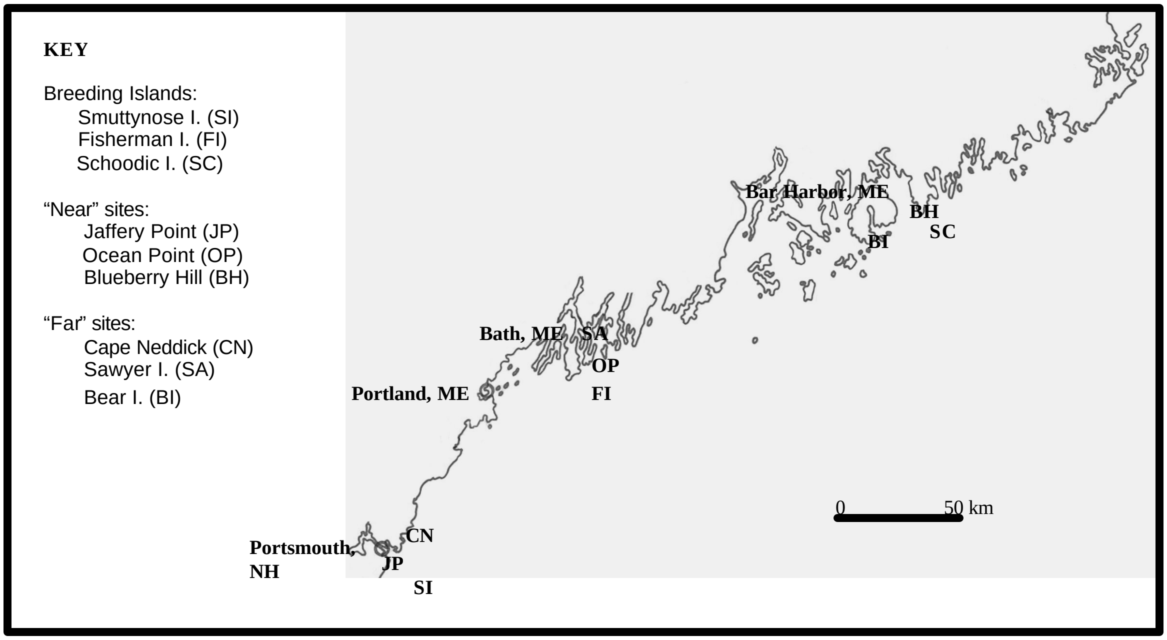

Fig. 1. Map of the nine study sites along the coast of Maine.

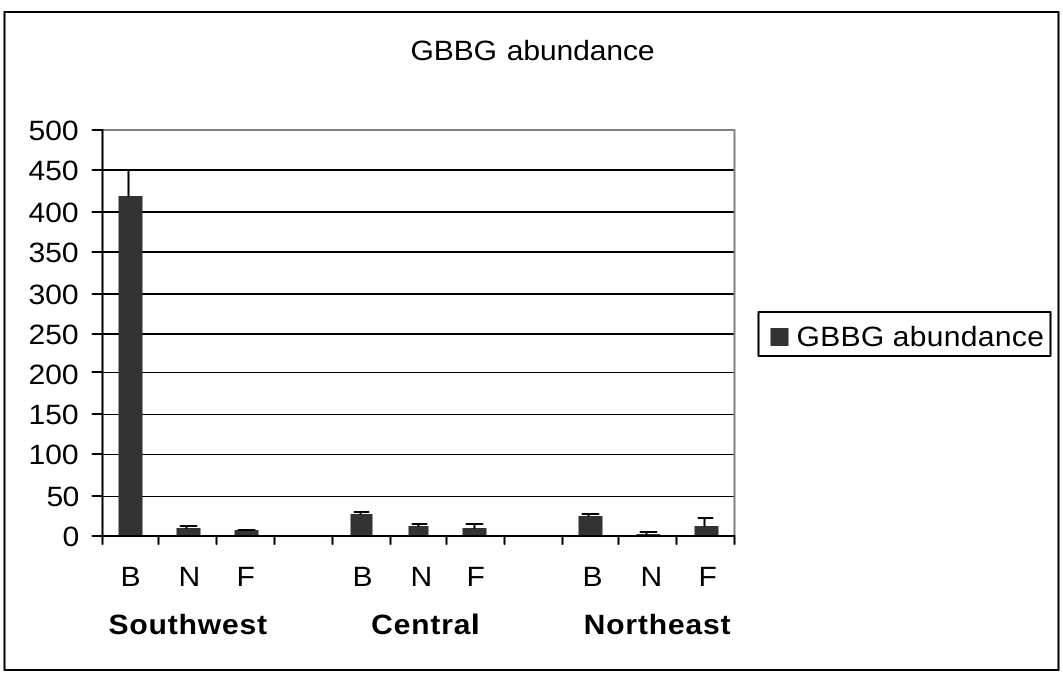

Fig. 2. Mean number of total Great Black-backed Gulls per km on the shore at all sites.

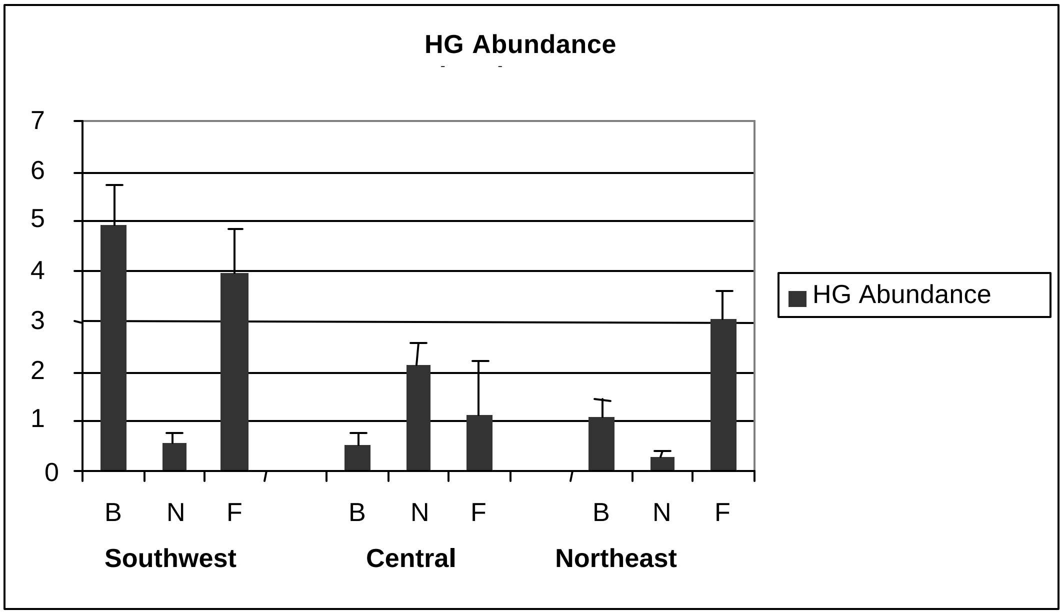

Fig. 3. Mean total density of Herring gulls per km on the shore at each of the sites.

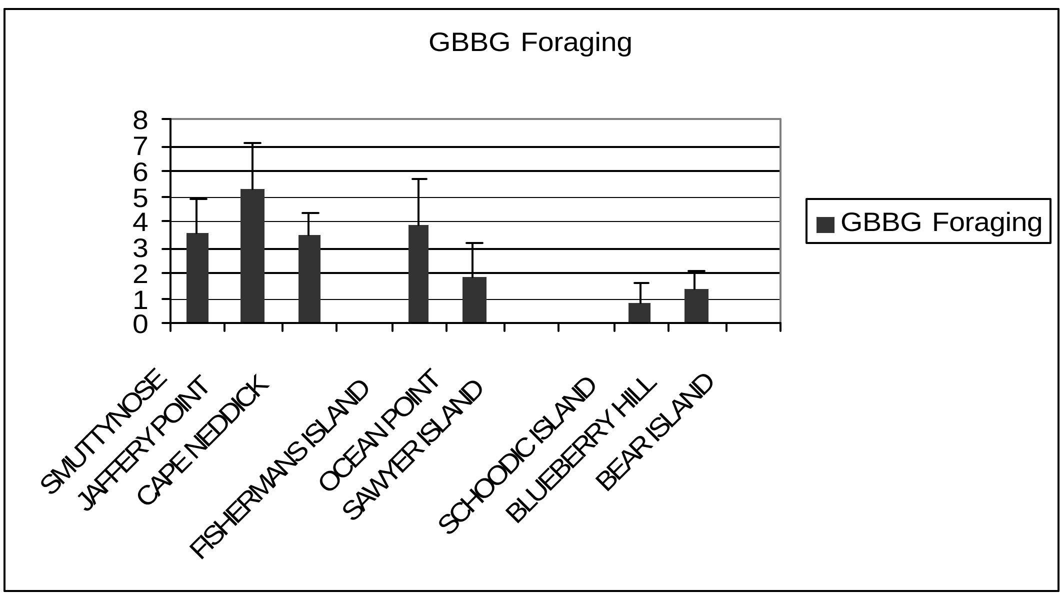

Fig. 4 Mean number of foraging Great Black-backed Gulls per km at all the sites

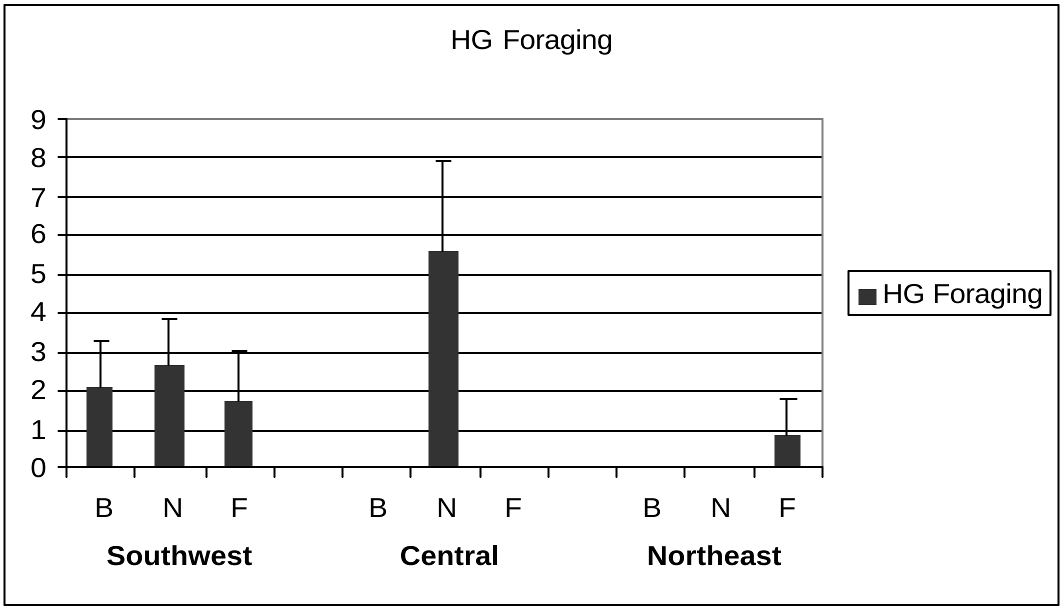

Fig. 5. Mean number of foraging Herring gulls per km at all sites.

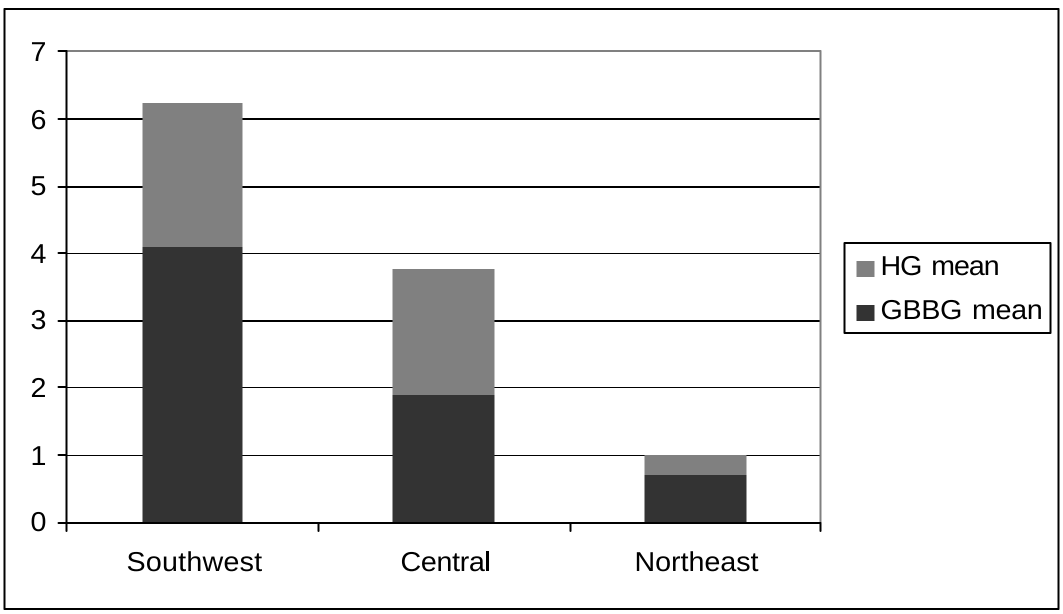

Fig. 6. Mean number of foraging gulls per km for both species at each region.

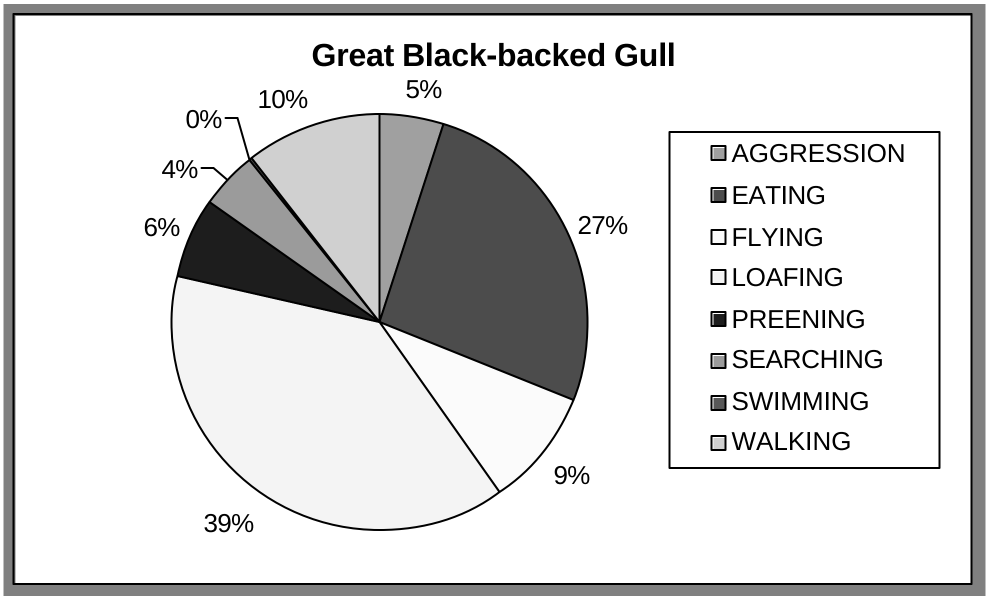

Fig. 7. The percent of time spent at each activity for the Great Black-backed Gull during an average low tide

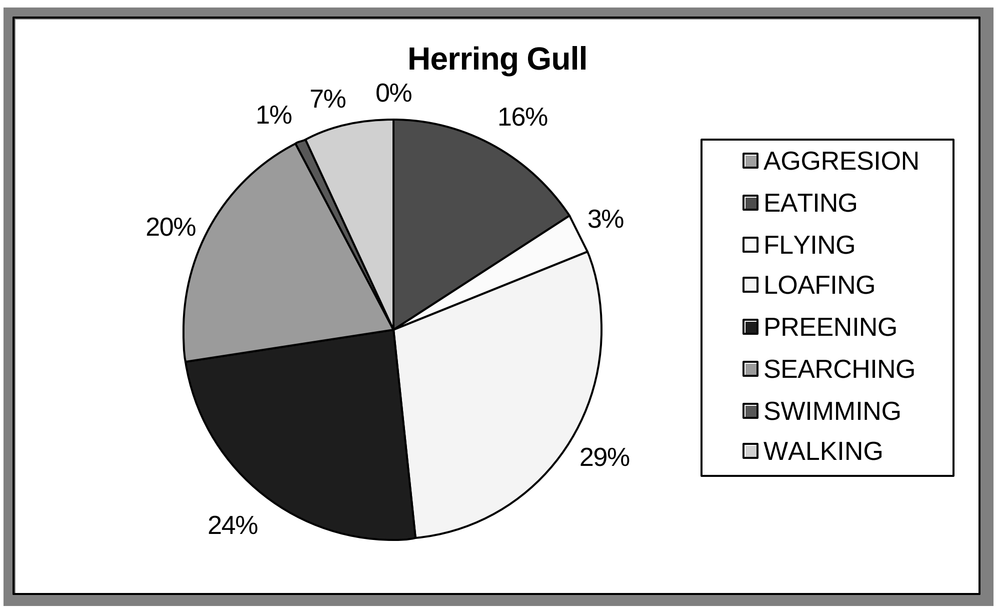

Fig 8. The percent of time spent at each activity for the Herring Gull during an average low tide

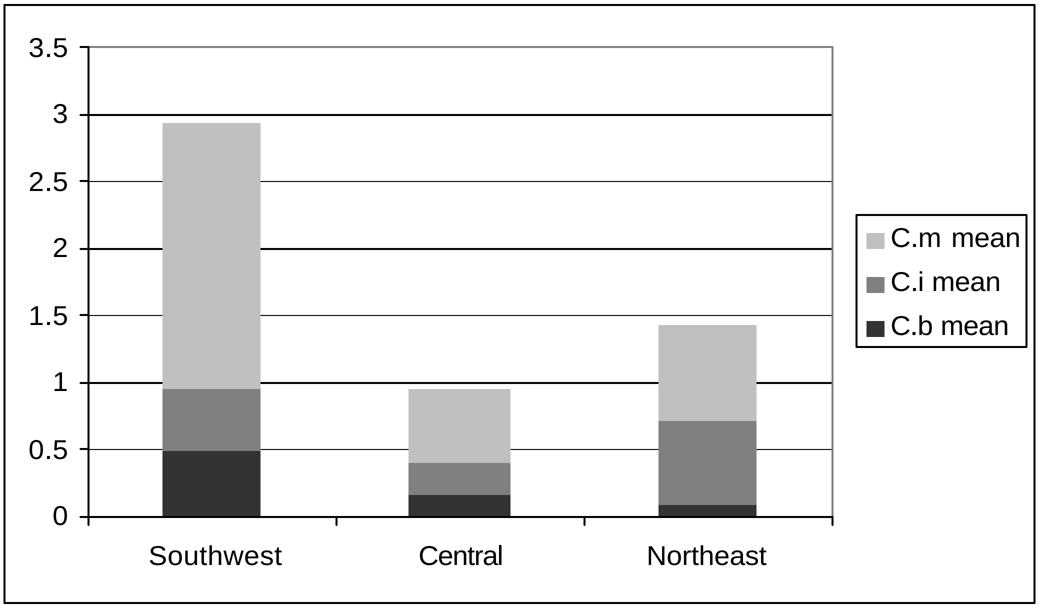

Fig. 9. Mean density of the three crab species per m^2 among regions.

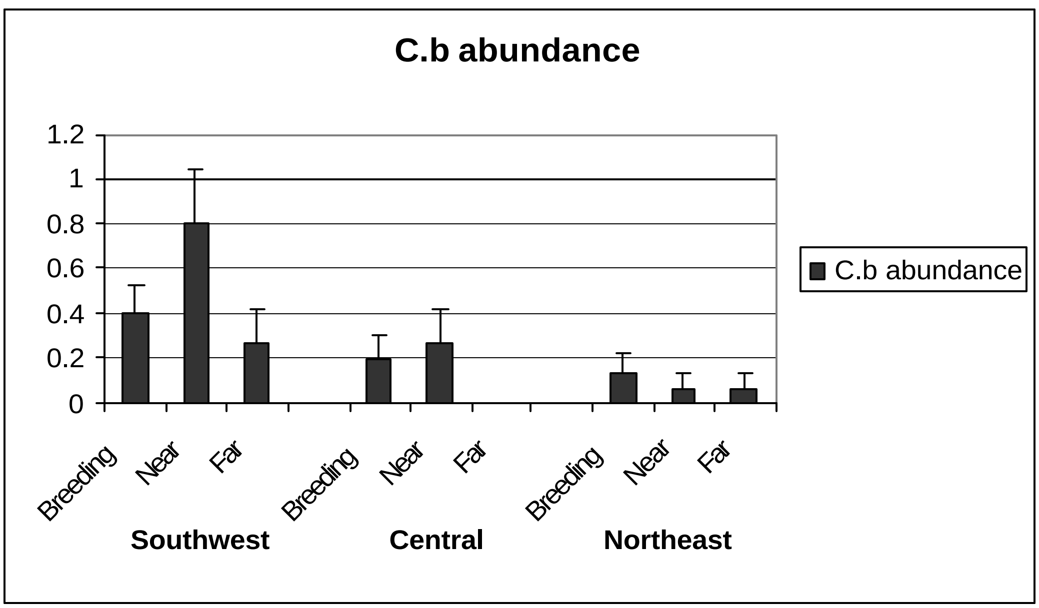

Fig. 10. Mean density of *Cancer Borealis* per m^2 at all of the sites.

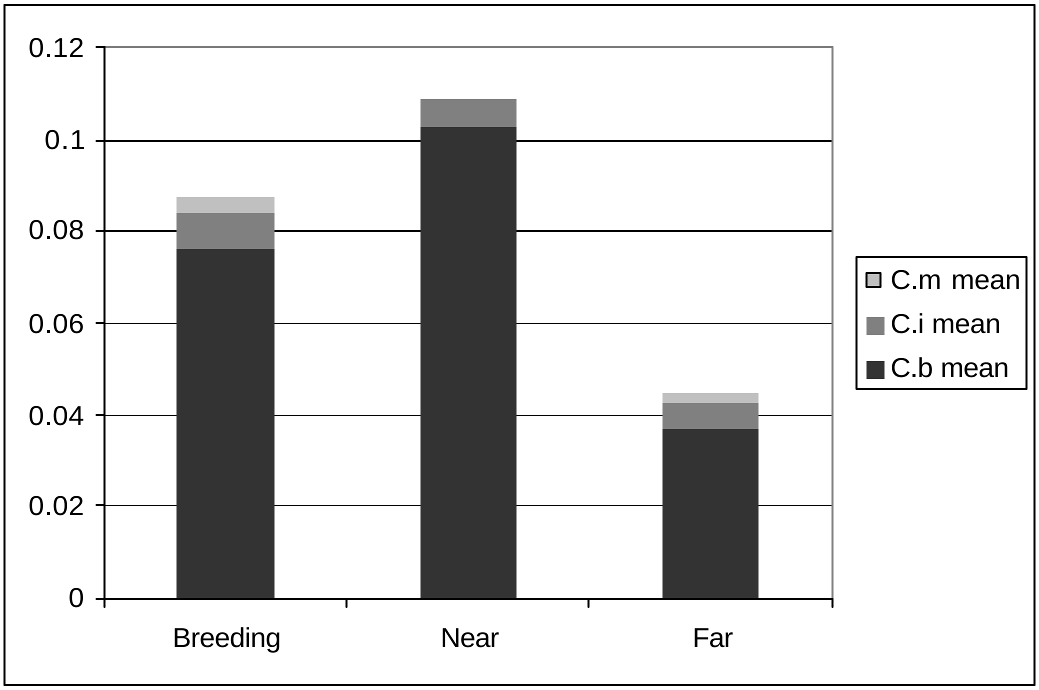

Fig. 11. Mean number of all three species consumed per m for the three site types.

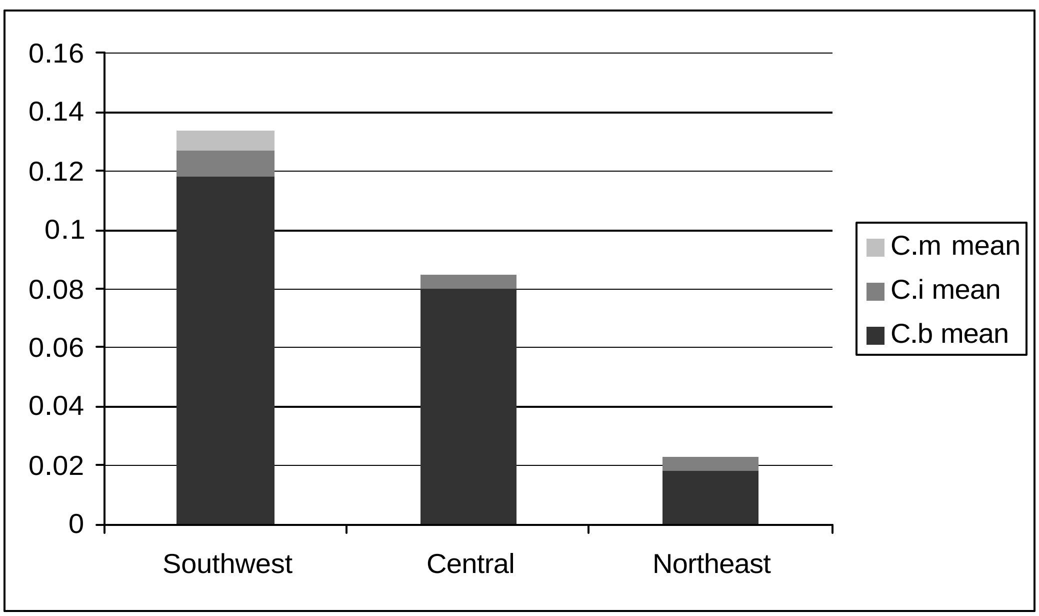

Fig. 12 Mean number of all three crab species consumed per m for the three regions

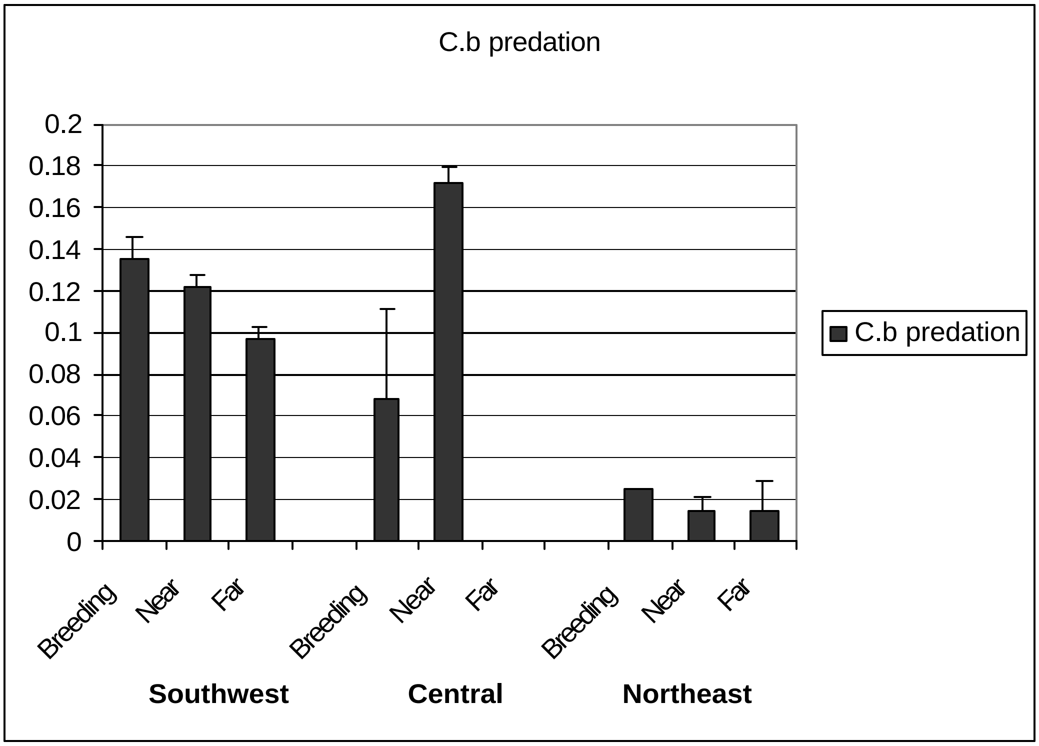

Fig. 13. Mean number of Cancer borealis consumed per m^2 at all sites.

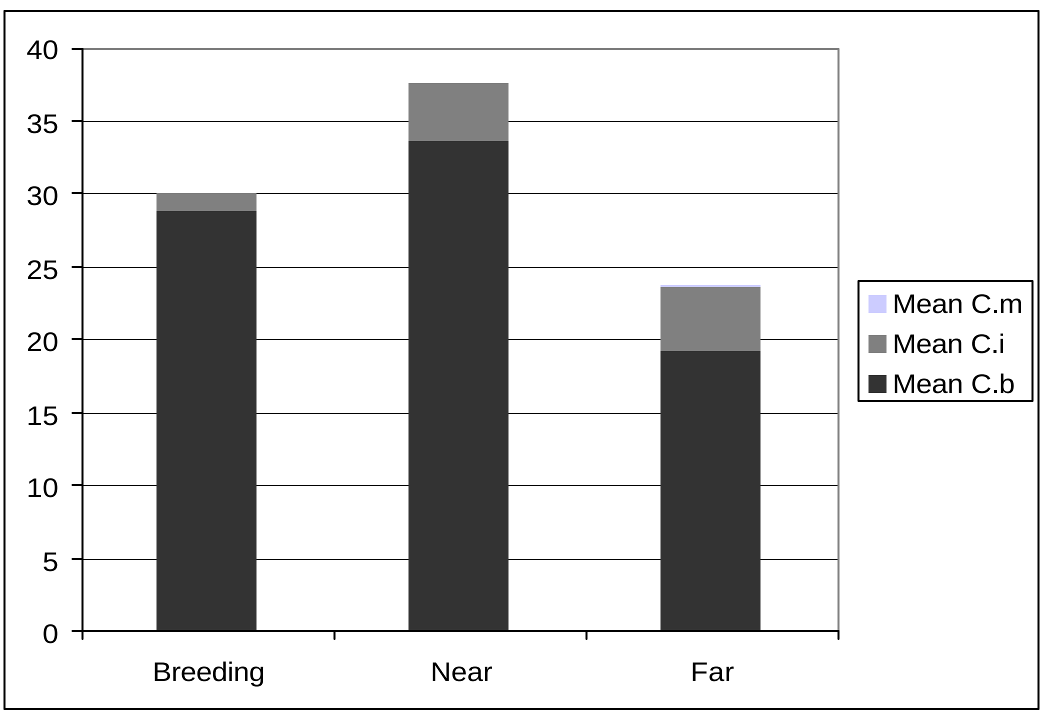

Fig. 14. Percent of available crabs pulled from the intertidal at each low tide at each site type.

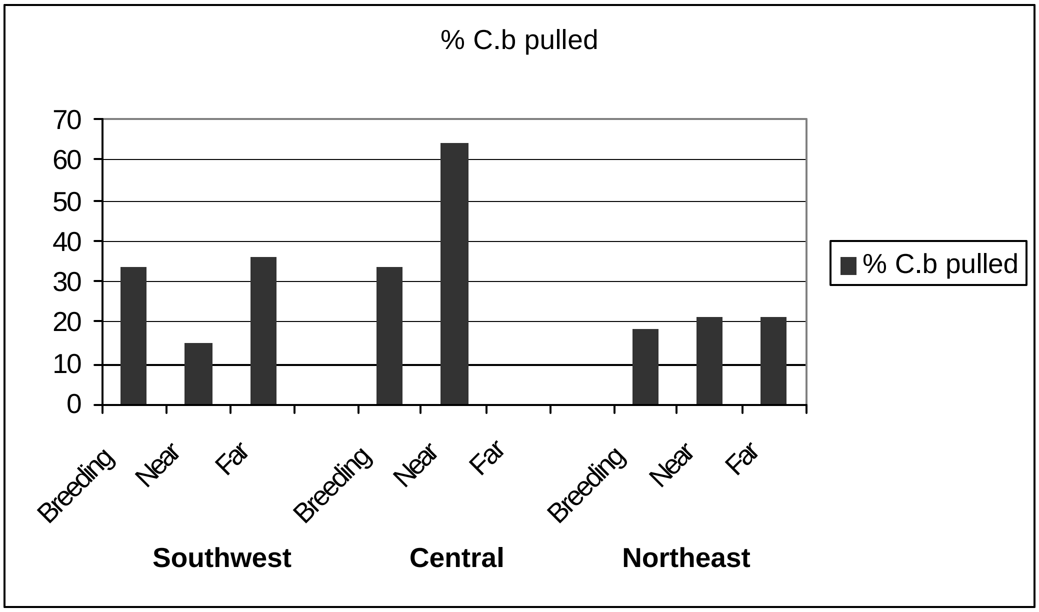

Fig. 15. Percent of available *C. borealis* removed each low tide for all sites

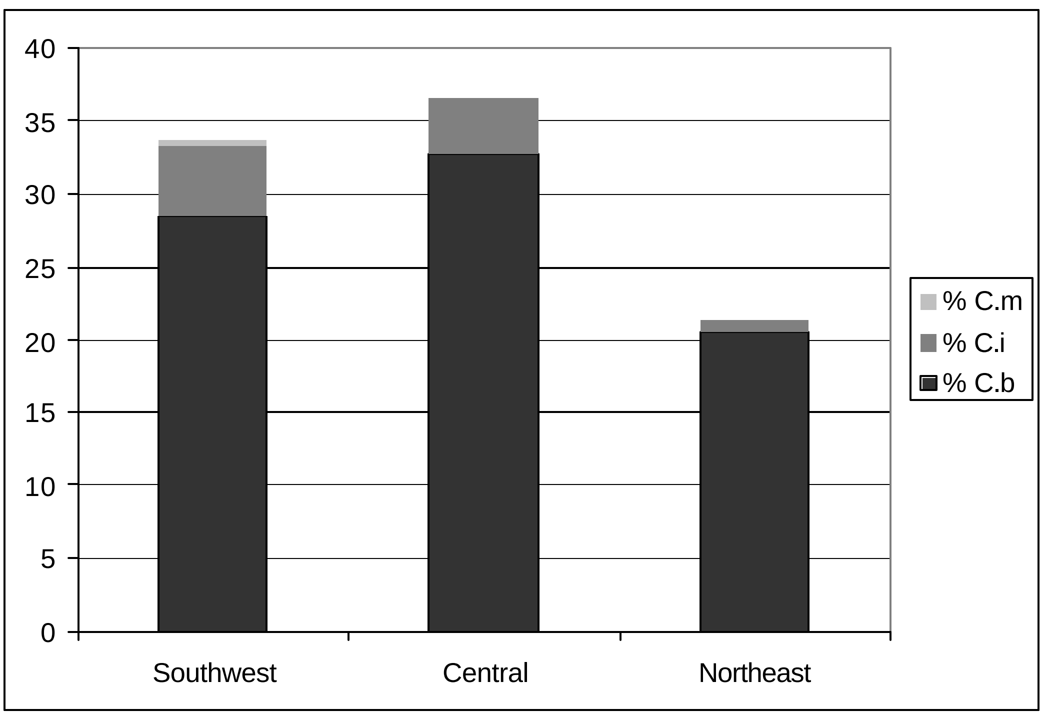

Fig 16. Percent of available crabs removed by gulls each low tide for each region.

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I conducted a geographical comparison of gull predation rates on the crab *Cancer borealis*. Past studies on the Isle of Shoals have shown that as many as 50 percent of the available *C. borealis* crabs in the intertidal are removed by gulls each tide. These studies were conducted on breeding islands, Smuttynose and Appledore, where gull numbers are inflated. I surveyed nine sites up and down the coast of Maine to determine if these high predation rates were simply a breeding island phenomenon or could be generalizable throughout the entire Gulf of Maine. I found high predation rates at all but one site (At this site we found no *C. borealis*.) This suggests that gulls may significantly impact the intertidal population of *C. borealis* and limit their upper distribution in the intertidal. *C. borealis* is an important predator in the intertidal and such high predation rates by gulls may impact lower trophic levels.

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