

Foraging ecology of Herring Gulls (*Larus argentatus*) and Great Black-backed Gulls (*Larus marinus*), with a focus in New England rocky intertidal

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Abstract:

Populations of Great Black-backed Gulls (*Larus marinus*) and Herring Gulls (*L. argentatus*) along coastal New England have fluctuated dramatically during the last century. Currently, populations of *L. marinus* are increasing as *L. argentatus* are precipitously declining. Studies in North America examining competitive interactions between these two species of gulls have demonstrated that *L. marinus* displaces *L. argentatus* from breeding habitats. Quality of nesting and foraging habitat are strong determinates of reproductive success; however, interactions between these two species in foraging habitats have been largely ignored. Within New England, these two species utilize the intertidal as important foraging habitat and can be important intertidal predators within intertidal marine communities. Thus, the foraging behaviors and interactions between *L. marinus* and *L. argentatus* within the intertidal have important implications for future gull population trajectories, as well as their potential predatory impacts on marine communities.

In the first chapter, I explore the diet, prey preference, and the intertidal foraging distributions and behaviors for *L. argentatus* and *L. marinus*. Diet and prey preferences of the two species greatly overlapped, although *L. marinus* tended to have a larger proportion of the most preferred prey items. In general, there was an inverse relationship between the density of foraging *L. argentatus* and *L. marinus*. All aggressive interspecific interactions were initiated by *L. marinus* and resulted in movement of *L. argentatus* from the immediate area. In September, when *L. marinus* begin to leave the island for overwintering grounds, 1) the size of *C. borealis* increased in *L. argentatus* remains, 2) the density of *L. argentatus* foraging and consuming crabs in the intertidal increased, 3) there was a higher proportion of *L. argentatus* foraging in high density areas and 4) interspecific aggressive interactions decreased.

In the second chapter, I explore the basis of *L. argentatus* and *L. marinus* preference for *C. borealis*. I address three possible hypotheses for the basis of this preference, including: 1) behavioral defenses, 2) crypticity and 3) tissue taste. In tethering experiments, both species of gulls preferred *C. irroratus* without claw defense behavior and *C. maenas* in patches cleared of algae, indicating that behavioral defenses and crypticity may limit gull capture of *C. irroratus* and *C. maenas*. However, when all three species of crabs were tethered 1) without any behavioral defense and 2) in a cleared patch, both species of gulls preferred *C. borealis*. When the meat of all crab species was offered to *L. argentatus* and *L. marinus* in colonies, there was no preference for a crab species. For all tethering experiments, selection choices were not statistically different between *L. argentatus* and *L. marinus*. These results indicate that *L. argentatus* and *L. marinus* have a very strong preference for *C. borealis*. Behavioral defenses as well as crypticity may limit capture of *C. irroratus* and *C. maenas*, although manipulating these factors does not alter the preference for *C. borealis*.

In conclusion, these findings suggest that *L. argentatus* and *L. marinus* overlap in diet, prey preferences, and the basis of the preference for *C. borealis*, indicating an overlap in resource utilization and a high potential for competition with intertidal foraging habitats. Furthermore, these findings suggest that aggressive *L. marinus*, at high densities, may suppress *L. argentatus* ability to forage and obtain larger *C. borealis* from the intertidal on Appledore Island.

CHAPTER 1:

Foraging ecology and interactions between Herring Gulls (*Larus argentatus*)
and Great Black-backed Gulls (*Larus marinus*) in New England Rocky
Intertidal, ME

Abstract

Populations of Great Black-backed Gulls (*Larus marinus*) and Herring Gulls (*L. argentatus*) along coastal New England have fluctuated dramatically during the last century. Currently, populations of *L. marinus* are increasing at the expense of *L. argentatus*. Studies in North America have demonstrated that *L. marinus* displaces *L. argentatus* from breeding habitats. Quality of both nesting and foraging habitat are strong determinates of reproductive success; however, interactions of these two species in foraging habitats have been largely ignored. On Appledore Island, ME, these two species utilize the intertidal as important foraging habitat. In this study, we: 1) compared diet and prey preferences of the two species, and 2) examined spatial and temporal patterns in foraging behavior and interspecific interactions in the intertidal. Diet and prey preferences of the two species greatly overlapped. However, patterns in foraging behavior differed: *L. marinus* foraged in a clumped pattern, creating foraging “hotspots,” whereas foraging *L. argentatus* were more evenly distributed around the island. At foraging hotspots, all aggressive interspecific interactions were initiated by *L. marinus* and resulted in movement of *L. argentatus* from the immediate area. The number of aggressive interactions peaked around the time of maximum foraging and was most intense in the lower intertidal. In September, when some *L. marinus* begin to leave the island for overwintering grounds, 1) the size of *C. borealis* increased in *L. argentatus* remains, 2) the density of *L. argentatus* foraging and consuming crabs in the intertidal increased, 3) there was a higher proportion of *L. argentatus* foraging in high density areas and 4) interspecific aggressive interactions decreased. These findings suggest that aggressive *L. marinus*, at high densities, may suppress *L. argentatus* ability to forage and obtain larger crabs from the intertidal on Appledore Island.

Introduction

Interspecific competitive interactions are a major factor determining niche breadth (MacArthur, 1972; Cody, 1974; Pianka, 1982) and may reduce resource overlap of ecologically similar species via partitioning of time, space, food resources or competitive exclusion (Schoener, 1974; Pianka 1973, 1976). In seabird communities, the coexistence of multiple species from one family has been documented in European and North American habitats (Cody, 1973; Fasola et al., 1989; Arcos et al. 2001). Ecological isolating mechanisms promoting the coexistence of multispecific seabird communities have been shown to include body size (Cody, 1973; Fasola et al, 1989), asynchronous breeding seasons (Cody 1973), foraging habitats (Cody, 1973; Hunt and Hunt, 1973; Mudge and Ferns, 1982) and prey items (Garthe et al., 1999; Arcos et al., 2001). Elucidating the degree of resource overlap and competitive interactions for currently coexisting species is necessary in order to predict population trajectories.

The partitioning of foraging habitats and interspecific interference for prey items have important fitness consequences, especially for gull communities during the breeding season. The quality of foraging habitat and diet during the breeding season are strong determinants of reproductive success (Pierotti and Annett 1990, 1991; Annett and Pierotti, 2000). In Western Gulls (*L. occidentalis*), the quality of diet for chicks was positively correlated with growth and survival (Annette and Pierotti, 2000).

In New England, Great Black-backed Gulls (*Larus marinus*) and Herring Gulls (*L. argentatus*) currently coexist on several off-shore breeding islands, whereas *L. argentatus* nearly exclusively bred on many of these islands in the first half of this century (Borrer and Holmes, 1995). Although *L. argentatus* have been more abundant than *L. marinus* in New England in the past century, *L. marinus* are currently increasing at the expense of *L. argentatus* (McGill-

Harlestad, 1985; Cavanaugh, 1992; Pierotti and Good, 1994; Good, 1998; Figure 1). Studies examining competitive interactions between these two species in North America have demonstrated that *L. marinus* displaces *L. argentatus* from prime breeding habitats on offshore islands (McGill-Harelstad, 1985; Good, 1998).

Although competition for nest sites has been examined, only a handful of studies have focused on interactions between the two species in foraging habitats. In New England, Hunt and Hunt (1973) describe habitat partitioning among *L. marinus*, *L. argentatus*, and Laughing Gulls (*L. atricilla*). *L. argentatus* tended to utilize mussel beds and mud flats more often than *L. marinus*, however, both species heavily relied upon human refuse areas as foraging habitat (Hunt and Hunt, 1973). Since that study, the availability of refuse in New England has decreased (Goodale, 2000), suggesting that the use of and reliance on more natural habitats has increased. As a consequence, interspecific interactions may also increase in these habitats.

European studies of *L. argentatus* and *L. marinus* interactions suggest a competitive foraging advantage for *L. marinus*, although this has not been explored in North American populations (Verbeek 1979, Furness 1992, Pierotti and Good 1994). *L. marinus* is the largest gull in North America, whereas *L. argentatus* is considered a medium sized gull and nearly 1/3 the size and weight of *L. marinus* (Pierotti and Good 1994). In general, larger-sized birds have a competitive advantage in interspecific interactions (Burger and Shisler, 1978; Burger, 1983). In Europe, in areas of clumped resources, such as the rocky intertidal, there was a lower abundance of smaller gulls in the presence of larger gulls and, the smaller gulls generally foraged in less productive regions (Hunt and Hunt 1973). While both species are considered kleptoparasites, *L. marinus* have been observed stealing prey from *L. argentatus* at landfills and in intertidal

foraging areas (Verbeek 1979). In Europe, *L. marinus* out-competes *L. argentatus* for fisheries waste and limited marine fish stocks (Furness 1992).

In New England, *L. marinus* are currently increasing while *L. argentatus* are precipitously declining. In 1993, *L. marinus* outnumbered *L. argentatus* for the first time this century in the Isles of Shoals (Borrer and Holmes, 1995). While it has been shown that *L. marinus* displaces *L. argentatus* in breeding habitats, the degree of resource overlap and the potential for competition within foraging habitats has been largely overlooked. The intertidal is an important natural foraging habitat for gulls during the breeding season on islands off the coast of New England (Ellis et al., in review; Good, 1998). In this study, I investigated the potential for competition and interactions between these two species of gulls within the intertidal on Appledore Island, an off-shore breeding island. The questions I addressed were: 1) What are *L. marinus* and *L. argentatus* diet? 2) What are the prey preferences of *L. marinus* and *L. argentatus*? 3) What are the spatial and temporal foraging distributions and behaviors of *L. marinus* and *L. argentatus*? and 4) What is the frequency and outcome of aggressive interaction between the two species of gulls in the intertidal? *L. argentatus* diet, foraging distribution and behavior, and intensity of aggressive interactions were examined at high and low densities of *L. marinus*, depending on the time into the breeding season. I hypothesized that if *L. marinus* have an impact on *L. argentatus* foraging behavior or diet, when the density of *L. marinus* decreases, there will be a shift in *L. argentatus* foraging behavior and diet.

Materials and Methods

Study Site

This study was conducted at the Shoals Marine Laboratory, Appledore Island, in the Gulf of Maine (42 58'N; 70 37'W). Appledore Island is part of a nine island archipelago and located approximately 10km off the coast of New Hampshire, USA. The east side, facing the Atlantic Ocean, is exposed to heavy wave action, whereas the western side is protected. The shoreline is comprised of exposed rocky headlands and boulder coves.

While both species were endangered in the late 1800's in New England, legal protection of seabirds and food supplementation from human refuse and fisheries discard have contributed to the large increase in gull populations (Kadlec and Drury, 1968; Good, 1998). *L. argentatus* abundance peaked at the Isles of Shoals by mid-1900's, whereas *L. marinus* were virtually absent at the beginning of the century (Borrer and Holmes, 1995). Since 1975, the breeding population of *L. argentatus* has declined by half, while *L. marinus* have more than doubled at the Isles of Shoals (Borrer and Holmes, 1995). The most recent published breeding bird census estimated that 1083 *L. argentatus* and 841 *L. marinus* breeding pairs inhabit Appledore Island (Borrer and Holmes, 1995).

L. argentatus form pairs, breed and tend to young on Appledore Island from late March to September whereas *L. marinus* inhabit the island from mid March to late August. Therefore, *L. marinus* migrate from Appledore to the mainland approximately 1 month before *L. argentatus*.

Both species forage within the intertidal and shallow subtidal around the island, as well as landfills on the mainland and open ocean (i.e. lobster fisheries discard). Common prey consumed by *L. argentatus* and *L. marinus* from the intertidal include crabs (*Cancer borealis*, *C.*

irroratus, *Carcinus meanus*), sea urchins (*Strongylocentrotus droebachiensis*), and mussels (*Mytilus edulis*) (Dumas, 1990; Pierotti and Good, 1994; Good, 1998; Ellis et al., in review). Generally, both species plunge dive in order to obtain subtidal crabs, and neither species can dive below 1-2 m (personal observation, Good 1998).

The rocky intertidal and shallow subtidal, where gulls forage, can be divided into three distinct zones characterized by the predominant sessile species: the barnacle zone (2.1-2.7m relative to MLLW), *Ascophyllum* zone (0.6m-2.1m), and *Chondrus* zone (0.6m to shallow subtidal). Gulls also forage in the “near shore” zone, which is the shallow subtidal zone adjacent to the shore. These zonation heights were determined using data from an ongoing intertidal monitoring study on Appledore (M. Dethier, personal communication).

I. What are L. argentatus and L. marinus diets throughout the breeding season?

Adult gulls bring prey items to the nest to feed mates and juveniles. Evidence of these prey items can be found in: 1. pellets of indigestible parts of prey regurgitated by adults and chicks and 2. prey remains not ingested (e.g. crab carapaces). Previous studies comparing pellets, stomach contents, chick and mate feeding, and regurgitations indicate that pellets and prey remains accurately reflect dietary composition (Spaans, 1971; Annette and Pierotti, 1987, 1990). I also observed gull-feeding behavior in colonies and intertidal foraging habitats to ensure that collections of prey remains accurately reflected the breadth of gull diet.

I assessed *L. argentatus* and *L. marinus* diets by collecting pellets and prey remains from nesting territories. I collected prey remains from 15-20 haphazardly chosen nests in each of six *L. argentatus* and *L. marinus* sub-colonies around Appledore Island (Figure 2). The *L. marinus*

colony was generally located at a slightly higher elevation than the *L. argentatus* colony. Prey remains were collected approximately every 2 weeks, from June - September 2001.

During each collection, I separated all prey remains into the following five categories: fish, human refuse, terrestrial vertebrates and insects, crab, and other intertidal prey items. If a collection of prey remains (i.e. crab carapace and chelipeds) resembled one individual at a single nest, only one piece was collected in order to prevent recollection. All remains were cleared from each nest site at the end of each collection period. The first collection (June 9) was not included in the analysis since it was not possible to determine whether these prey items had accumulated from the past months.

Since crabs are the most important intertidal prey item for gulls on Appledore Island (Ellis et al. in review), I compared the species and sizes of crab carapaces in *L. argentatus* and *L. marinus* remains. All crab carapaces and chelipeds were identified to species, either *C. borealis*, *C. irroratus*, or *C. meanaus*, and the maximum carapace width was measured. Novak (2000) found the following regression relating *C. borealis* chelae length (ChL) to maximum carapace width (CW) ($CW = (0.379 \text{ ChL} - 0.00476 \text{ ChL}^2 + 3.5)^2$). I measured all *C. borealis* chelae and calculated carapace width according to the equation above.

For each of the 6 collection dates, I calculated the proportion of remains per prey remains category and per crab species. Prey and crab remains data were transformed (\sqrt{x} arcsin) to correct for normality and homogeneity of variances. I used a one-way repeated-measures ANOVA to test for the effect of species over time.

I performed a one-way ANOVA to determine if *C. borealis* carapace size differed between *L. argentatus* and *L. marinus* remains. Another one-way ANOVA was performed, separately for *L. argentatus* and *L. marinus*, to determine if a difference in crab size existed

between early summer remains (June-early August) and late summer remains (late August-September).

II. What are L. argentatus and L. marinus prey preferences?

II a. Overall Prey Preference

To compare the prey preferences between *L. argentatus* and *L. marinus*, five common prey items were offered to gulls. Prey items included herring (*Clupea harengus*), mussel (*Mydulis edulis*), *C. borealis*, *C. maenas*, and a BBQ chicken wing, which is a typical refuse prey item. Fish and crabs were offered dead to gulls, in order to control for mobility. All trials were conducted from mid-late June 2001.

All trials were conducted in the colonies since adult gulls forage for the offered prey items in multiple locations (i.e. intertidal, mainland, etc). For each trial, I randomly placed each food item in one of five sections on a board. I offered the prey items to a single gull and observed the order in which all items were eaten or handled from at least 15 m away. All experiments were ended after 30 minutes.

I ran experiments in six sub-colonies, with three gulls of each species at each sub-colony (Figure 2). The specific order that each gull chose the prey items was summarized into a sequence. A G-test was conducted to determine if sequences differed between species.

II b. Crab Species Preference

In order to compare *L. argentatus* and *L. marinus* preferences among crab species, I tethered live crabs in the lower intertidal (i.e *Chondrus* zone). All tethering experiments were conducted during low tide, when the lower intertidal is exposed and readily accessible to gull

foraging. All tethered crabs were collected from the intertidal around Appledore Island. Crabs were tethered in areas dominated by a single gull species in order to determine preferences with limited interference from the other species. Thus, all trials were conducted in either a *L. argentatus* or *L. marinus* dominated area of foraging, Babb's Cove or Larus Ledge, respectively (Figure 2).

Crab carapace tethers were constructed using a small nylon cable loop that was fastened to the posterior portion of the carapace with a marine epoxy (A-788 Splash Zone Compound, Kop Coat). The epoxy was painted with a maroon or black nail polish to closely match carapace color. To limit crab movement, I attached carapace tethers to exposed *Chondrus* plants with a dark, tarred nylon rope, of approximately 20 cm long. Plants were separated by approximately 30 cm. Thus, the tethered crabs were independent of each other. Preliminary observations indicated that the crabs could not cut ropes with their claws or break free from tethers.

In each trial, I tethered a set of three crabs, one of each of the following species: *C. borealis*, *C. irroratus*, *C. maenas*. These are the only crab species found in gull prey remains. I controlled for the size of crab by using crabs of similar carapace area, since gulls are considered visual predators. From at least 15m away, I observed and recorded the first crab eaten or handled.

A χ^2 test was conducted in order to determine if a non-random pattern of crab species selection occurred. χ^2 tests were conducted separately for *L. argentatus* and *L. marinus*. A G-test was conducted to determine if crab species preferences differed between gull species.

II c. Crab Size Preference

To determine *L. argentatus* and *L. marinus* size preferences for *C. borealis*, I tethered 3 size classes of *C. borealis*. The three size classes were large (105-90mm), medium (85-70mm), and small (65-50mm). Tethering occurred in the same method as described above in *IIB*.

A χ^2 test was conducted in order to determine if a non-random pattern of crab size selection occurred. χ^2 tests were conducted separately for *L. argentatus* and *L. marinus* trials. A G-test was conducted to determine if size preferences differed between gull species.

III. What are L. argentatus and L. marinus foraging distributions and behaviors within the intertidal throughout the breeding season?

IIIa. Foraging distribution and behaviors around Appledore Island

We conducted surveys to determine the regional distribution, zonation, and foraging behaviors of gulls on Appledore Island. I completed 9 surveys, every 1-2 weeks, from June - September 2001 on the following days: 6/13, 6/24, 7/1, 7/11, 7/21, 7/25, 8/6, 8/23, 9/16 with the following lowtides, 1.1, -1.3, 0.6, 0.7, -1.3, -1.0, 0.3, -0.9, 0.7, respectively. During each survey, we circled the island twice in a boat, 15-20 m away from shore; so that we did not disturb foraging gulls (ie. cause flight or cessation of feeding). The perimeter of the island was divided into 12 regions (Figure 2), and the species, zone and foraging activity for all gulls in the intertidal was recorded in each region. On a topographic map, I measured the linear distance of shoreline within each of these regions, and I converted abundance data to number of gulls per 1 km of shoreline.

Gull behavior was categorized as either foraging or non-foraging. Foraging behavior was subdivided into the following three categories: 1. Consuming crab: visually able to see gull

eating crab (>50mm carapace width) 2. Picking: gull repeatedly raising and lowering head into substrate 3. Searching: head pointed down at least a 45° towards the ground (Dumas 1990)

A one-way repeated measures ANOVA was performed to test for the effect of species over time, for all foraging and non-foraging gulls. Only foraging gulls were included in the following two analyses. I used a two-way repeated measure ANOVA to test for effects of species and zonation over time. Using foraging data from the *Ascophyllum* and *Chondrus* zones, the zones with the highest density of foraging gulls (Ellis et al. in review), I performed a two-way repeated-measures ANOVA to test for effects of species and foraging behavior over time. Circle 1 and Circle 2 were analyzed separately. All data were transformed ($\sqrt{(x + 1)}$) to correct for normality and homogeneity of variances.

III. b. Species abundances in areas of high foraging density

Previous surveys on Appledore Island indicated that foraging gulls concentrated in two main regions: Larus Ledge and Malaga Cut (Ellis et al. in review; Figure 2). Since areas of concentrated foraging efforts may indicate habitats with high quality, abundance and availability of prey (Schoener 1971), I chose to focus on the temporal patterns of gull abundances in these two regions. I observed Larus Ledge and Malaga Cut once a month, June - August 2001. In June, observations began 90 minutes before low tide until 30 minutes after low tide. In order to observe the dynamics between *L. argentatus* and *L. marinus* from high tide to low tide, peak foraging time (Ellis et al. in review), July -August observations began when the *Ascophyllum* zone was first exposed after high tide, 240 minutes before low tide. Binoculars and a spotting scope were used to view gulls at Malaga Cut from a vantage point on a neighboring island, and

at Larus Ledge from a vantage point on a cliff top. Instantaneous scan sampling was performed every 15 minutes (Altman 1974) to note the species, location, and behavior, of gulls in the area.

Foraging *L. argentatus* and *L. marinus* abundances were averaged for the -45min, -30min, -15min, 0, 15min, until low tide scan samples and this foraging data was used to conduct a one-way repeated measure ANOVA to test for the effect of species over time.

IV. How do interspecific aggressive interactions in the intertidal vary spatially and temporally?

Preliminary observations from island surveys suggested that within a single region on the island, there tended to be an inverse relationship between the density of *L. argentatus* and *L. marinus*. Past studies have suggested that *L. marinus* may interfere with *L. argentatus* foraging via aggressive interactions (Good, 1992). In order to examine direct inter-specific interference on intertidal foraging, I observed the frequency of inter-specific aggressive interaction at Larus Ledge, Malaga Point, and Babb's Cove, areas of relatively high gull foraging density (Figure 2). An aggressive interaction was defined as any action in which one gull moved, made noise, or raised their wings towards a second gull, resulting in cessation of activity of the second gull, as well as movement from the immediate area. The three areas were observed once a month, June-August 2001, using instantaneous scan samples (Altman 1974). The initiating species and location of all interspecific aggressive interactions was recorded.

Results

I. What are L. argentatus and L. marinus diets throughout a breeding season?

Ia. Overall diet

Overall, both species had very similar diets (Figure 3a,b). The proportion of crab was significantly higher in *L. argentatus* than *L. marinus* remains, whereas the proportion of fish and terrestrial prey was significantly greater for *L. marinus* than *L. argentatus* (Table 1).

In the diet of both species, the proportion of fish decreased significantly from June-September 2001, whereas the proportion of crab increased over time (Table 1).

Ib. Crab Species

C. borealis was the most abundant crab species found in *L. marinus* and *L. argentatus* remains, although the proportion of this species was higher in *L. marinus* remains (Table 2; Figure 4a,b). The proportion of *C. irroratus* was higher in *L. argentatus* remains (Table 2).

Ic. Crab Size

C. borealis carapaces in *L. marinus* remains were significantly larger than in *L. argentatus* remains (one-way ANOVA, $t=7.628$, $df=980$, $p<0.0001$; Figure 5). In *L. argentatus* remains, *C. borealis* were significantly larger in late August- September than in June - early August (one-way ANOVA, $t = 7.062$, $df= 526$, $p<0.0001$).

II. What are L. argentatus and L. marinus prey preferences?

IIa Overall Prey Preference

When gulls were offered five prey items, there were a total of six sequences of the order in which the items were consumed and handled (Table 3). There was no significant difference

between the sequences chosen by *L. argentatus* and *L. marinus* (G-test, $\chi^2 = 8.53$, $df=5$, $p>0.05$). Fish was chosen first in 100% of the *L. marinus* trials and in 88.9% of the *L. argentatus* trials.

Ib Crab Species

In crab species preference experiments, *C. borealis* was chosen significantly more often than *C. irroratus* and *C. maenas* by both *L. argentatus* ($\chi^2=12.35$, $df=2$, $p=0.004$) and *L. marinus* ($\chi^2= 17.45$, $df=2$, $p=0.001$; Figure 6). There was no significant difference between *L. argentatus* and *L. marinus* preference for *C. borealis* (G-test, $\chi^2=0.14$, $df=3$, $p>0.05$).

Ic. Crab Size

In crab size preference experiments, *L. argentatus* chose medium crabs most often ($\chi^2= 14.56$, $df=2$, $p=0.002$); whereas *L. marinus* chose the largest crabs most often ($\chi^2= 8.87$, $df=2$, $p=0.044$; Figure 7). However, there was no significant difference between the *L. argentatus* and *L. marinus* preferences for crab size (G-test, $\chi^2=6.40$, $df=3$, $p>0.05$).

III. What are L. argentatus and L. marinus foraging distributions and behaviors within the intertidal around Appledore Island throughout the breeding season?

IIIa. Foraging distribution and behaviors around Appledore Island throughout a breeding season:

Densities of foraging gulls ranged from 3.27 to 33.17 gulls/km within a single region (Figure 8a). Density of foraging *L. marinus* was patchy, whereas foraging *L. argentatus* were

more evenly distributed. Within a single region, there tended to be an inverse relationship between the density of foraging *L. argentatus* and the density of foraging *L. marinus*.

Throughout summer 2001, total gull density and foraging density peaked in July and in September, although densities did not significantly differ between *L. marinus* and *L. argentatus* and (Table 4). *L. argentatus* total and foraging density increased with time where as *L. marinus* decreased with time (Table 4; Figure 8b).

Density of foraging gulls in the various intertidal zones varied over time, although the *Chondrus* zone was used most often by both species (Table 5).

Of the three foraging behaviors, searching was observed significantly more often than consuming crabs or picking (Table 5). *L. marinus* consumed crab more often than *L. argentatus* whereas *L. argentatus* picked more often (Figures 9a,b). For both species, the density of gulls consuming crabs increased from June- September 2001 (Table 5).

III. b. Species abundances in areas of high foraging density

Island surveys indicated two regions of overall high foraging densities, Larus Ledge and Malaga Cut (Figure 2). In these areas, gull foraging abundance at low tide peaked in July and decreased in late August (Table 6). Significantly more *L. marinus* foraged in these areas than *L. argentatus* (Table 6). The abundance of foraging *L. argentatus* increased with time, and peaked in late August, when *L. marinus* begin to migrate to mainland (Table 6; Figure 10).

The proportion of *L. argentatus* was greater near high tide, and decreased until low tide in July and August (Figure 11 a, b). In August, a higher proportion of *L. argentatus* was observed.

IV. How do interspecific aggressive interactions in the intertidal vary spatially and temporally?

Of the 27 inter-specific aggressive interactions observed, all were initiated by *L. marinus*. The number of inter-specific aggressive interactions per gull tended to increase throughout the falling tide and peaked at low tide: the period of maximum gull foraging density (Ellis et al., in review; Figure 12a). The intensity of aggressive interaction increased from the high intertidal to the low intertidal/near shore zone (Figure 12b). Aggressive interactions per gull peaked in July, and were lowest in August (Figure 12c).

Discussion

Multi-specific seabird communities have been shown to coexist by varying in breeding season, size, foraging habitat and prey species. In many situations, interspecific competition drives these ecologically separating mechanisms (Cody, 1973, Fasola et al., 1989, Arcos et al., 2001). In New England, *L. marinus* displaces *L. argentatus* from prime nesting habitats on breeding islands (McGill-Harlestad 1985, Good, 1998), although, prior to this study, little was known about the competitive interactions between these two species in foraging habitats. This study demonstrated that: 1) *L. marinus* and *L. argentatus* had similar diets, indicating an overlap in resource utilization and a high potential for competition between the two species in the intertidal, 2) *L. marinus* and *L. argentatus* had similar prey preferences, 3) *L. marinus* consumed more crabs in the intertidal than *L. argentatus* and dominated all high density foraging habitats, and 4) *L. marinus* won all aggressive interactions, which were most intense at low tide and in the lower intertidal. A natural “exclusion” experiment occurred when *L. marinus* began to migrate from Appledore Island to the mainland a month prior to *L. argentatus*. At lower *L. marinus*

density 1) the size of *C. borealis* increased in *L. argentatus* remains, 2) the density of *L. argentatus* foraging and consuming crabs in the intertidal increased, 3) there was a higher proportion of *L. argentatus* foraging in high density areas and 4) interspecific aggressive interactions decreased. These findings suggest that aggressive *L. marinus*, at high densities, suppress *L. argentatus* ability to forage and obtain larger crabs from the intertidal on Appledore Island.

Overlap in L. argentatus and L. marinus diet and prey preferences

I found that *L. argentatus* and *L. marinus* have similar diets and prey preferences, indicating an overlap in resource utilization and a high potential for competition. Other studies of *L. argentatus* and *L. marinus* indicate that both species consume similar prey items, such as marine invertebrates, fish, insects, and human refuse (Hunt and Hunt, 1973; Pierotti and Good, 1994; Good, 1998; Ellis et al., in review). While the diet is similar, *L. marinus* tended to have a larger proportion of the most preferred food items (fish, *C. borealis*, large/medium crabs), suggesting that *L. marinus* has a competitive advantage in foraging.

Fish was the most preferred prey item for both species of gulls, although there was a higher proportion in *L. marinus* than *L. argentatus* prey remains. In Europe, Furness (1992) found that *L. marinus* out-competes *L. argentatus* for limited fishery discard. Likewise, within the Gulf of Maine, anecdotal observations also suggests that *L. marinus* obtain discarded bait more often than *L. argentatus*, despite the larger number of *L. argentatus* attempting to compete for the bait at lobster boats (personal observation; Goodale, 2000). Fish is a profitable prey item, especially for chicks during the breeding season. Fish contain more calories per unit than human food scraps at garbage dumps (Pierotti and Annett, 1987), seabirds, and invertebrate prey (Good,

1998). *L. occidentalis* chicks that were fed fish, had higher growth and survival rates than chicks fed refuse (Pierotti and Annette, 2000). At Appledore Island, the largest source of fish is from old macerated bait on near-by lobster boats. Thus, a short travel time to obtain fish is an additional factor making fish a profitable prey item.

In my study, refuse is a major component of gull diet, comprising 25-45% of prey remains. Past studies have suggested that reliance on “unnatural” food sources, such as refuse, has lessened competition in more natural habitats, such as the intertidal, between *L. argentatus* and *L. marinus* (Hunt and Hunt, 1973; Good, 1992). Refuse adds a supplemental foraging habitat thereby permitting species with high overlap in natural habitats to coexist. However, current trends indicate that the availability of human refuse is decreasing (Goodale, 2000). A study in Maine, USA conducted 20 years earlier indicated that *L. marinus* and *L. argentatus* utilized refuse habitats for 50% to 71% of total foraging time (Hunt and Hunt, 1973). A study on Appledore Island in 1991 showed that human refuse comprised 54% of *L. marinus* diet (Good 1998). A lower percentage of refuse in gull diet in my study, 25-45%, further suggests that there is a decreasing availability of refuse.

On Appledore Island, the intertidal is an important foraging ground for both species of gulls. Prey items from this habitat, mainly *C. borealis* crabs, comprised nearly 50% of *L. argentatus* and *L. marinus* prey remains. In New England, previous studies indicate that, during the breeding season, the intertidal is more intensely utilized as foraging habitat on breeding island than on mainland. For example, on the mainland of Maine, USA, *L. marinus* and *L. argentatus* spent only 5% to 8%, respectively, of total habitat time in intertidal habitats (Hunt and Hunt 1973). Studies from Appledore Island demonstrated a higher reliance on intertidal habitats, with *L. marinus* diet comprised of 27% (Good, 1998) to 35 % (Ellis et al., in review) of

intertidal prey items. When gulls inhabit offshore islands during the breeding season, the intertidal is one of the closest foraging habitats. Travel time directly reduces the time spent attending territories, which results in negative fitness consequences; with lower nest attendance there is a higher frequency of territory intrusion and predation on chicks (Piettori 1982, 1987, Morris & Black 1980). Intertidal invertebrate organisms also provide essential nutrients for breeding females and their chicks (Bayne 1976, Pierotti and Annett 1987, 1990).

This study shows that there is a higher proportion of crab in *L. argentatus* prey remains than *L. marinus* remains. However, this does not necessarily indicate that *L. argentatus* are consuming more crabs than *L. marinus*. Crabs are either 1) eaten in the intertidal or 2) brought back to the colonies to be fed to mates and juveniles. Therefore, it is possible that *L. argentatus* travel from the intertidal to colonies to consume crabs, perhaps to avoid interference from *L. marinus*. *L. marinus* are kleptoparasites that often steal crabs from *L. argentatus* in the intertidal (personal observation, Verbeek 1979). Island survey data indicates that the density of *L. argentatus* consuming crabs in the intertidal does not increase until August, when *L. marinus* aggressiveness and abundance decreases. In addition, I observed *L. argentatus* returning to the colonies with freshly caught crabs more often than did *L. marinus*.

Of all intertidal prey items, *C. borealis* were consumed most often and also more preferred by both gull species in prey preference experiments. This prey choice is especially noteworthy because the most abundant crab species in the intertidal is *C. maenas* (Ellis et. al, in review), whereas *C. borealis* is relatively much less abundant. Other New England studies have also indicated that *L. argentatus* and *L. marinus* consume *C. borealis* more often than other available crab species (Dumas, 1990; Good, 1992; Ellis et al., in review). However, the basis for

this preference is unclear. Possible explanations include size, profitability, crypticity, as well as defense and escape behavior. Chapter 2 further explores these hypotheses.

In size preference experiments, *L. argentatus*, a medium sized-gull, preferred medium-sized crab whereas *L. marinus*, the largest gull in North America, preferred the largest crabs. Seabird body size often correlates with the size of their prey (Fasola et al., 1989). Prey remains indicate that *L. marinus*, on average, consume medium sized crabs, whereas *L. argentatus* do not consume medium sized crabs until late August - September. *L. argentatus* may be unable to obtain larger crabs due to interference from *L. marinus* earlier in the breeding season. In Nahant, MA, where there are approximately 80% *L. argentatus* foraging in intertidal habitats, *L. argentatus* consumed the largest *C. borealis* (Dumas, 1990), further suggesting that *L. marinus* impact the ability of *L. argentatus* to forage on the largest crabs.

In this study, *L. marinus* had a larger proportion of the most preferred prey items. An ability to attain these prey items may have important fitness consequences if these more profitable prey items are of limited abundance. In this case, the larger proportion within *L. marinus* remains would indicate that *L. argentatus* are driven to forage for less profitable prey items. In the Dutch Wadden Sea, direct competition for fish between *L. argentatus* and Lesser Black-backed Gulls (*L. fuscus*), has led *L. argentatus* to specialize on marine invertebrates, and may be responsible for declines in their breeding success since the 1960's (Noordhuis and Spaans 1992).

While a lower quality diet may have indirect fitness consequence, anecdotal evidence from prey remains suggests that *L. marinus* can have a direct impact on *L. argentatus* fitness. On Appledore Island, *L. marinus* frequently prey upon *L. argentatus* chicks, whereas *L. argentatus* never consumed *L. marinus* chicks. Currently, the number of *L. marinus* specializing on *L.*

argentatus chicks on Appledore Island is increasing (Good, 1998). Other studies, in North America and Europe, have also shown that *L. marinus* regularly prey upon *L. argentatus* chicks and comprise an important component of *L. marinus* diet (Lock, 1973; Pierotti, 1979; Mudge and Ferns, 1982).

Intertidal foraging distribution and behaviors

While both species utilize the intertidal on Appledore Island, several lines of evidence suggest that *L. marinus* may dominate the most profitable foraging regions and that interspecific aggressive interactions are a possible mechanism to explain the foraging distribution and patterns of *L. argentatus*. *L. argentatus* may not be as abundant in the most profitable foraging regions if 1) aggressive interactions from *L. marinus* directly drive them out, or 2) *L. argentatus* prefer to forage in less profitable areas that provide spatial refuges from *L. marinus* interference. Less productive areas may be more profitable for less aggressive individuals if there is high competitive interference at high quality foraging sites (Sutherland and Parker, 1985). In patchy foraging habitats in Europe, smaller gulls tended to forage in less productive areas when in the presence of larger gulls (Hunt and Hunt, 1973).

This study indicates that *L. marinus* generally obtain large crabs from the lowest intertidal zones, whereas *L. argentatus* generally pick smaller organisms, such as small crabs (<50cm carapace width), sea stars, or mussels, from higher zones. Lower zones typically contain greater prey densities of larger individuals than in higher zones (Irons, 1986; Menge, 1983). Although upper zones have smaller organisms, there is shorter handling and searching times in these zones (Irons, 1986). Since gulls in higher intertidal zones also have a lower intensity of

aggressive interactions, *L. argentatus* may forage in these upper zones in order to quickly consume prey and avoid interference from *L. marinus*.

In a similar study on the coast of NH, approximately 10 km inshore of Appledore Island, there was three times the amount of *L. argentatus* in the intertidal than *L. marinus* (Good, 1992). The mainland, therefore, may provide a second spatial refuge from *L. marinus* interference during the breeding season. However, this mainland study was conducted at a time when *L. marinus* were approximately 65% as abundant as at the time of my study (Borror and Holmes 1995). Therefore, the difference in numbers between the two studies may be indicative of past population trends and suggest that interference from *L. marinus* has been increasing during the past 10 years.

High gull foraging densities may be indicative of a preferred and highly profitable foraging habitat. Areas of concentrated foraging efforts are indicative of habitats with high abundance, availability and quality of prey items (Schoener, 1971). At Larus Ledge and Malaga Cut, sites with moderately exposed headlands with high gull foraging densities, there was a higher abundance of *L. marinus*. *L. argentatus* abundance increased when aggressive interactions decreased, suggesting that *L. marinus* may be excluding *L. argentatus* from a preferred foraging habitat. In Nahant, MA, which is dominated by *L. argentatus*, gulls concentrated in moderately exposed headlands (Dumas, 1990). My findings and these studies suggest that *L. argentatus* are unable to concentrate in preferred foraging regions due to interference from *L. marinus*.

The intensity of aggressive interactions peaked in July and decreased in late August. Similarly, in breeding colonies, mean aggression rate is highest in July, right after chicks hatch for both species of gulls (Burger 1983, Pierotti 1987).

Implications

MacArthur and Levins (1967) determined a theoretical limit of resource overlap between two species. Before this study, it was known that *L. argentatus* and *L. marinus* have similar breeding seasons and habitats. This study indicates that *L. argentatus* and *L. marinus* have similar diets and prey preferences. Furthermore, this study suggests that resource partitioning on Appledore Island, in terms of prey size and foraging regions, may underlay the current coexistence of these species on a breeding island.

Currently, it is unclear whether *L. marinus* will continue to increase at the expense of *L. argentatus*, leading to competitive exclusion, or whether population growth trends will stabilize. Past gull population trends have been heavily influenced by human activity. In the 19th century, *L. marinus* and *L. argentatus* were virtually absent from coastal areas as seabirds were hunted for food and the millinery trade (Drury, 1973). Throughout the 20th century, gull populations have soared in part from legal protection of seabirds and food supplementation from human sources (William and Drury, 1968). However, the extreme increase in gull densities high has resulted a plethora of negative social and ecological impacts, such as harming endangered bird species, fouling of building, and interference with airport safety. Therefore, *L. marinus* and *L. argentatus* are currently controlled throughout New England. Since this study and past research indicates that *L. marinus* are increasing at the expense of *L. argentatus*, it is important for managers to consider this "natural" control on *L. argentatus* when planning control programs.

In addition to direct population control, the availability of refuse is an important determinant of the degree of competitiveness between the two species and influence on future population trajectories. Refuse, and other food "supplements" from anthropogenic sources, decrease the degree of resource overlap between these two species of gulls in more natural habitats (Hunt and Hunt, 1973). If the availability of refuse continues to decrease, as suggested

by this study, there will most likely be an increase in the competition in more natural habitats, such as the rocky intertidal (Hunt and Hunt, 1973; Good, 1992).

In conclusion, human management of gull populations and competitive interactions between the two species will have significant indirect and direct effects on the growth or decline of *L. marinus* and *L. argentatus*.

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Figures:

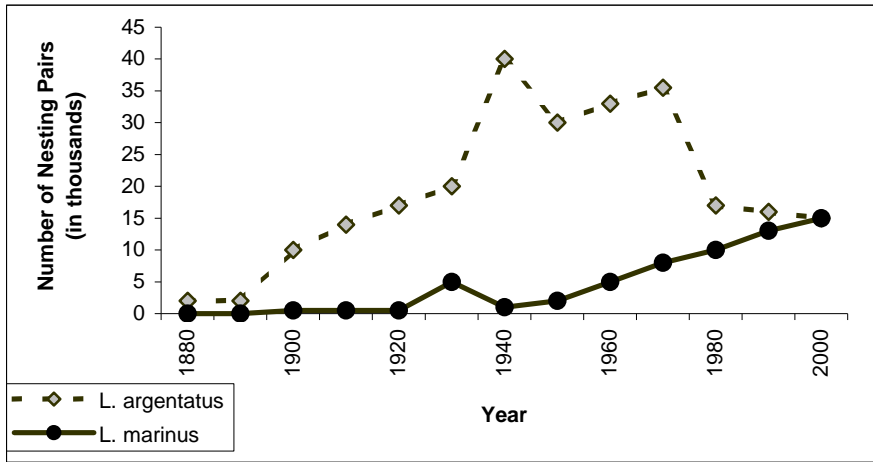


Figure 1: Population trends for *L. marinus* and *L. argentatus* in Maine, USA during the twentieth century.

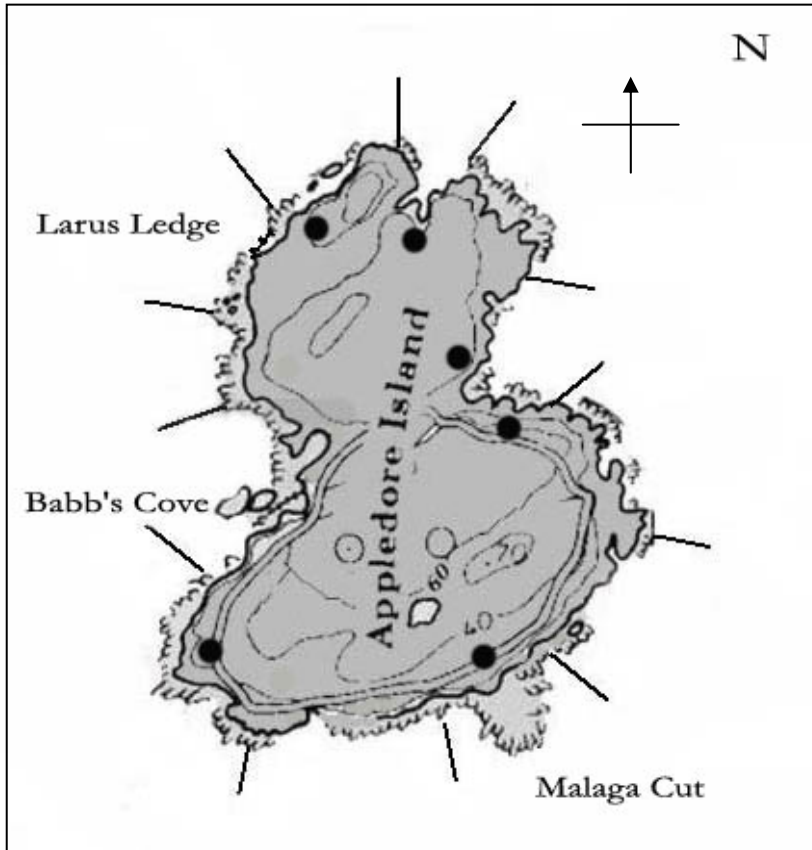


Figure 2: Map of Appledore Island, Maine, USA (42° 58' N; 70° 37' W) in the Gulf of Maine, approximately 10km off the coast of New Hampshire. Black dots indicate sites of prey remain collections and overall prey preference experiments. Babb's Cove and Larus Ledge are areas of high *L. argentatus* and *L. marinus* foraging density, respectively, and therefore used for all crab tethering experiments. Black lines indicate a division among regions for island surveys. Larus Ledge and Malaga Cut were areas of high gull foraging densities and therefore used as sites for scan samples. Scan samples for aggressive interaction observations occurred at Larus Ledge, Malaga Cut, and Babb's Cove.

Figure 3a. *L. argentatus*

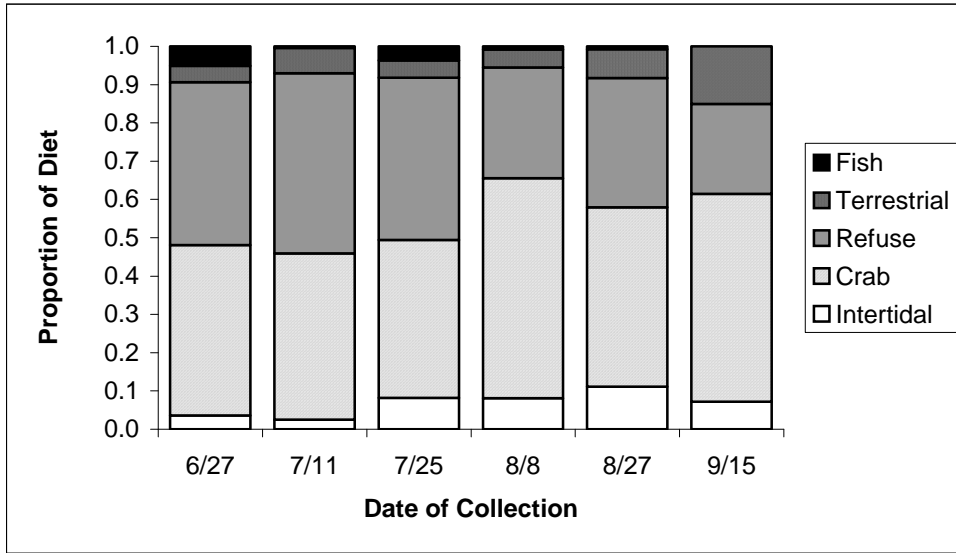


Figure 3b. *L. marinus*

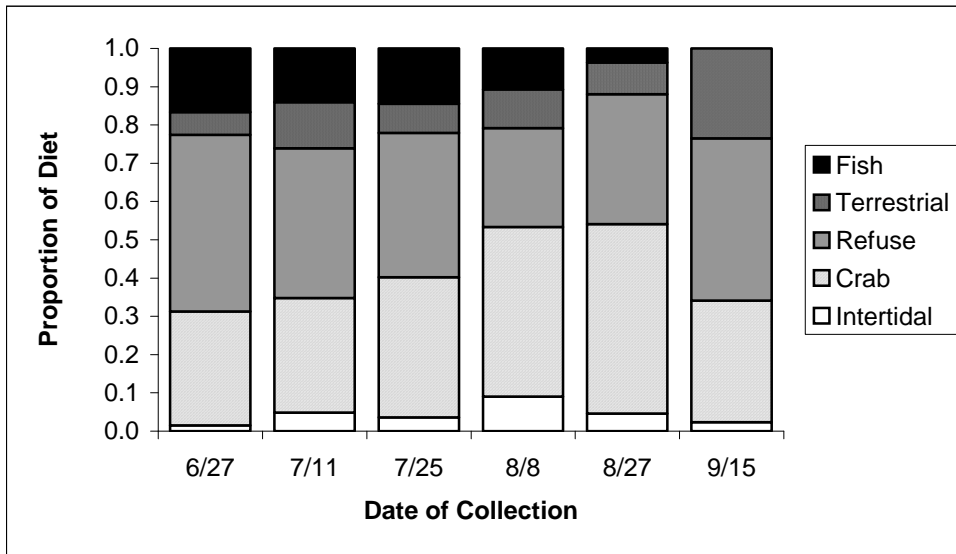


Figure 3. Proportion of prey remains collected from (a) *L. argentatus* and (b) *L. marinus* sub-colonies on Appledore Island, ME from June-September 2001. $n=1245$ prey remains in *L. argentatus* collections and $n = 1521$ prey remains in *L. marinus* collections

Figure 4a: *L. argentatus*

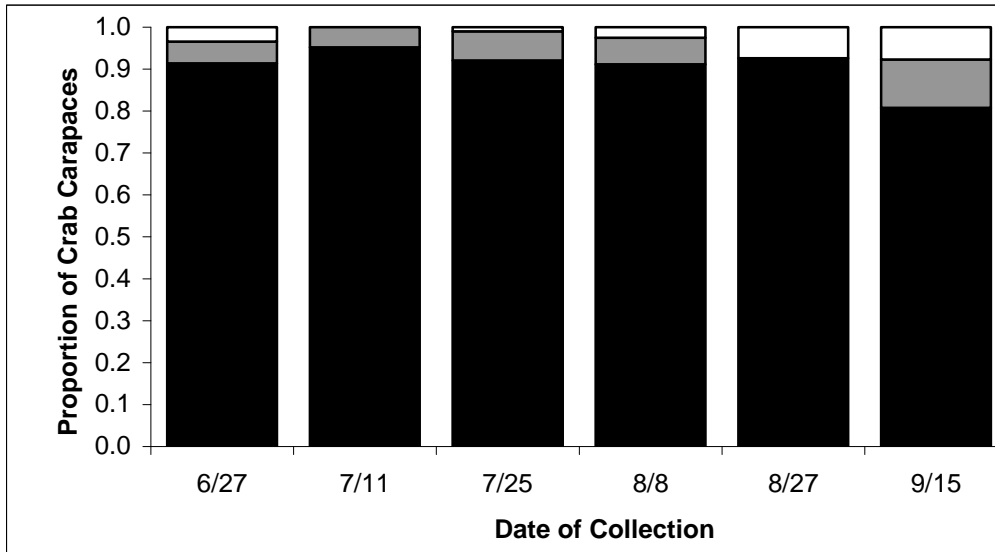


Figure 4b. *L. marinus*

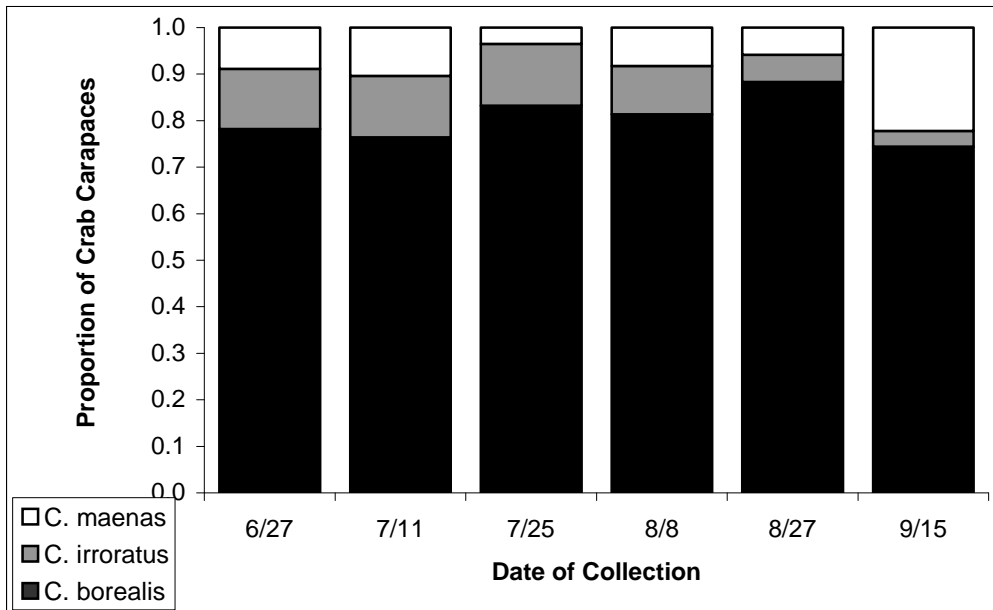


Figure 4. Proportion of three crab species represented in carapace collected from (a) *L. argentatus* and (b) *L. marinus* sub-colonies on Appledore Island, ME from June-September 2001. $n=718$ carapaces in *L. argentatus* collections and $n = 539$ carapaces in *L. marinus* collections

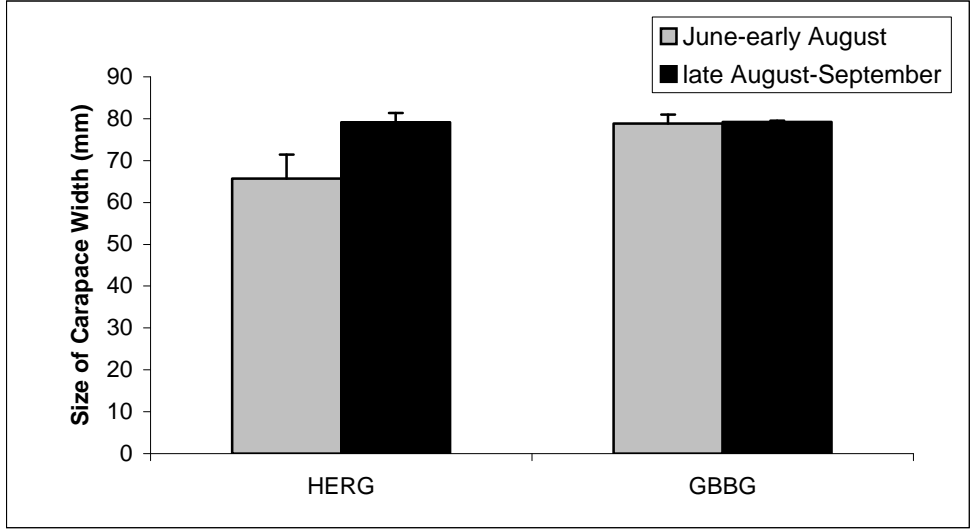


Figure 5. The maximum carapace width for all *C. borealis* carapaces in *L. argentatus* and *L. marinus* remains in the June- September 2001. Carapace width was significantly greater in *L. marinus* remains than *L. arentatus*. In *L. argentatus* remains, carapace width was significantly greater at the end of the breeding season than earlier in the breeding season. Error bars represent ± 1 SE.

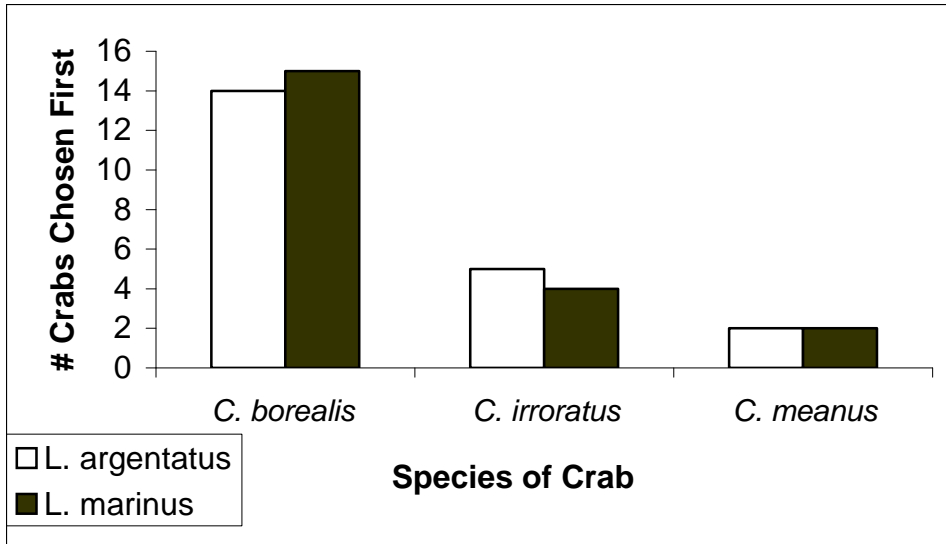


Figure 6. Results from crab species preference experiments. Both *L. argentatus* and *L. marinus* preferred *C. borealis* and there was no significant difference between there preferences. $n=21$ for *L. argentatus* and $n=21$ for *L. marinus*

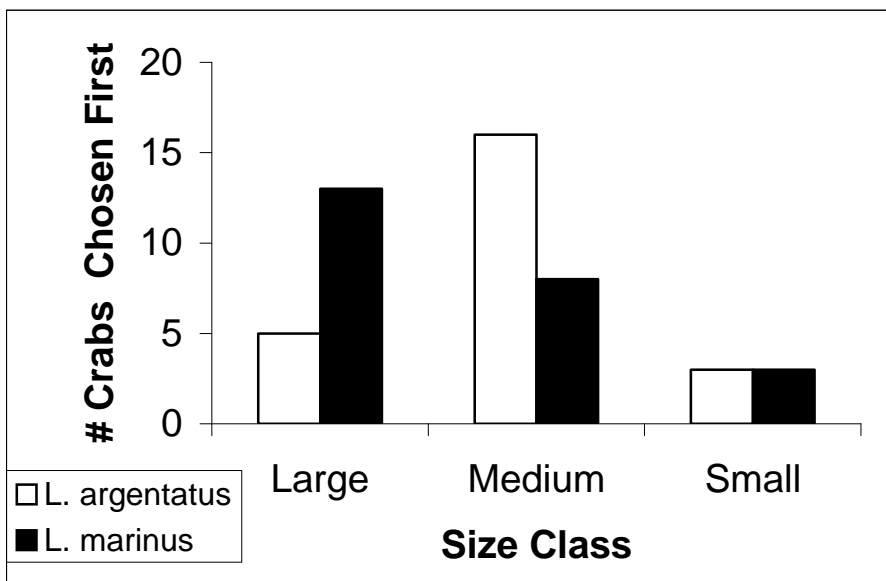


Figure 7. Results from *C. borealis* size preference experiments. *L. argentatus* prefer medium sized whereas *L. marinus* preferred the largest crabs. $n=24$ for *L. argentatus* and $n=24$ for *L. marinus*

Figure 8a. *L. argentatus* and *L. marinus* foraging density June-August 2001

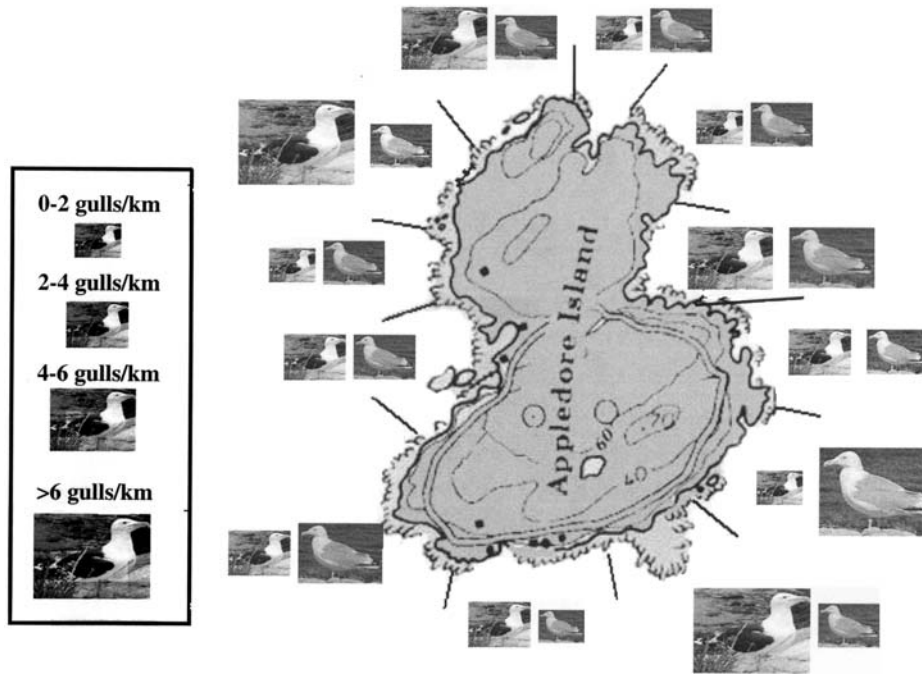


Figure 8b. *L. argentatus* foraging densities in June-August and in September (in boxes) 2001

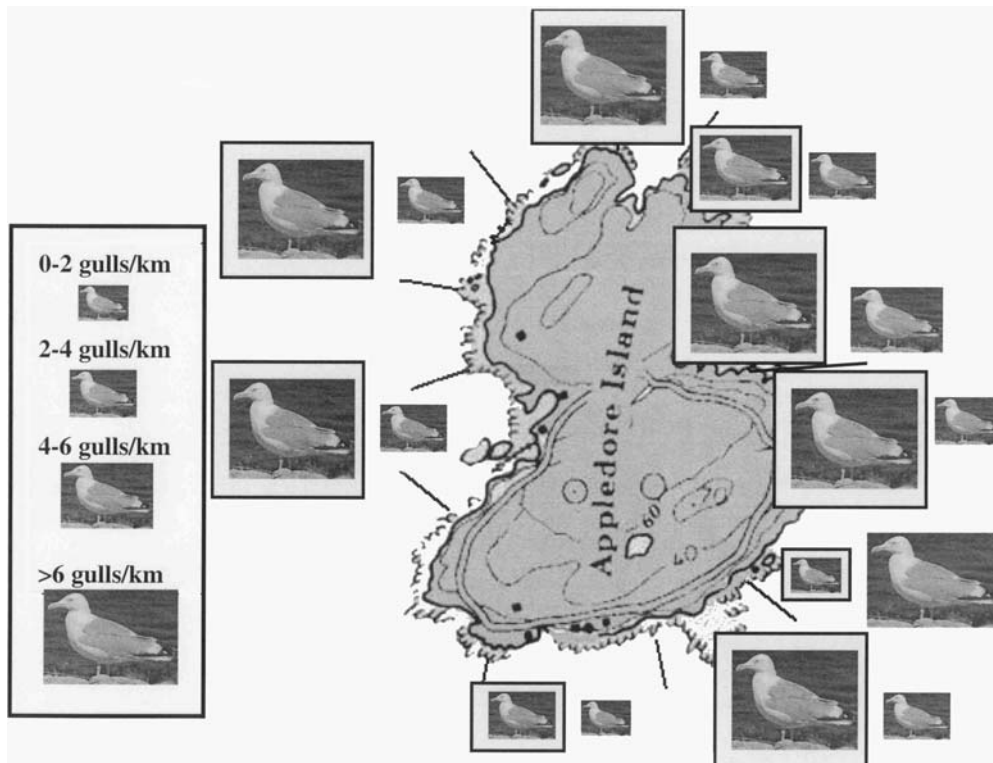


Figure 8. Densities of foraging gulls divided among the 12 regions at Appledore Island. Gull icons represent foraging densities (individual km^{-1}). (a) *L. argentatus* and *L. marinus* foraging densities from June - August 2001 island surveys. (b) *L. argentatus* foraging density in June-August and in September. Icons in grey boxes indicated September densities. September foraging data was only included in regions where *L. marinus* density decreased.

Figure 9a. Consuming crabs

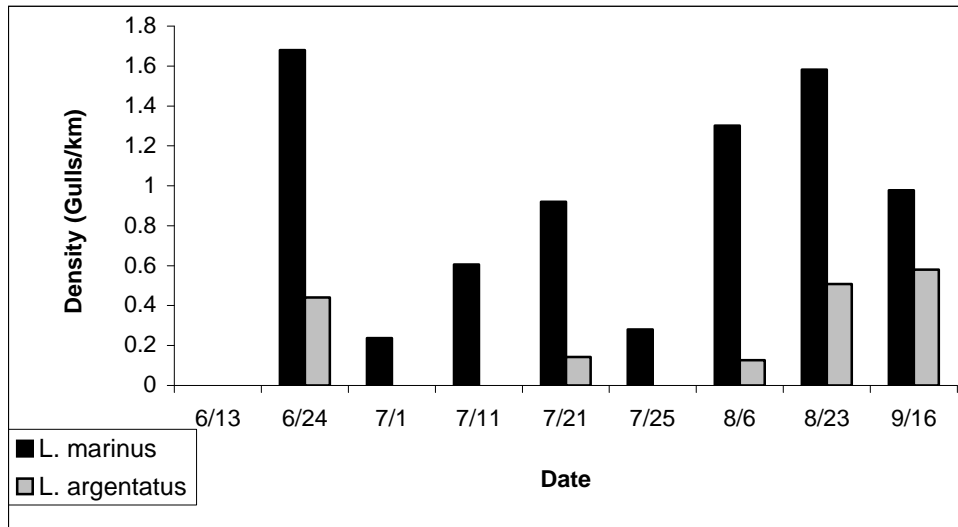


Figure 9b. Picking

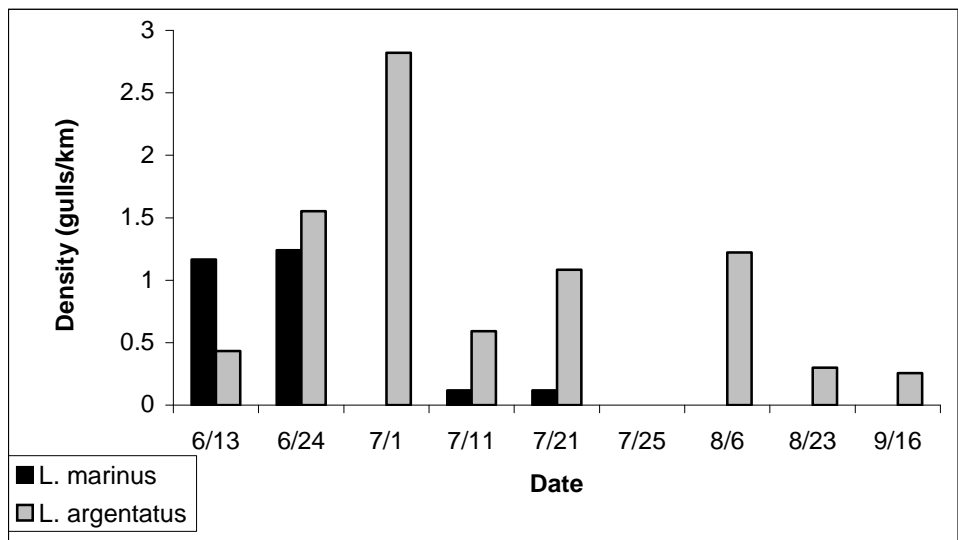


Figure 9. Densities of *L. argentatus* and *L. marinus* (a) consuming crabs and (b) picking during island surveys from June-September 2001.

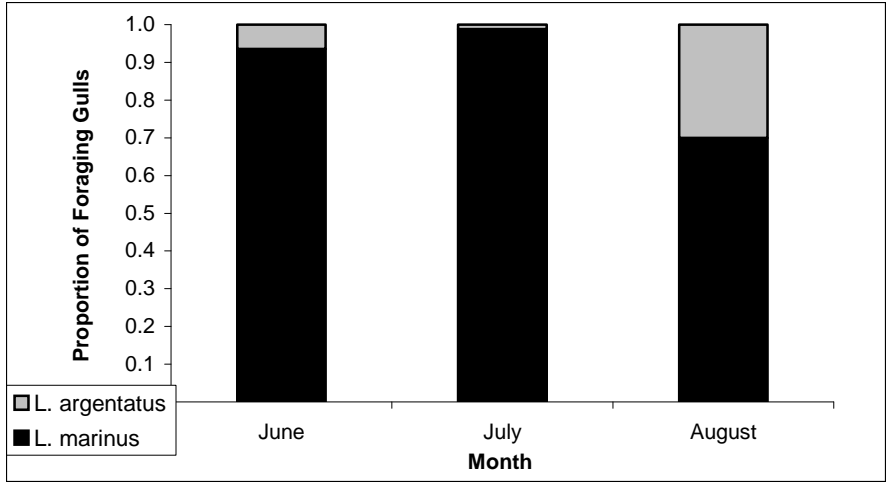


Figure 10. Proportion of foraging *L. argentatus* and *L. marinus* from -45, -30, -15, 0, and +15 minutes till low tide scan samples. Observations were conducted at Larus Ledge and Malaga Cut.

Figure 11a. July

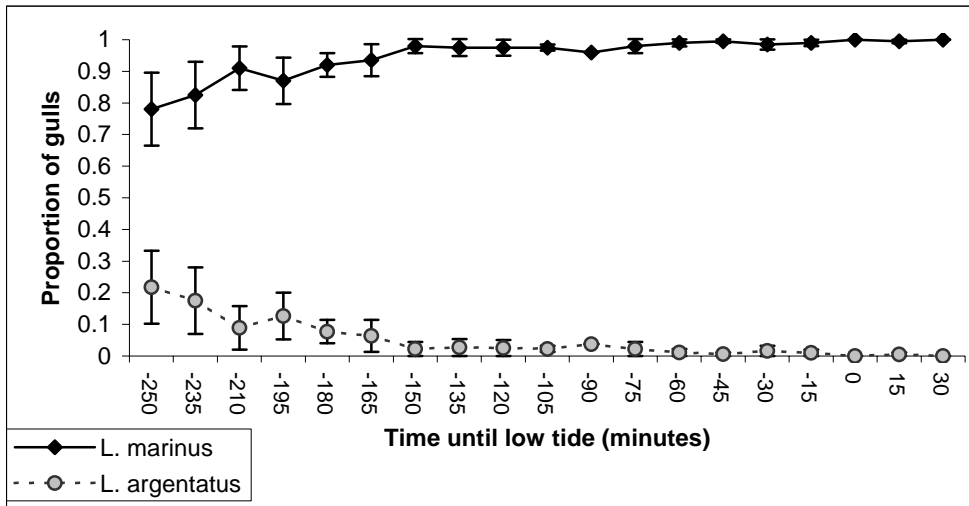


Figure 11b. August

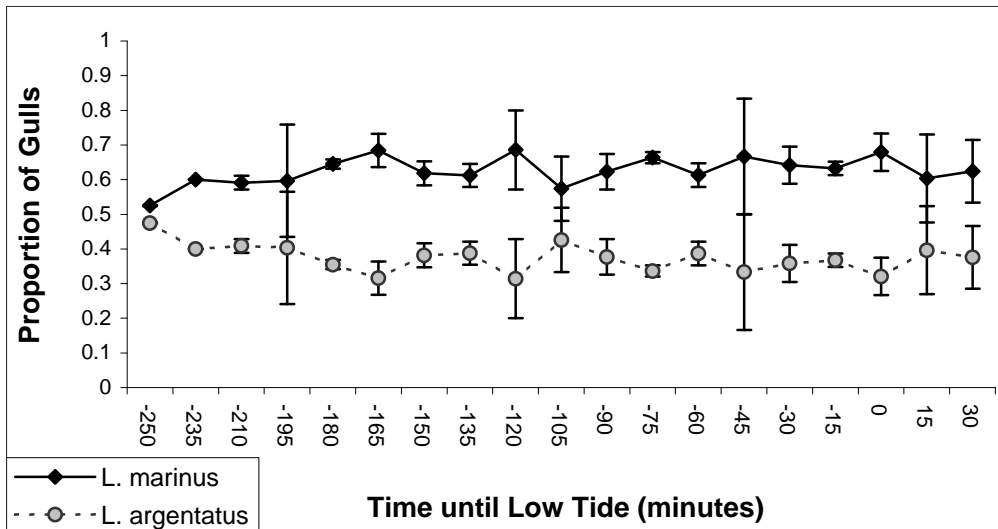


Figure 11. Proportion of *L. argentatus* and *L. marinus* during falling tides in (a) July and (b) August. Observations were conducted at Larus Ledge and Malaga Cut (Figure 2).

Figure 12a: Aggressive interactions during a falling tide

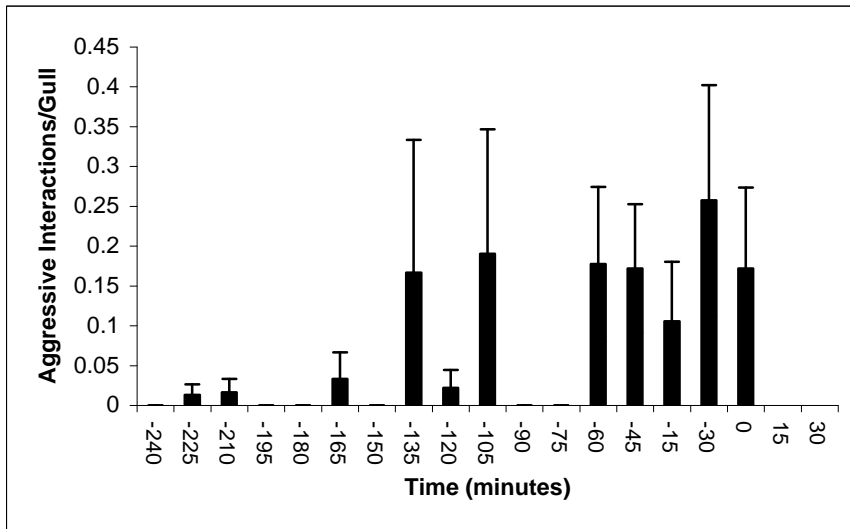


Figure 12b. Aggressive interactions from the high to low intertidal

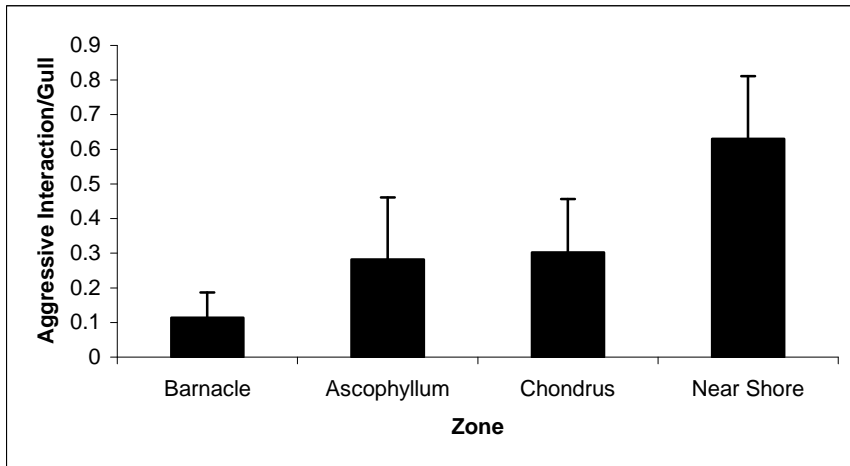


Figure 12c. Aggressive interactions from June- August 2001

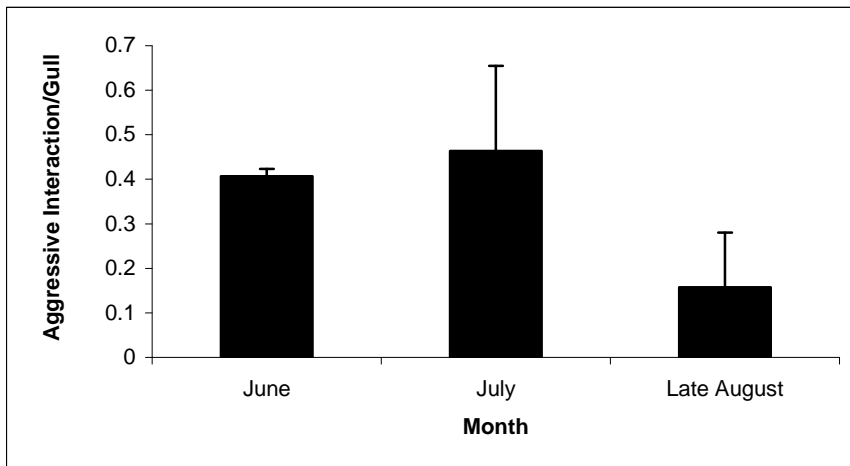


Figure 12. The number of aggressive interactions/gull (a) during a falling tide, (b) from the high intertidal to the low intertidal/shallow subtidal, (c) from June-August 2001. All aggressive interactions were won by *L. marnius*. Observations were conducted at Larus Ledge, Malaga Cut, and Babb's Cove (Figure 2).

	F value	df	p value
Fish			
Species	21.8958	1	0.0009 **
Time	17.7220	5	0.0016 *
Refuse			
Species	0.1123	1	0.7444
Time	8.4751	5	0.0108
Terrestrial			
Species	11.9548	1	0.0061 *
Time	1.6498	5	0.2788
Crab			
Species	5.1985	1	0.0458 *
Time	4.2444	5	0.0536
Other Intertidal			
Species	0.2383	1	0.1537
Time	1.9120	5	0.2264

Table 1. Results from one-way repeated measures ANOVA testing for the effect of species over time. Separate tests were run for fish, refuse, terrestrial vertebrates and insects, crabs, and other intertidal prey items. * indicates significant values (*p≤0.05; ** p≤0.001; ***p≤0.0001)

	F value	df	p value
<i>C. borealis</i>			
Species	12.1220	1	0.0059 *
Time	0.8954	5	0.5385
<i>C. irroratus</i>			
Species	12.8222	1	0.0050 *
Time	2.9194	5	0.1123
<i>C. meanas</i>			
Species	2.4231	1	0.1506
Time	0.7245	5	0.6296

Table 2. Results from one-way repeated-measures ANOVA testing for the effect of species over time. Separate tests were run for each crab species. * indicates significant values (*p≤0.05; ** p≤0.001; ***p≤0.001)

Order Food Item Chosen	<i>L. argentatus</i>	<i>L. marinus</i>
Fish, Chicken, <i>C. borealis</i> , <i>C. meanas</i> , mussel	11	15
Fish, Chicken, <i>C. borealis</i> , NT- <i>C. meanas</i> , NT-mussel	3	2
Fish, Chicken, <i>C. borealis</i> , mussel, NT- <i>C. meanas</i>	1	1
Chicken, Fish, <i>C. borealis</i> , mussel, NT- <i>C. meanas</i>	1	0
Fish, mussel, chicken, <i>C. borealis</i> , <i>C. meanas</i>	1	0
Chicken, Fish, <i>C. borealis</i> , <i>C. meanas</i> , NT-mussel	1	0

Table 3. The order in which *L. argentatus* and *L. marinus* handled or consumed prey items offered during overall prey preference experiments in breeding colonies. There was no significant difference between *L. argentatus* and *L. marinus* preferences (G-test, $\chi^2 = 8.53$, $df=5$, $p>0.05$).

	<u>Circle 1</u>			<u>Circle 2</u>		
	<i>F Value</i>	<i>df</i>	<i>p value</i>	<i>F value</i>	<i>df</i>	<i>p value</i>
Overall Density						
Species	0.7856	1	0.3850	0.7835	1	0.3850
Time	13.1475	7	<0.0001 ***	8.3760	8	0.0002 **
Species x Time	3.7937	7	0.0129 *	1.7368	8	0.1699
Foraging Density						
Species	0.4232	1	0.5176	0.2793	1	0.5989
Time	5.6496	7	<0.0001 ***	4.2353	8	0.0005 **
Species x Time	2.9036	7	0.0112 *	3.3714	8	0.0030 *

Table 4. Results of repeated-measures ANOVA examining the effect of species over time for overall and foraging densities of *L. argentatus* and *L. marinus* from island surveys June-September 2001. * indicates significant values (* $p \leq 0.05$; ** $p \leq 0.001$; *** $p \leq 0.0001$)

	<i>Circle 1</i>			<i>Circle 2</i>		
	<i>F value</i>	<i>df</i>	<i>p value</i>	<i>F value</i>	<i>df</i>	<i>p value</i>
Zonation						
Zone	34.8957	2	<0.0001 ***	28.1711	2	<0.0001 ***
Zone x Spp	1.5583	2	0.2183	0.6521	2	0.5243
Zone x Time	2.8959	14	0.0009 **	3.6509	16	<0.0001 ***
Zone x Time x Spp	2.40	14	0.0054 *	2.36	16	0.0044 *
Foraging Behaviors						
Activity	15.7956	2	<0.0001 ***	22.8348	2	<0.0001 ***
Activity x Spp	9.4977	2	0.0002	5.0789	2	0.0089 *
Activity x Time	4.0041	14	<0.0001 ***	3.8876	16	<0.0001 ***
Activity x Time x Spp	3.0257	14	0.0005	2.7389	16	0.0010 **

Table 5. Results of two-way repeated-measures ANOVA examining the effects 1) of species and zone and 2) species and foraging behaviors in the *Chondrus* and *Ascophyllum* zones from island surveys. * indicates significant values (* $p \leq 0.05$; ** $p \leq 0.001$; *** $p \leq 0.0001$)

	F value	df	p value
Species	20.106	6	<0.0001 ***
Time	5.596	5	0.053
Species x Time	7.9425	5	0.028 *

Table 6. Results of one-way repeated-measures ANOVA examining the effect of species over time in high density foraging areas, Larus Ledge and Malaga Cut. Observations were conducted once a month June-August 2001. * indicates significant values (* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$)

CHAPTER 2:

The basis for Herring Gull (*Larus argentatus*) and Great Black-backed Gull (*Larus marinus*) preference among three species of intertidal crabs in New England

Abstract

Gulls are important intertidal predators within rocky intertidal communities. Past studies have indicated that Herring Gulls (*L. argentatus*) and Great Black-backed Gulls (*L. marinus*) preferentially consume *C. borealis* more often than other intertidal crab species. This study addresses three possible hypotheses for the basis of this preference, including: 1) behavioral defenses, 2) crypticity and 3) tissue taste. In tethering experiments, both species of gulls preferred *C. irroratus* without claw defense behavior and *C. maenas* in patches cleared of algae, indicating that behavioral defenses and crypticity may constraint gull ability to obtain *C. irroratus* and *C. maenas*. However, when all three species of crabs were tethered 1) without any behavioral defense and 2) in a cleared patch, both species of gulls preferred *C. borealis*. When the meat of all crab species was offered to *L. argentatus* and *L. marinus* in colonies, there was no preference for a crab species. When the meat of all crab species was offered to *L. argentatus* and *L. marinus* in colonies, there was no preference for a single crab species. These results indicate that *L. argentatus* and *L. marinus* have a very strong preference for *C. borealis*. Behavioral defenses as well as crypticity may limit gulls from capturing *C. irroratus* and *C. maenas*, although manipulating these factors does not alter the preference for *C. borealis*.

Introduction:

In marine and terrestrial communities, prey selection and preference can have community-wide ramifications in terms of the distribution of prey species (Connell, 1961; Witman 1985), community structure (Janzen, 1970) and biodiversity (Paine, 1966). Although generalist predators may have a broad diet, many selectively consume, and therefore prefer, certain prey species within a local habitat (Annett and Pierotti, 1984; Ebersole and Kennedy, 1995).

Optimal foraging theory predicts that prey preferences are based on maximum energetic profitability of prey (MacArthur and Pianka, 1966; Charnov, 1976). However, other studies have indicated that a variety of other factors, including interference from competitors, prey defenses, and the ability to recognize and locate prey, strongly influence prey preferences. Within marine environments, the degree of predatory defenses has been an important determinant of prey selection and preference (Waters, 1973; Edmunds et al., 1974; Schmitt, 1982; Annett and Pierotti 1984). In other studies, non-cryptic species were selected over more profitable, cryptic prey if search time is higher for hard to recognize species (Hughes, 1979; Erichsen et al., 1980).

In New England rocky intertidal habitats, Herring Gulls (*Larus argentatus*) and Great Black-backed Gulls (*Larus marinus*) are important predators of crabs (Good, 1992b; Ellis et al., in review; see Chapter 1). Although both species are considered generalist, past studies have indicated that gulls consume the rock crab, *Cancer borealis*, more often than the other two available crab species, *C. irroratus*, *Carcinus maenas* (Dumas, 1990; Good, 1992a; Ellis et al., in review; see Chapter 1). Ellis et al. (in review) found the proportion of *C. borealis* consumed to be significantly higher than the proportion available in the intertidal on Appledore Island, ME.

Moreover, when these three species of crab were made equally available to foraging gulls, *L. argentatus* and *L. marinus* selected *C. borealis* most often (see Chapter 1).

When attacked by a predator, *C. maenas* and *C. irroratus* are generally very aggressive and lift their claws in defense, whereas *C. borealis* generally tucks its claws under the carapace (personal observation). *C. maenas* is a dark green crab, and may be more cryptic within the dominant intertidal algal assemblage (*Ascophyllum*, *Chondrus*, *Fucus*) than pink *Cancer* spp (Gosner 1971). Dumas and Witman (1993) found *C. maenas* more susceptible to gull predation in tidepools without mussels than *C. irroratus*.

While it is clear that *C. borealis* is a preferred prey item, the basis for preference has been unclear. In this study, I examined the role of crab species crypticity, behavioral defense, and tissue taste in determining *L. marinus* and *L. argentatus* foraging success and preferences. This study compares *L. marinus* and *L. argentatus* preferences to continue to examine the interspecific potential for competition for *C. borealis*, as initially explored in Chapter 1.

Materials and Methods:

Study Site

This study was conducted at the Shoals Marine Laboratory, Appledore Island, in the Gulf of Maine (42 58'N; 70 37'W; Fig 1). Appledore Island is part of a nine island archipelago and located approximately 10km off the coast of New Hampshire, USA. The east side, facing the Atlantic Ocean, is exposed to heavy wave action, whereas the western side is protected. The shoreline is comprised of exposed rocky headlands and boulder coves. The most recent published

breeding bird census estimated that 1083 *L. argentatus* and 841 *L. marinus* breeding pairs inhabit Appledore Island (Borrer and Holmes, 1995).

Gulls on Appledore Island forage within the intertidal and shallow subtidal around the island, as well as at mainland landfills and open ocean (i.e. lobster fisheries discard). Ellis et al. (in review) indicated that the intertidal is an important foraging habitat for breeding gulls on Appledore Island. In New England, common prey for *L. argentatus* and *L. marinus* from the low intertidal and shallow subtidal include crabs (*Cancer borealis*, *C. irroratus*, *Carcinus meanus*), sea urchins (*Strongylocentrotus droebachiensis*), and mussels (*Mytilus edulis*) (Dumas, 1990; Good, 1998; Ellis et al., in review). Generally, both species plunge dive in order to obtain subtidal crabs, and neither species can dive below 1-2 m (personal observation, Good 1998).

General Tethering Methods:

In order to understand what factors influence *L. argentatus* and *L. marinus* preference for *C. borealis*, I tethered live crabs in the low intertidal (i.e. *Chondrus* zone, 0.6m to shallow subtidal; M. Dethier, personal communication). All tethering experiments were conducted during low tide, when the *Chondrus* zone was exposed and readily accessible to gull foraging. This is also the period of maximum gull foraging (Ellis et al., in review). All tethered crabs were collected from the intertidal around Appledore Island. Crabs were tethered in areas dominated by a single gull species in order to determine preferences with limited interference from the other species. Thus, all trials were conducted in either a *L. argentatus* or *L. marinus* dominated area of foraging, Babb's Cove or Larus Ledge, respectively (Figure 1).

Crab carapace tethers were constructed using a small nylon cable loop that was fastened to the posterior portion of the carapace with a marine epoxy (A-788 Splash Zone Compound, Kop Coat). The epoxy was painted with a maroon or black nail polish to closely match carapace color. To limit crab movement, I attached carapace tethers to exposed *Chondrus* plants with a dark, tarred nylon rope, approximately 20 cm long. Tethered crabs were separated by approximately 30 cm. Thus, the tethered crabs were independent of each other. Preliminary observations indicated that the crabs could not cut ropes with their claws or break free from tethers.

Crab size may play an important role in determining prey choice (see Chapter 1). Therefore, size of crabs was controlled in all preference experiments by tethering crabs of similar carapace area, since gulls are considered visual predators. I observed and recorded the first crab eaten or handled from at least 15 m away, either in a boat off shore or behind nearby boulders.

Hypothesis I: Behavioral defenses

*Ia. The relative deterrence factor for *C. irroratus* and *C. borealis* claw defense behavior*

In order to determine how claw defense behavior deterred gull foraging, I tethered *C. irroratus* with and without claw defense behavior. I paired similar sizes of *C. irroratus* for each of the two treatments. In the first treatment, I wrapped a 4-inch cable-tie around the claws of each crab. I set cable-tied crabs in sea-tables for at least 2 hours, or until they showed normal walking behavior. In the second treatment, crabs had complete movement of their claws for defense. Each set of two crabs, one of each treatment, were considered a replicate.

The two treatments were repeated with *C. borealis* in order to determine the relative deterrence factor for *C. irroratus* and *C. borealis* claw defense behavior. *C. maenas* were not included in this experiment in order to isolate the effects of crypticity with defense behavior.

2. Preference of immobile *C. borealis*, *C. irroratus*, *C. maenas*

Since preliminary results from the above experiment indicated that defense behavior limit gull captures for *C. irroratus*, I tethered all crab species without defense abilities in order to determine if gull preference for *C. borealis* would change. I tethered sets of one dead crab from each species as explained above. A set of one *C. borealis*, one *C. irroratus*, and one *C. maenas* was considered a replicate.

Hypothesis II: Crypticity

*Ila. The relative role of a cryptic refuge for *C. maenas* and *C. borealis**

To examine whether intertidal algae provides a cryptic refuge for *C. maenas*, I paired similar sizes of *C. maenas* in areas with and without an algal background. In the first treatment, I tethered *C. maenas* to a small rock and placed the crab and rock in the center of a cleared patch, approximately 100 x 50 cm. When the algae were cleared, the rock substrate was a light gray. In the second treatment, I tethered *C. maenas* to a small rock and placed it on algae in the low intertidal, covered mainly by *Chondrus* spp and *Fucus* spp. Areas with short algae were used in order to prevent crabs from hiding. Each set of two crabs was considered one replicate.

This procedure was repeated with *C. borealis* to examine the relative role of crypticity in limiting gull capture for *C. maenas* and *C. borealis*. Thus, pairs of *C. borealis* were tethered in cleared and algal patches, as described above.

Iib. Preference of C. borealis, C. irroratus, C. maenas in cleared patches

Since preliminary results from the above experiment indicated that crypticity limit gull captures for *C. maenas*, I tethered *C. borealis*, *C. irroratus*, and *C. maenas* in cleared patches to determine gull preferences without a cryptic background. I tethered each crab to a small rock, and placed the rock in the cleared area. Each set of three crabs was considered one replicate trial.

Hypothesis III: Tissue Taste

Separating meat from crabs eliminates searching or handling constraints. Meat of different species might provide differential amounts of secondary compounds, minerals, proteins or nutrients. In general, marine invertebrates provide certain minerals and proteins necessary for physiological requirements of gulls, especially during the breeding season (Annett and Pierotti, 1987).

Crabs, collected from the intertidal around Appledore Island, were dissected and all internal meat and organs, which gulls consume, were removed. The mixture was crushed and homogenized. I then filled a mold, 3.5 cm in diameter, with the crabmeat and froze them.

I placed three frozen patties of crabmeat, one of each crab species, within a gull territory. I offered the crabmeat to three *L. argentatus* and three *L. marinus* within a single sub-colony, for a total of 6 sub-colonies spaced around the island (Figure 1).

Statistical Analysis

A χ^2 test was conducted in order to determine if a non-random pattern of crab species selection occurred. χ^2 tests were conducted separately for *L. argentatus* and *L. marinus*. A G-test was conducted to determine if crab species preferences differed between gull species.

Results:

Hypothesis I: Behavioral defenses

Ia. The relative deterrence factor for C. irroratus and C. borealis claw defense behavior

Both *L. argentatus* and *L. marinus* selected *C. irroratus* with limited defense ability more often than *C. irroratus* with complete claw movement. However, gulls showed no preference for *C. borealis* that were with or without claw movement (Table 1; Figure 2a). In addition, there was no significant difference between *L. argentatus* and *L. marinus* preference for *C. irroratus* with limited defense ability (G test, $\chi^2 = 0.1181$, $df=1$, $p>0.05$).

Ib. Preference of immobile C. borealis, C. irroratus, C. maenas

When dead crabs were offered to gulls, *C. borealis* was chosen most often by *L. argentatus* and *L. marinus* (Table 1; Figure 2b). There was no significant difference between *L. argentatus* and *L. marinus* preference for *C. borealis* (G test, $\chi^2 = 1.014$, $df=2$, $p>0.05$).

Hypothesis II: Crypticity

Ila. The relative role of a cryptic refuge for C. maenas and C. borealis

C. maenas in cleared patches was selected more often than in non-cleared patches by both species of gulls. However, gulls showed no preference for *C. borealis* that were in cleared or non-cleared patches (Table 2; Figure 3a). There was no significant difference between *L. argentatus* and *L. marinus* preference for *C. maenas* (G test, $\chi^2 = 0.1056$, $df=1$, $p>0.05$).

Ilb. Preference of C. borealis, C. irroratus, C. maenas in cleared patches

When gulls were offered the three species of crabs in cleared patches, *C. borealis* was chosen most often by both species of gulls (Table 2; Figure 3b). There was no significant difference between *L. argentatus* and *L. marinus* preference for *C. borealis* (G test, $\chi^2 = 1.445$, $df=2$, $p>0.05$).

Hypothesis III: Tissue Taste

When gulls were offered crabmeat, neither *L. argentatus* nor *L. marinus* had a preference for crab species (Table 3; Figure 4). There was no significant difference between *L. argentatus* and *L. marinus* crab preference (G test, $\chi^2 = 0.1540$, $df=2$, $p>0.05$).

Discussion:

These results indicate that *L. argentatus* and *L. marinus* strongly prefer *C. borealis*, despite the low abundance of this crab in intertidal and shallow subtidal habitats of New England (Good, 1992a,b; Ellis et al., in review). The results of this study indicated that claw defense and crypticity restrict capture of *C. irroratus* and *C. maenas*, whereas the size of crab and tissue taste

can be eliminated as possible factors driving the preference for *C. borealis*. Manipulated crab or environmental conditions did not alter gull preference for *C. borealis*. The preference for *C. borealis* may be a combination of factors, either tested in this study, i.e. claw defense and crypticity, or other untested factors, i.e. profitability, microhabitat use and escape behavior.

This study indicates that *C. irroratus* without claw defense abilities are selected more often than *C. irroratus* with claw defense behaviors. However, eradicating defense behaviors for all three species of gulls did not alter the strong gull preference for *C. borealis*. *C. borealis* defense behavior has evolved with lobster predation, by which *C. borealis* pull their claws under their carapace in order to prevent a lobster claw from getting hold of it (L. Harris, personal communication). However, this defense behavior, tucking in claws, is highly ineffective for avian predators which attack from above and are able to fit the entire carapace into their bills. Thus, aggressive defense behavior may be a constraint for gulls to obtain *C. irroratus*.

Cryptic coloring of *C. maenas* may constrain gulls from locating *C. maenas* in the intertidal, but eliminating the cryptic algal background does not change gull preference for *C. borealis* over *C. maenas* and *C. irroratus*. Dumas and Witman (1993) found *C. maenas* more susceptible to gull predation in tidepools without mussels than *C. irroratus*. These results further suggest that the cryptic intertidal algal and organism assemblages provide more of a predation refuge for *C. maenas* than *Cancer* spp.

Crabmeat experiments suggest that the meat of *C. borealis* do not provide a greater benefit, such as taste, mineral content, secondary compounds, etc., than *C. maenas* or *C. irroratus* meat. Moreover, these results suggest that searching and handling constraints of the other crabs species may better explain the preference for *C. borealis*, rather than a benefit in the energetic or nutritional benefits from *C. borealis* meat. However, direct analysis of possible

secondary compounds, minerals, nutrients, and calories of the meat should be examined to fully test this hypothesis.

For all manipulations, there was no significant difference between the prey preferences of *L. argentatus* and *L. marinus* preferences. This suggests that both gull species prefer *C. borealis* for similar reasons. These results, along with the findings of Chapter 1, further suggest that there is a strong potential for foraging competition between *L. argentatus* and *L. marinus* for *C. borealis* on Appledore Island.

Irons (1986) found that Glaucous-winged Gulls develop a search image for prey items. On Appledore Island, *L. argentatus* and *L. marinus* may have created a search image for *C. borealis* over long time scale. *C. maenas* has been introduced to this habitat in the past century, further providing evidence for this hypothesis. However, this explanation seems unlikely since gulls were relatively rare on Appledore Island until the beginning of the nineteenth century (Borrer and Holmes, 1995). Furthermore, gulls are opportunistic foragers and have taken advantage of other modern prey items, such as garbage, as soon as it became readily available in the twentieth century (Kadlec and Drury, 1968; Hunt and Hunt, 1973).

Gulls are highly mobile predators with a high metabolic rate; thus, gulls can be important, although historically under appreciated, component of rocky intertidal food webs (Edwards, 1982; Feare and Summers, 1986; Marsh, 1986; Wootton, 1992; Ellis et al., in review). Predation pressure from gulls has impacted mussel recruitment patterns (Marsh 1986) and abundances of seastars, *Asterias forbesi* (Dumas 1996). Within the rocky intertidal at Appledore Island, high predation from gulls may limit the upper bounds of *C. borealis* in the intertidal (Good, 1994; Ellis et al, in review). Furthermore, *C. borealis* are important predators of *Littorina littorea*, and regulate their abundance and distribution (Kraft, 2002; Carlson, 2002). Thus, the selective

predation for *C. borealis* may have a strong impact on *C. borealis* zonation and community-wide effects.

This study suggests that claw defense behavior and crypticity are factors which limit gulls from capturing *C. irroratus* and *C. maenas*. However, when these factors were eradicated and all crab species were made available, gulls continued to prefer *C. borealis*. Thus, it is important for further studies to continue to examine the basis of the *C. borealis* preference. Other possible factors include profitability, escape behavior, and use of microhabitat. Gulls regularly plunge dive while foraging and unsuccessfully capture crabs. However, it is unclear which species of crabs are best able to avoid gull predation during natural predatory events. Observations of these attacks in nature may also provide further insight into these predator-prey interactions.

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Figures:

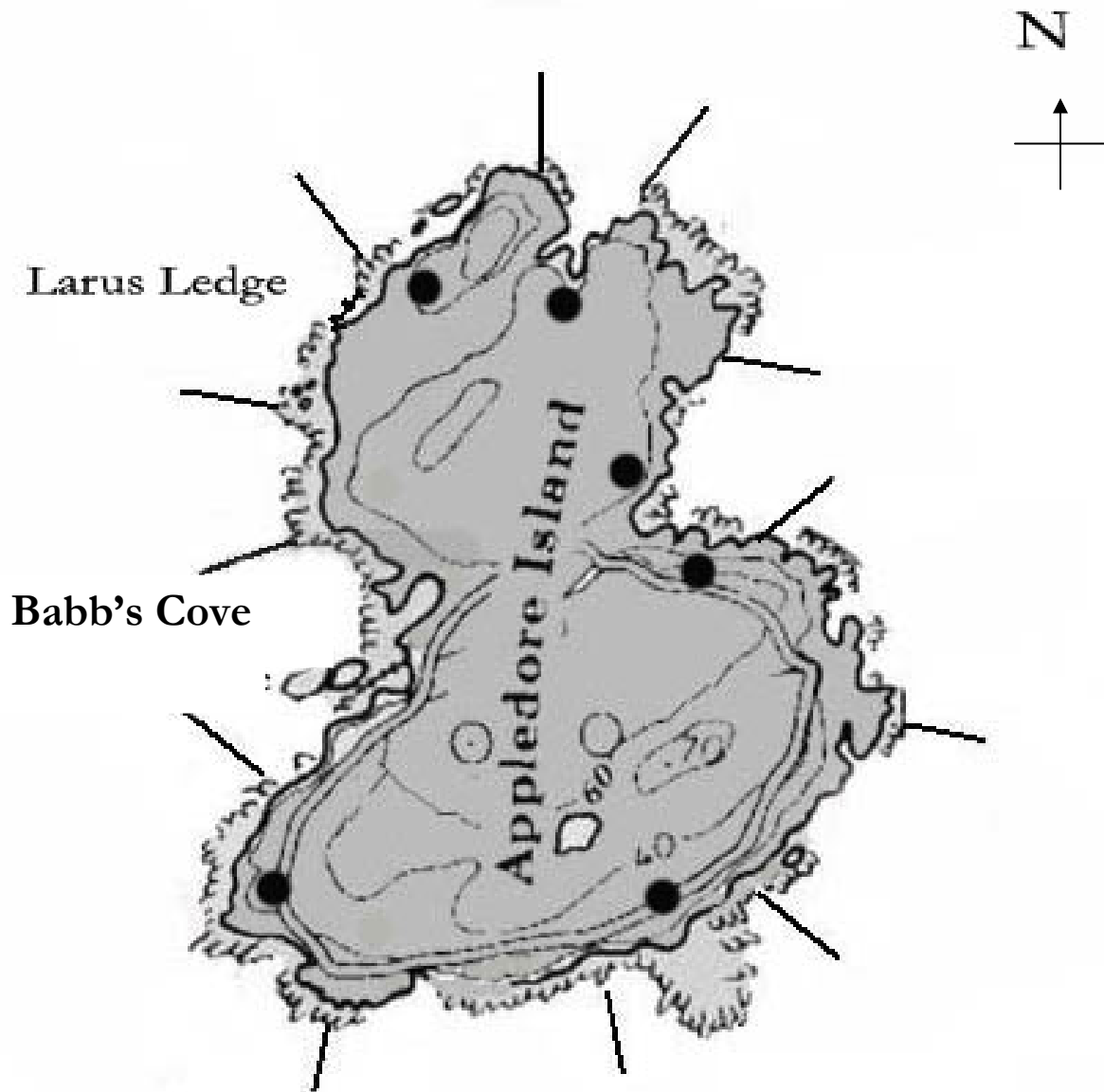


Figure 1. Map of Appledore Island, Maine, USA (42° 58' N; 70° 37' W) in the Gulf of Maine, approximately 10 km off the coast of New Hampshire. Black dots indicate sites of meat experiments in gull sub-colonies. Babb's Cove and Larus Ledge are areas of high *L. argentatus* and *L. marinus* foraging density, respectively, and therefore used for all crab tethering experiments.

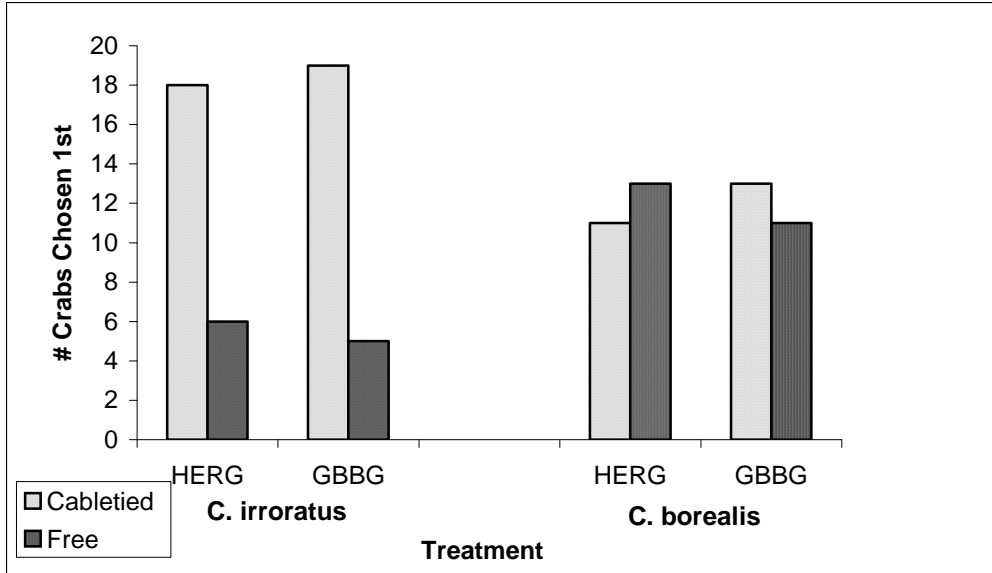


Figure 2a. Gull preference for *C. borealis* and *C. irroratus* with and without claw mobility

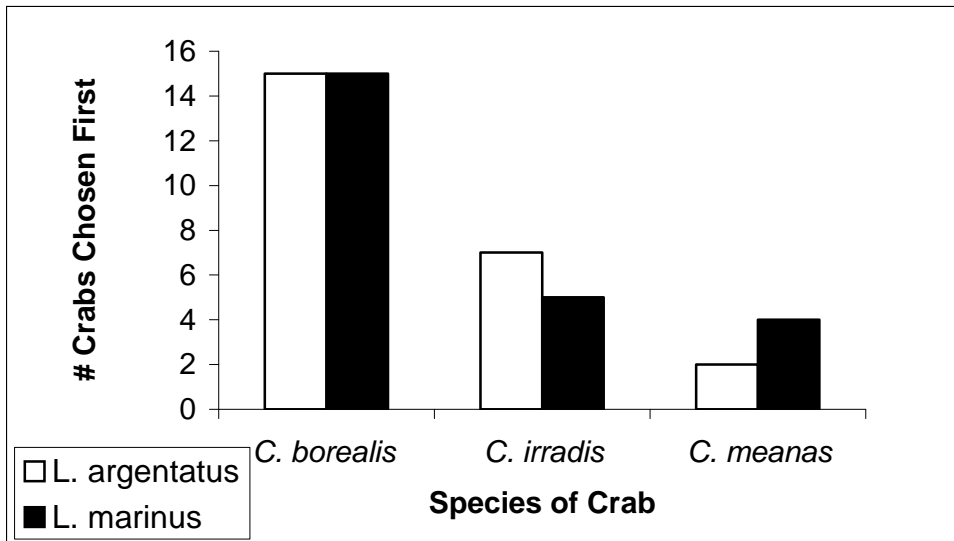


Figure 2b. Gull preference for immobile *C. borealis*, *C. irroratus*, and *C. maenas* $n=24$ for *L. argentatus* and $n= 24$ for *L. marinus*

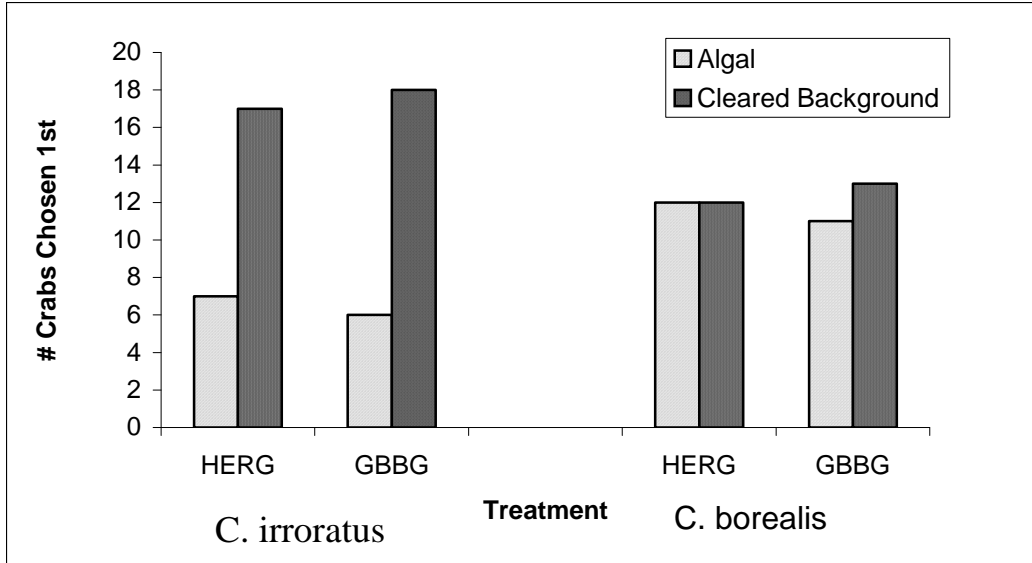


Figure 3a. Gull preference for *C. borealis* and *C. maenas* in cleared and uncleared patches

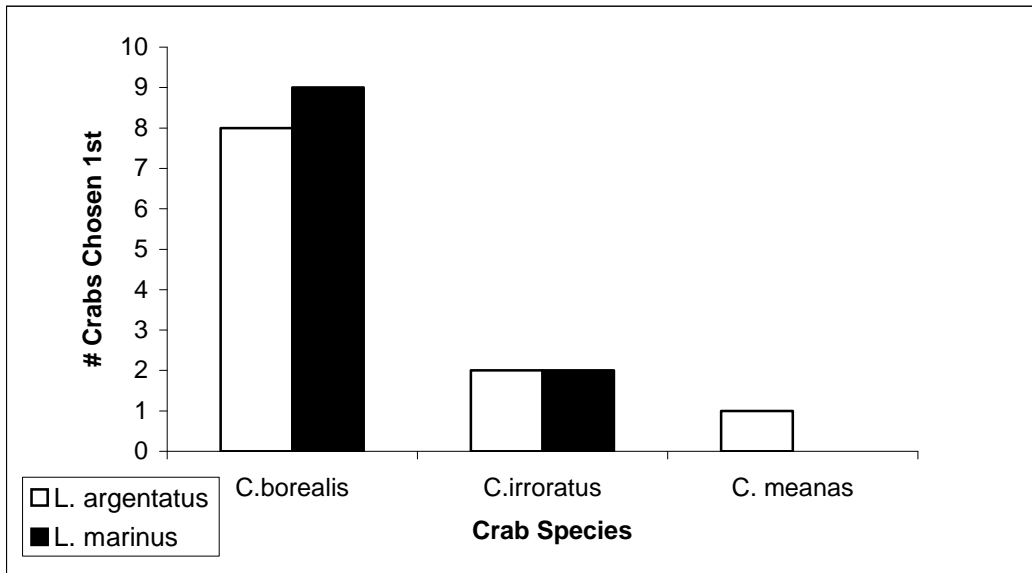


Figure 3b. Gull preference for *C. borealis*, *C. irroratus*, and *C. maenas* in cleared patches of the lower intertidal $n=12$ for *L. argentatus* and $n=12$ for *L. marinus*

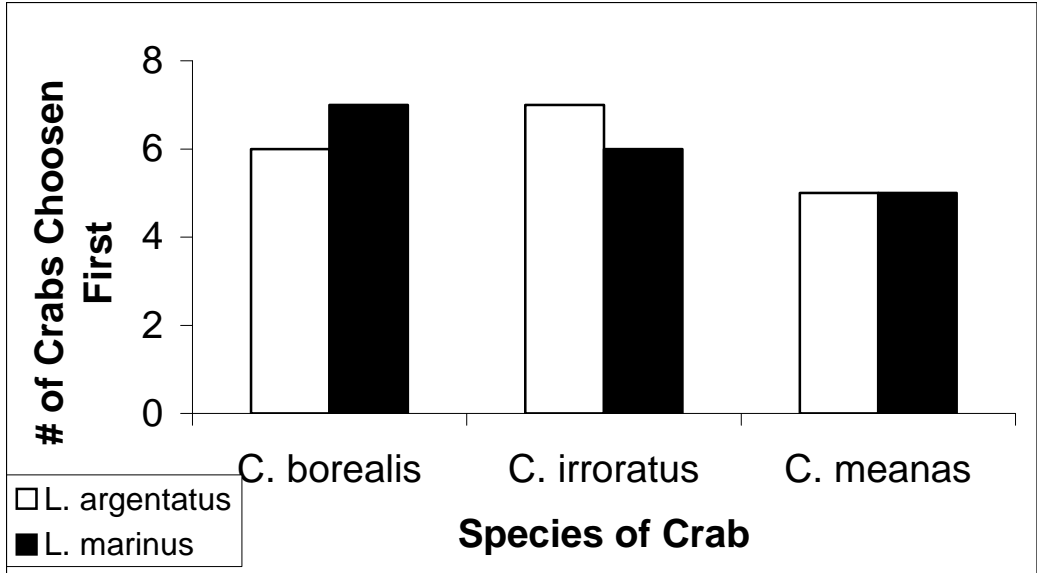


Figure 4. Gull preference for *C. borealis*, *C. irroratus*, and *C. maenas* meat. $n=18$ for *L. argentatus* and $n =18$ *L. marinus*

Tables:

	χ^2 value	df	p value
<i>C. borealis</i>			
<i>L. argentatus</i>	0.7363	1	> 0.05
<i>L. marinus</i>	0.9673	1	> 0.05
<i>C. irroratus</i>			
<i>L. argentatus</i>	12.8222	1	0.014 *
<i>L. marinus</i>	18.9643	1	0.041 *
All Crab Species			
<i>L. argentatus</i>	16.7843	2	0.005 *
<i>L. marinus</i>	10.2345	2	0.01 *

Table 1. Results from crab tethering experiments for *C. borealis*, with and without claw defense behavior, *C. irroratus*, with and without claw defense behavior, and when all three species were tethered immobile. All χ^2 were run separately for *L. argentatus* and *L. marinus* experiments. * indicates significant values (*p≤0.05; ** p≤0.001; ***p≤0.0001)

	χ^2 value	df	p value
<i>C. borealis</i>			
<i>L. argentatus</i>	1.7234	1	> 0.05
<i>L. marinus</i>	0.0673	1	> 0.05
<i>C. maenas</i>			
<i>L. argentatus</i>	18.9643	1	0.041 *
<i>L. marinus</i>	12.8222	1	0.014 *
All Crab Species			
<i>L. argentatus</i>	15.8893	2	0.006 *
<i>L. marinus</i>	9.2536	2	0.03 *

Table 2. Results from crab tethering experiments for *C. borealis*, in cleared and non-cleared patches, and *C. irroratus*, in cleared and non-cleared patches, and when all three species were tethered in a cleared patch. All χ^2 were run separately for *L. argentatus* and *L. marinus* experiments. * indicates significant values (*p≤0.05; ** p≤0.001; ***p≤0.0001)

	χ^2 value	df	p value
<i>L. argentatus</i>	0.3458	2	> 0.05
<i>L. marinus</i>	0.5596	2	> 0.05

Table 3. Results from crab meat preference experiments in *L. argentatus* and *L. marinus* colonies.