



Choosing among mobile prey species: Why do gulls prefer a rare subtidal crab over a highly abundant intertidal one?

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ABSTRACT

In New England, Herring Gulls (*Larus argentatus*) and Great Black-backed Gulls (*L. marinus*) are generalist predators that forage on highly mobile prey in intertidal and shallow subtidal zones, including three species of crabs: *Cancer borealis*, *C. irroratus*, and *Carcinus maenas*. *Carcinus* is more abundant than are *C. irroratus* and *C. borealis* and yet both *Cancer* species are more common in the diet of gulls. In this study we used a series of experiments to examine why gulls exhibit disproportionately higher predation on *C. borealis* relative to the two other crab species. We found that gulls do not discriminate among crab species when presented crab tissue “patties” indicating that gulls do not select crabs based on differences in palatability. At smaller size ranges (<75 mm carapace width), *C. irroratus* had lower dry tissue weight than the other two species, thus gulls should prefer similar-sized *C. borealis* and *Carcinus* based on their caloric value. At carapace widths greater than 80 mm, *C. irroratus* had higher available dry tissue weight than *C. borealis*. However, *C. borealis* is generally larger than *C. irroratus* in the intertidal and shallow subtidal zones so this difference is unlikely to contribute to a preference for *C. irroratus*. Our experiments showed that algal species dominating rocky ledges provide a cryptic refuge for *Carcinus* thereby reducing the likelihood of attack by gulls. We found that the “lateral merus” display exhibited by *C. irroratus* appears to deter attacks by gulls; in contrast, *C. borealis* withdraw their chelae in response to attack, which likely facilitates their capture by gulls. During simulated gull attacks, *Carcinus* exhibited escape behavior whereas *C. borealis* remained stationary. Lack of escape behavior likely facilitates capture of *C. borealis* by gulls. In sum, our findings suggest that gulls have formed a search image for *C. borealis*, which is likely a result of the relative ease of capture and profitability of *C. borealis* compared to *Carcinus* and *C. irroratus*. Gull preference for *C. borealis* has important consequences for crab distributions and the structure of rocky intertidal and shallow subtidal zones in New England. In particular, gulls create a refuge for *Carcinus* in the intertidal zone by reducing densities of *C. borealis*, a potential predator and competitor, and by avoiding preying upon *Carcinus*.

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1. Introduction

Predation can have strong ecological effects, influencing population sizes, community composition, and species diversity. However, the impact of predators depends on their prey choices. Selection of dominant versus inferior competitors, or abundant versus rare species, can greatly alter the magnitude of a predator's impact on the ecological community. Predators also exert strong selection on prey populations, with subsequent evolution of prey defenses that in turn may alter the choices made by future generations of predators. Thus, understanding how predators choose among multiple prey species contributes to a greater understanding of selection pressures on prey and the influence of predators on communities.

In coastal New England, Herring Gulls (*Larus argentatus* Pontoppidan, 1763) and Great Black-backed Gulls (*L. marinus* Linnaeus, 1758) are generalist predators that regularly forage on highly mobile intertidal and subtidal prey (Ellis et al., 2007; Good, 1992). Included in the diet are three species of crabs: *Cancer borealis* (Stimpson, 1859), *C. irroratus* (Say, 1817), and *Carcinus maenas* (Linnaeus, 1758) (henceforth referred to as *Carcinus*). Predation by gulls results in the virtual exclusion of *C. borealis* from the low-mid intertidal zone and produces a trophic cascade through enhancement of snail (*Littorina littorea*) and mussel (*Mytilus edulis*) populations (Ellis et al., 2007). Gull predation on *C. borealis* also results in increased populations of two other mesopredators, *Carcinus* and the carnivorous snail, *Nucella lapillus*. Interestingly, gulls consume *C. borealis* at disproportionately high rates relative to its abundance in the intertidal and shallow subtidal zones (Ellis et al., 2005; Rome and Ellis, 2004). Most strikingly, *Carcinus* is far more abundant than are *C. irroratus* and *C. borealis* (Donahue et al., 2009) and yet both *Cancer* species are much more common in the diet of gulls (Ellis et al., 2005).

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Prey may suffer disproportionately higher rates of predation due to a variety of reasons: differences in profitability (calories/handling-time), abundance, palatability, digestibility, search time (including effects of prey crypticity), escape behaviors and defensive capabilities. There is an extensive literature documenting prey behavior and decision making under predation risk, but predator foraging decisions in relation to prey characteristics have been less well studied (Lima, 2002; Shultz and Finlayson, 2010) but, see (Van Gils et al., 2005). Numerous studies suggest that foraging predators select prey based on their encounter frequency or relative abundance; searching predators should show biases toward the most abundant prey types (Pulliam, 1974; Sherratt and Harvey, 1993; Yearsley, 2003). Much of the evidence supporting frequency-dependent selection by predators comes from foraging experiments using passive or immobile prey; however, predator choice has been shown to be very different when predators feed on mobile prey (Sih and Christensen, 2001). That is, encounter rates for mobile prey are not simply a function of prey densities, but instead are modified by mobility as well as crypticity. The majority of studies that examine prey selection by predators in rocky intertidal zones have focused on sessile or slow-moving prey including limpets, sea urchins, mussels, sea stars, snails, sea anemones, and chitons (Donahue et al., 2009; Irons et al., 1986; Lopez et al., 2010; Silva et al., 2010; Snellen et al., 2007; Yoshiyama et al., 1996). Prey mobility and defensive behaviors are likely to affect prey selection, but studies are lacking for intertidal and shallow subtidal predators of such prey.

In this study we first determine gull prey preferences when different crab species are equally available and unable to use escape or defense behaviors. We then address the question of why gulls exhibit disproportionately higher predation on *Cancer* spp. relative to *Carcinus*, and on *C. borealis* relative to *C. irroratus*, and the related question of how gulls distinguish among crab species. We consider a number of hypotheses and perspectives: (1) Palatability may differ among the crab species; (2) Crabs of the same size but different species may vary in tissue mass available to gulls; (3) Differences in coloration (crypticity) or shape among crab species may affect the likelihood of predation by gulls; (4) Behavioral defenses by the crabs may influence gull prey selection; and/or (5) Escape responses may differ among the crab species and affect the likelihood of successful predation by gulls.

2. Methods

2.1. Study site and species

The 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 located 10 km east of the coast of New Hampshire. The eastern side of the island is exposed to heavy wave action from the Atlantic Ocean, whereas the western side is relatively protected. The shoreline is dominated by rock ledges and boulder coves.

In the Gulf of Maine, Herring Gulls and Great Black-backed Gulls forage in the rocky intertidal and shallow subtidal zones (Ellis et al., 2007), mainland landfills, the open ocean, and behind fishing boats (Good, 1998; Pierotti and Good, 1994). Gulls capture prey in shallow subtidal areas by paddling on or flying close to the water, then plunging to a maximum depth of 1 m below the water surface (Good, 1998). Gulls also forage in the intertidal zone during low tide by walking along the shoreline and capturing prey from within the algal canopy or from rock crevices. The rocky intertidal zone where gulls forage can be divided into three distinct zones characterized by the predominant sessile species: the barnacle zone (2.1 – 2.7 m above mean lower low water [MLLW]), the *Ascophyllum* (*A. nodosum*) zone (0.6 – 2.1 m), and the *Chondrus* (*C. crispus*) zone (0.6 m to shallow subtidal). Gulls primarily feed in the *Chondrus* and *Ascophyllum* intertidal zones, as well as the shallow subtidal zone adjacent to the shore (Ellis et al., 2005; Rome and Ellis, 2004).

Gulls capture crabs during ebbing tides, typically while paddling on the surface of the water and plunge diving. Gulls sometimes swallow small crabs whole, but gulls grab most crabs by a leg or claw and transport them to shore where they are dismembered prior to consumption. After dropping the crab on the shore, the gull flips the crab over on its dorsal side, rips off the legs and claws, pierces the ventral carapace, and then consumes the muscles and organs contained within the dorsal carapace.

The three crab species on which gulls forage are (in order of increasing body and chela size): *Carcinus maenas* (family Portunidae), *Cancer irroratus* and *C. borealis* (family Cancridae) (Fig. 1). All three species share trophic and spatial resources and have morphological characteristics typical of predatory decapods, including large chelate first thoracic appendages (Jeffries, 1966). *Carcinus* and *C. irroratus* are generally fast moving and highly active on open substrates (Elner, 1981; Jeffries, 1966; Moody and Steneck, 1993). In contrast, *C. borealis* are slower but have stronger chelae (Jeffries, 1966; Moody and Steneck, 1993). Both *C. irroratus* and *Carcinus* respond to threats by either fleeing or performing a stereotypical lateral merus display during which the crabs raise and extend their chelipeds (Novak, 2004; Richards, 1992). In contrast, *C. borealis* crouches down rather than fleeing and folds its appendages to cover its mouthparts and ventral surface (Novak, 2004; Richards, 1992). The two crab genera are quite different in coloration. *Carcinus* has a dark green exoskeleton, which matches the color of dominant algae in the low- and mid- rocky intertidal zones of New England. In contrast, the two *Cancer* species have pink exoskeletons, which match the coralline algae that often cover the rocky substrate in sea urchin barrens (Dumas and Witman, 1993). Though the two *Cancer* species are very similar in color and general shape, subtle differences include a much smoother carapace texture for *C. irroratus*, and larger, coarser carapace teeth for *C. borealis*.

2.2. Palatability of different crab species

One possible explanation for the disproportionate rates of predation is that the 3 crab species differ in palatability. To test this hypothesis, we constructed an experiment to determine whether gulls showed any preferences among crab tissue when all visual cues as to species identity had been removed, and no prey defenses were present. We dissected individuals of each of the three species of crabs and removed all internal meat and organs, which were then crushed and homogenized. The homogenized tissue was placed into a circular mold (3.5 cm diameter × 2.5 cm in height) and frozen into crab patties. In each experimental trial, we placed three crab patties (one per species) in a line within the territory of a gull pair, and recorded which patty was eaten first and whether all three patties were eaten. Each trial was conducted in a different gull territory and the spatial ordering of crab patties was randomized for every trial. A total of 36 trials (18 per gull species) were conducted in gull breeding colonies on Appledore Island.

2.3. Differences in tissue mass among crab species

Gulls may select among crab species based upon differences in available calories provided by otherwise similar-sized crabs. To determine whether this might explain the different rates of predation on the 3 crab species, we examined the relationship between crab size (carapace width) and the dry mass of the tissues consumed by the gulls. Here we explicitly assume that the proportion of dry tissue mass that is digestible by the gulls is similar among the three species of crabs. We collected 20–40 individuals of each crab species from intertidal and shallow-subtidal areas around Appledore Island. These crabs represented the range of sizes encountered by foraging gulls (Rome and Ellis, 2004). Maximum carapace width was measured and then the soft tissue in the carapace (muscles, stomach, gonads, gills, cartilage, and other organs/tissues) was dissected from each crab. Muscle tissues in the legs

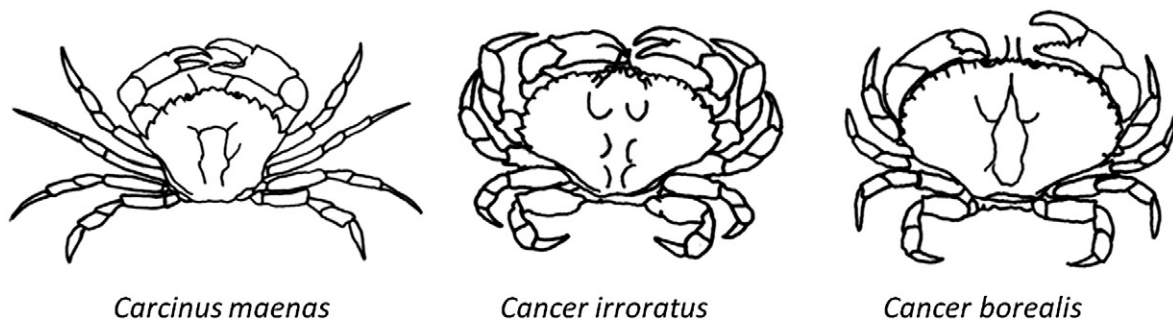


Fig. 1. The three crab species commonly preyed upon by gulls: *Carcinus maenas* (family Portunidae), *Cancer irroratus* and *C. borealis* (family Cancridae). Drawings adapted from Pollock (1999).

and chelae were not included, as gulls typically only ingest meat taken from the carapace (except for very small crabs). Tissue samples were dried at 100 °C to a constant weight.

The three species of crabs collected from the intertidal and shallow subtidal zones at Appledore Island varied in size (carapace-width) distribution [*C. borealis*: \bar{x} = 85.9 mm \pm 2.8SE (range: 52–115, N = 39); *C. irroratus*: \bar{x} = 64.5 mm \pm 3.1SE (range: 43–103, N = 26); *Carcinus*: \bar{x} = 47.1 mm \pm 3.0SE (range: 31–71, N = 16)]. Because *Carcinus* available to the gulls were restricted to a much smaller size range than the two *Cancer* species, we performed two separate analyses of the relationship between size and tissue weight: (1) a comparison of all three crab species that excluded *Cancer* individuals \geq 75 mm carapace width; and (2) a comparison of *C. borealis* and *C. irroratus* of all sizes. For each of these analyses, we used an ANCOVA to look at the effect of species on tissue dry-weight (g) with carapace width as a covariate. Both carapace width and tissue dry-weight were log-transformed to meet the assumptions of the model.

2.4. Prey preference experiments: general methods

In order to determine what factors influence prey selection by gulls, we conducted a series of prey preference experiments in June–August 2001 and 2006 that involved varying carapace color or shape, crab behaviors, or backgrounds of tethered crab prey. These experiments were performed in the *Ascophyllum* or *Chondrus* zones during the two hours prior to low tide, when intertidal foraging by gulls is at its highest rate (Ellis et al., 2005). To determine whether the two species of gulls differ in prey preference, we performed these experiments at two sites located on the west (protected) side of Appledore Island: (1) Babb's Cove, where Herring Gulls predominated, and (2) Larus Ledge, where Great Black-backed Gulls were far more common.

Crab tethers were constructed by fastening a small nylon loop (cable tie) to the posterior portion of the carapace with marine epoxy (A-788 Splash Zone Compound, Kop Coat). The epoxy was painted with dark-pink or black nail polish in order to closely match the carapace color of the *Cancer* spp. and *Carcinus*, respectively. A fine black nylon line was tied to the loop on the carapace and the crabs were tethered by attaching the free end of the 20 cm long line to either a *Chondrus* frond or a rock. Pilot experiments indicated that the crabs could not cut the lines with their claws or break free from tethers.

In order to eliminate the possibility that gulls were choosing crabs based on differences in size, we ensured that all crabs in a trial had similar carapace widths. Crabs were deployed in sets of 2 or 3; each individual in a trial was tethered a minimum of 30 cm from its neighbor(s). After crabs were deployed in the intertidal zone, we observed the experiment from either a boat offshore or behind a boulder on the shore; observers were located at least 15 m away in order to avoid disturbing the gulls. In each experimental trial, we assessed prey preference by recording the identity of the first crab handled or eaten by a gull.

Except where specifically noted, we analyzed our results using binary logistic regression (SPSS version 17) with crab chosen first as the response variable and experimental treatment (e.g., restrained versus unrestrained chelipeds, substrate type), gull species, and the interaction term as explanatory variables.

2.5. Effects of potential cryptic coloration on crab vulnerability to gull predation

We designed an experiment to test whether the dark-green color of intertidal algae provides a cryptic refuge for *Carcinus*. Areas of the *Chondrus* zone, approximately 100 \times 50 cm in size, were cleared of all algae, exposing grey granitic rock substrate. A trial consisted of *Carcinus* deployed in pairs; one individual was tethered to *Chondrus* fronds, and the other tethered to a small rock in the center of a cleared patch (N = 24 trials per site). Efforts were made to place the former in areas with short algae in order to prevent crabs from hiding in the algal canopy. The same procedure was repeated using pairs of *C. borealis* (24 per site) in order to examine the relative role of crypticity in protecting each species from attack by predatory gulls.

Results from these experiments showed that gulls chose *Carcinus* tethered on bare rock substrate more often than those tethered on an algal background. In order to determine whether gulls would continue to exhibit a preference for *Cancer* crabs over *Carcinus* if crypticity were eliminated, we conducted another experiment in which individuals of all three species were tethered in cleared patches. A trial consisted of three live crabs, one of each species, tethered to a rock in a cleared patch (N = 11 trials per site). We compared these results to the identical experiment carried out in algal-covered habitat by Rome and Ellis (2004).

2.6. Effects of cheliped extension behavior in *Cancer* crabs

The previous experiments (see Results), as well as field data (Rome and Ellis, 2004), showed gulls exhibited a preference for *C. borealis* over *C. irroratus*. One possible explanation is that *C. irroratus* frequently responds to threats by extending its chelipeds (lateral merus display) (Novak, 2004). To test this hypothesis, we conducted an experiment in which gulls could choose between crabs with unrestrained chelipeds and crabs whose chelipeds were restrained by cable ties that attached each chela to the merus. An experimental trial consisted of two tethered *Cancer* crabs of the same species, one with unrestrained and one with restrained chelipeds. The experiment was conducted with both *C. irroratus* and *C. borealis* at Babb's Cove and Larus Ledge (N = 24 trials per crab species per site).

2.7. Prey preference when crabs lack behavioral defenses

An earlier study (Rome and Ellis, 2004) had shown that gulls, when offered live individuals of all three crab species, showed strong preferences for *Cancer borealis*. We designed an experiment to

address the question of whether gulls exhibit preferences when the crabs were unable to use escape or defensive behaviors. To eliminate possible behavioral responses to the predator, we used frozen crabs. In each experimental trial, we placed 3 crabs, one of each species, 30 cm apart in the *Chondrus* zone and recorded which crab was consumed first. We performed 24 trials at each of the two study sites. We compared these results to the identical experiment carried out with live crabs (Rome and Ellis, 2004) to determine whether removing behavioral responses altered prey preference by the gulls.

2.8. Effects of carapace shape and texture on gull selection of *Cancer* crabs

C. borealis and *C. irroratus* are similar in appearance, but gulls can readily distinguish between the two species. We designed experiments to test whether gulls discriminate the *Cancer* species based on differences in their carapace shape or texture. In the two sets of experiments, we eliminated behavioral differences between the two species by restraining the chelae of each crab using nylon cable ties. In all trials, pairs of crabs were deployed in the *Ascophyllum* zone at Larus Ledge, which is dominated by Great Black-backed Gulls. In the first experiment, we tested whether gulls distinguish between *Cancer* species based on carapace shape. We eliminated differences in carapace color by painting the carapace and top of each leg of each crab the same color using a permanent waterproof red paint marker; the color was applied thickly so it was completely opaque. A trial (N = 8) consisted of a pair of painted crabs (one *C. irroratus* and one *C. borealis*).

In the second experiment we tested whether gulls differentiate between *Cancer* species based on the shape or number of teeth on the anterior end of the carapace. We dried the carapace of each crab and applied a layer of white, air-hardening modeling material (Creative Paperclay®) to the anterior edge of the carapace covering the teeth. A thin layer of polymer clay in “Brick Red” (Sculpey®) was applied over the white layer in order to approximate the carapace color of the crabs. Carapace tethers were made from 20-gauge steel wire; one end of the wire was wrapped in a loop around the pterygostomial region of the carapace and the bases of the walking legs so as not to overlap with the clay covering the carapace teeth. An experimental trial consisted of two tethered *Cancer* crabs (one *C. borealis* and one *C. irroratus*), both with modified carapaces (N = 21 trials).

For these two experiments, we used a binomial test to determine whether the frequency with which a crab species was chosen first differed significantly from the null hypothesis of 0.5.

2.9. Difference in escape behavior between *Cancer borealis* and *Carcinus maenas*

A possible explanation for gull preferences among crab species is differences in escape behaviors. Gulls may learn not to attempt to attack a species of crab when previous attempts have been unsuccessful. To explore differences in escape behavior, we exposed *C. borealis* and *Carcinus* to a gull model and recorded the distances the crabs moved. A sea table (185 × 75 × 50 cm) with a plexiglass viewing window on one side was used to create a semi-natural shallow subtidal habitat. The bottom was covered with a layer of gravel and small rocks and the aquarium filled with seawater to a depth of 50 cm. An air pump was installed at each corner of the sea table to ensure that the water remained oxygenated. To construct a model that would appear similar to a gull from the perspective of a crab, we attached two wooden sticks (the size and shape of gull legs and feet) to the underside of a white ellipsoid buoy (40 cm long, 15 cm in diameter). During trials, the model was moved along the surface of the water and “bobbed” downward to mimic the behavior of a paddling and plunge-diving gull.

Carcinus and *C. borealis* (N = 19 per species) were collected from the intertidal and shallow-subtidal zones of Appledore Island and kept in flow-through sea tables until used in the experiment. Sizes (carapace width) of crabs ranged from 56.2–93.4 mm. Prior to the beginning of each experimental trial, a single crab was placed in the sea table 10 cm from one end and 30 cm from one side. Pilot experiments had shown that crabs initially moved around the sea table for a maximum of 7 min before becoming stationary. Therefore, we waited ten minutes for each crab to acclimate to the sea table before initiating a trial. After recording the crab's position in the sea table, we placed the “gull” on the water on the opposite end of the sea table and moved it along the water's surface toward the crab. When the model was above the crab, we repeatedly thrust the front end of the buoy into the water to simulate an attack by the gull. When the crab moved, we manipulated the model to follow as though paddling along the surface, and mimicked the “attack” again if the crab stopped moving. At the end of 2 min, the crab's position was recorded and the distance it had traveled was measured. We compared the frequency of escape responses in the two crab species in a contingency table analysis with Fisher's exact test.

3. Results

3.1. Palatability of different crab species

When gulls were offered frozen crab patties, neither species showed a preference among the crab species (Gull species × Crab species: $\chi^2 = 0.24$, $df = 2$, $P = 0.89$; Crab species: $\chi^2 = 0.74$, $df = 2$, $P = 0.69$; Fig. 2).

3.2. Differences in tissue mass among crab species

In comparing *Carcinus*, small *C. borealis* (<75 mm carapace width), and small *C. irroratus*, we found that species, as well as crab size, had a significant effect on log(dry tissue-weight) [ANCOVA: species, $F = 5.28$, $P = 0.009$; log(carapace-width), $F = 94.2$, $P < 0.0001$; Fig. 3]. Controlling for size, small *C. irroratus* had significantly lower dry-tissue weight than *Carcinus* and small *C. borealis* (both $p = 0.0025$). For crabs under 75 mm, the species did not differ in the slope of the relationship between log(carapace-width) and log(tissue dry-weight) [ANCOVA: species × log(carapace-width), $F_{2,2} = 0.05$, $P = 0.95$].

A comparison of the two species of *Cancer* across their entire size ranges showed that they differed significantly in the slope of the relationship between log (dry-tissue weight) and log (carapace width) [ANCOVA: species × log(width): $F = 8.7$, $p = 0.0045$]. At carapace widths larger than 80 mm, *C. irroratus* had higher available dry-tissue weight than *C. borealis*.

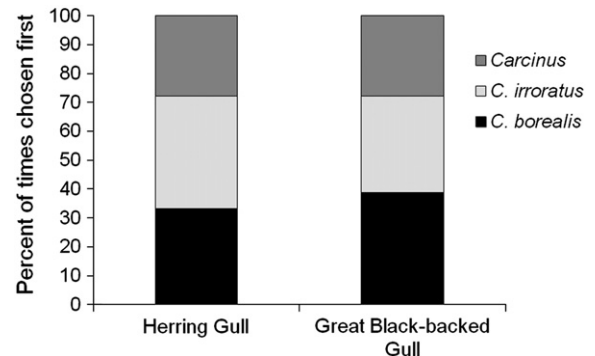


Fig. 2. Palatability experiment: percent of trials in which frozen meat patties composed of *C. borealis*, *C. irroratus*, or *Carcinus* were chosen first by two species of gulls. Neither species of gull showed a preference among the crab species.

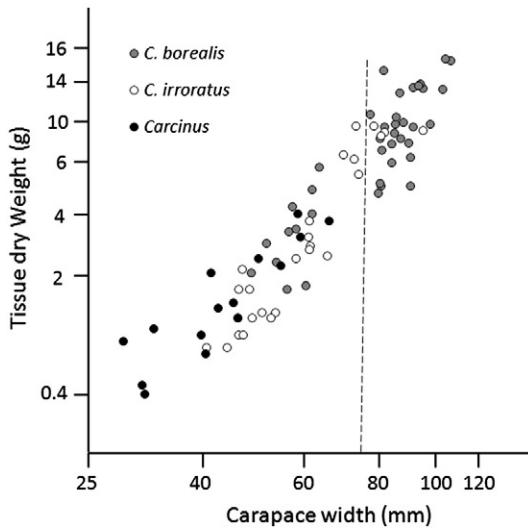


Fig. 3. Relationship between crab size (carapace width) and mass of tissues consumed by gulls. Species and crab size affected tissue weight (species: $P=0.009$, carapace width, $P<0.0001$); controlling for size, *C. irroratus* had significantly lower dry-tissue weight than the other two species. At carapace widths larger than 80 mm, *C. irroratus* had higher available dry-tissue weight than *C. borealis* ($P=0.0045$).

3.3. Effects of potential cryptic coloration on crab vulnerability to gull predation

When offered a choice between *Carcinus* tethered on algae versus *Carcinus* tethered on bare rock, both gulls chose crabs on bare rock substrate significantly more often (Substrate type: $\chi^2=18.6$, $df=1$, $P<0.0001$, Gull species \times Substrate type: $\chi^2=0.21$, $df=1$, $P=0.65$; Fig. 4). In contrast, when offered *C. borealis* on algae versus bare rock, gulls showed no preference (Substrate type: $\chi^2=0.0$, $df=1$, $P=1.0$, Gull species \times Substrate type: $\chi^2=0.17$, $df=1$, $P=0.68$; Fig. 4).

When gulls were offered all three species of crabs on bare rock substrate, *C. borealis* was chosen more often than *Carcinus* ($\chi^2=6.9$, $df=1$, $P=0.009$) and *C. irroratus* ($\chi^2=7.4$, $df=1$, $P=0.007$); gulls showed no difference in preference for *Carcinus* compared to *C. irroratus* ($\chi^2=0.37$, $df=1$, $P=0.54$; Fig. 5a). Gull species did not differ in their preferences (Gull species \times Crab species: $\chi^2=0.12$, $df=2$, $P=0.94$). To determine whether substrate affected gull preferences, we compared how often each crab species was chosen first when the crabs were tethered on bare rock substrate versus when the crabs were tethered on algae (the latter data set from Rome and Ellis, 2004). Prey

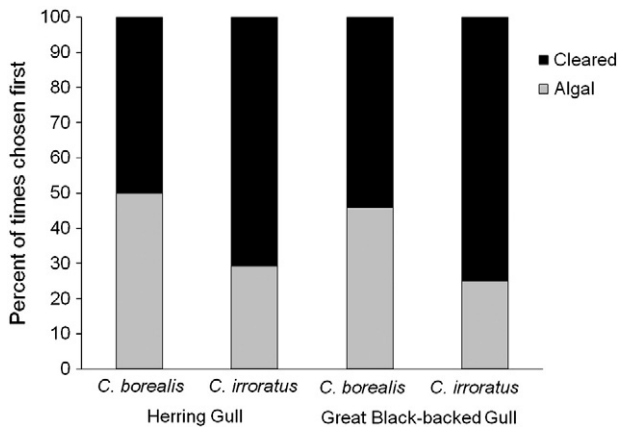


Fig. 4. Crypticity experiment: percent of trials in which *C. borealis* or *Carcinus* was chosen first on either bare rock substrate (cleared) or on algal substrate. Both species of gull chose *Carcinus* more often on bare substrate ($P<0.0001$), but showed no preference for *C. borealis* on either substrate type ($P=1.0$).

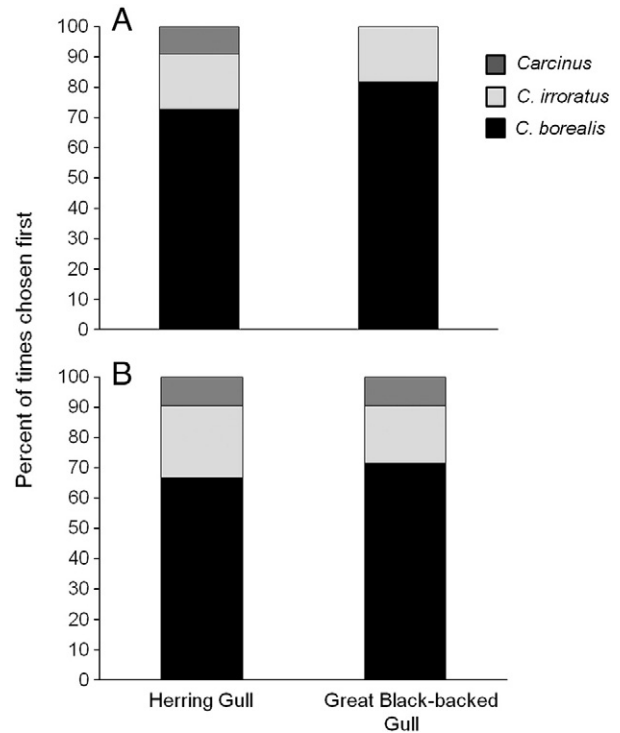


Fig. 5. Crypticity experiment: percent of trials in which *C. borealis*, *C. irroratus*, or *Carcinus* was chosen first on bare rock substrate. *C. borealis* was chosen more often than *Carcinus* ($P=0.009$) and *C. irroratus* ($P=0.007$) by both species of gull in the current study (A) and Rome and Ellis (2004) (B).

choices were very similar on the two substrates (Fig. 5a, b) and the statistical analysis showed no effect of substrate type on which crab species was chosen first by the gulls (Substrate \times Crab species: $\chi^2=1.13$, $df=2$, $P=0.57$; Crab species: $\chi^2=66.5$, $df=2$, $P<0.0001$).

3.4. Effects of cheliped extension behavior in Cancer crabs

When offered a choice between *Cancer irroratus* with restrained versus unrestrained claws, both species of gull selected the crab with restrained claws significantly more often (crab claw status: $\chi^2=10.9$, $df=1$, $P=0.001$, Gull species \times Crab claw status: $\chi^2=0.24$, $df=2$, $P=0.63$; Fig. 6). In contrast, when offered *C. borealis* with restrained

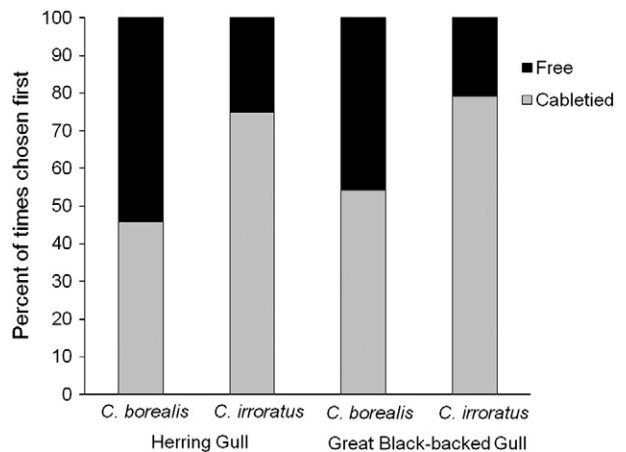


Fig. 6. Effects of cheliped extension behavior on gull preference: percent of trials in which *C. borealis* or *C. irroratus* with restrained or unrestrained chelipeds was chosen first by the two species of gulls. Both species of gulls chose *C. irroratus* with restrained chelipeds more often ($P=0.001$), but gulls showed no preference for *C. borealis* with or without restrained chelipeds ($P=0.56$).

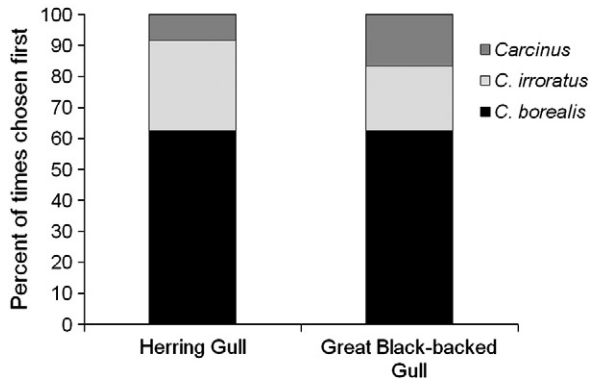


Fig. 7. Effects of crab behavioral defenses on gull preference: percent of trials in which dead *C. borealis*, *C. irroratus*, or *Carcinus* was chosen first by the two gull species. Both gull species chose dead *C. borealis* more often than dead *Carcinus* ($P=0.001$) and *C. irroratus* ($P=0.002$).

versus unrestrained claws, gulls showed no preference (Crab claw status: $\chi^2=0.33$, $df=1$, $P=0.56$, Gull species \times Crab claw status: $\chi^2=0.67$, $df=2$, $P=0.42$; Fig. 6).

3.5. Prey preference when crabs lack behavioral defense

When dead crabs (all three species) were offered, both gull species (Gull \times Crab species: $\chi^2=0.479$, $df=2$, $P=0.787$) chose *C. borealis* significantly more often than *Carcinus* ($\chi^2=11.7$, $df=2$, $P=0.001$) and *C. irroratus* ($\chi^2=9.3$, $df=2$, $P=0.002$); there was no difference in preference for *C. irroratus* compared to *Carcinus* ($\chi^2=1.4$, $df=2$, $P=0.234$; Fig. 7).

To determine whether lack of behavior affected gull prey preference, we compared the choices gulls made when offered the dead crabs to choices made when offered live crabs (the latter data from Rome and Ellis, 2004). Gulls showed similar crab-species preferences in both experiments (Figs. 7 vs. 5b; Dead/live \times Crab species: $\chi^2=0.79$, $df=2$, $P=0.67$; Crab species: $\chi^2=67.9$, $df=2$, $P<0.0001$).

3.6. Effects of carapace shape and texture on gull selection of *Cancer* crabs

When presented with pairs of *C. borealis* and *C. irroratus* that had been painted the same shade of dark pink, gulls chose *C. borealis* in 100% of the 8 trials (binomial test: $p=0.0039$). When colored clay was placed over the carapace teeth of both crab species, gulls chose *C. borealis* in only 66% of the trials ($N=21$), which did not differ significantly from the null hypothesis of 50% ($p=0.19$).

3.7. Difference in escape behavior between *Cancer borealis* and *Carcinus maenas*

Carcinus and *C. borealis* responded quite differently to the simulated attack by a foraging gull. Almost all (95%) of the *C. borealis* remained motionless (1 individual moved 10 cm), whereas 84% of the *Carcinus* moved when under attack and traveled considerable distances ($\bar{x}=150 \pm 27$ SE cm for the 16 *Carcinus* that moved). The difference in the proportion of individuals showing an escape response differed significantly between the two crab species (Fisher's exact test: $p=0.038$).

4. Discussion

In coastal New England, gulls consume *C. borealis* at disproportionately high rates relative to its abundance in the rocky intertidal and shallow subtidal zones (Ellis et al., 2005). Moreover, *Carcinus* is far more abundant in these habitats than are *C. irroratus* and

C. borealis, yet both *Cancer* species are much more common in the diet of gulls. An extensive literature suggests that foraging predators often select prey based on their encounter frequency or relative abundance, but the majority of these studies were based on relatively immobile prey (Shultz and Finlayson, 2010). In the present study, we examined why gulls exhibit disproportionately higher predation on *C. borealis* relative to the two other crab species.

We experimentally explored the possibility that palatability underlies the differences in predation rates on these crab species. However, gulls showed no discrimination among prey species when presented with just crab tissue "patties." Not only were there no differences in the crab species chosen first, but all patties were consumed, suggesting that the tissues of all three species are palatable.

Another hypothesis is that gulls prefer *C. borealis* because they provide more calories. In our experiments, gulls consistently preferred *C. borealis* even when offered crabs of the same carapace width. Our analysis of the relationship between this size metric and dry tissue weight in *Carcinus*, small *C. borealis* (<75 mm carapace width) and small *C. irroratus* showed that *C. irroratus* had significantly lower dry tissue weight than either of the other two species. Thus, gulls would obtain more calories from small *C. borealis* and *Carcinus* compared to small *C. irroratus*; this could explain why gulls prefer small *C. borealis* over small *C. irroratus*. However, when the two species of *Cancer* crabs were compared across their entire size ranges, we found that at carapace widths greater than 80 mm, *C. irroratus* had higher dry tissue weight than *C. borealis*. Gulls should, therefore, prefer large *C. irroratus* over similar-sized *C. borealis*. However, in the intertidal and shallow subtidal zones of the Isles of Shoals, *C. borealis* are generally much larger than the other two species (Donahue et al., 2009; Novak, 2004), thus on average would provide gulls more calories per prey item.

Coloration of the crab carapace has also been proposed to be important in prey selection by gulls (Dumas and Witman, 1993) and our experiments supported that hypothesis. When we tethered *Carcinus* on both bare rock and algal backgrounds, gulls chose the crabs on bare rock significantly more often. In contrast, there was no difference in attack rate on *C. borealis* on these two substrates. Dumas and Witman (1993) conducted similar tethering experiments with *Carcinus* and *C. irroratus* in mid-intertidal tidepools at Nahant, Massachusetts and found that *C. irroratus* was more vulnerable to predation from gulls than was *Carcinus*. They attributed this difference to the cryptic coloration of *Carcinus* on the dark backgrounds of blue mussel (*Mytilus edulis*) beds in the tidepools. The authors further suggested that *Cancer* spp are adapted to be cryptic in low intertidal and sublittoral habitats where urchin barrens dominated by pink crustose coralline algae are common, and that *Carcinus* is adapted to habitats where mussel cover predominates (mid to high-pools). Our experiments were conducted in mid- and low intertidal zones on emergent substrate, rather than in tide pools, but the results were similar. The algal species (*Ascophyllum*, *Chondrus*, *Mastocarpus*) that dominate rocky ledges in the low and mid-intertidal zones of moderately exposed shores appear to provide a cryptic refuge for *Carcinus* and reduce the likelihood of attack by gulls.

An important behavioral difference between *Cancer borealis* and *C. irroratus* is that only the latter shows any defensive behaviors in response to predator attacks. This study is the first we know of to investigate whether the extension of raised, opened chelipeds ("lateral merus" display) [(Novak, 2004; Richards, 1992)] by *C. irroratus* deters a potential predator. When presented with *C. irroratus* that had either restrained or unrestrained chelae, gulls attacked the crabs with restrained chelae significantly more often; in contrast, there was no increase in attack rate on *C. borealis* with restrained chelae. This finding suggests that the lateral merus display by *C. irroratus* can deter attacks by gulls, and may at least partly explain gull preference for *C. borealis*. When foraging for crabs, gulls typically plunge dive either from the water's surface or while flying overhead. A crab with

extended chelae may be more difficult to capture or put a gull at risk of injury.

During the simulated gull attacks, *Carcinus* exhibited escape behavior whereas *C. borealis* did not move away from the “attacking gull.” Instead, *C. borealis* remained still and withdrew its chelae in response to simulated attacks. This finding corroborates our observations of foraging by gulls in the field: gulls often only plunge dive once or twice before capturing *C. borealis*, suggesting that *C. borealis* remain stationary while being attacked rather than running away. Also, when crabs were collected from the intertidal zone, *Carcinus* were much more difficult to capture than were *C. borealis* because of their rapid, agile escape behaviors. Our experiments suggest that the absence of escape behavior in *C. borealis* likely facilitates its capture by predatory gulls.

In the absence of predation risk and dangerous prey, foraging theory and studies indicate that predators select prey based on profitability: calories per handling time (Stephens and Krebs, 1986; Sutherland, 1982; Zwarts et al., 1996). Prey handling time includes both capture time (including unsuccessful attempts) as well as time spent actually consuming the prey once captured. For gulls feeding on captured crabs, consumption time is relatively short [1.3 min ± 1.9 SD (N = 129 observations); unpubl data] and likely differs little among crab species. The escape and defense behaviors, however, differ considerably among the three species and suggest that average capture time (including unsuccessful attempts) is far lower for *C. borealis* than for either of the other two species. The combination of shorter capture times and higher calories (due to larger sizes) appears to make *C. borealis* a much more profitable prey item for gulls than *Carcinus* and *C. irroratus*.

Gulls at the Isles of Shoals appear to have formed a search image for *C. borealis*, which we were unable to alter in our experiments. In every experimental trial in which we offered *C. borealis* and another crab species to gulls, they typically attacked *C. borealis* first. This search image was likely formed as a result of the relative ease of capture and profitability of *C. borealis* compared to *Carcinus* and *C. irroratus*. Irons et al. (1986) also found that gulls foraging in the rocky intertidal on the Pacific coast exhibited distinct search images that were based on previous foraging experience. They compared prey selection by gulls and conducted prey preference experiments at multiple sites, and found that preferences in experimental trials differed between sites, reflecting differences in availability of species and sizes of prey. Moreover, handling times were significantly lower for prey that the birds were more experienced handling. There was only one experiment in which we were able to decrease the number of times that gulls attacked *C. borealis* first (before another species). When we altered the appearance of the carapace teeth on *C. irroratus* and *C. borealis*, gulls attacked *C. irroratus* first in 34% of trials. In contrast, when the carapaces of the two species of crabs were painted the same color, gulls continued to attack *C. borealis* first in 100% of trials. These results suggest that gulls distinguish between the two species based, at least in part, on differences in the shape and texture of their carapaces.

Gull preference for *C. borealis* has important consequences for crab distributions in intertidal and shallow subtidal zones. On Appledore Island, the three crab species show distinct differences in vertical and habitat distribution across intertidal and shallow subtidal zones: *Carcinus* is most abundant in the mid-intertidal zone, while *C. irroratus* and *C. borealis* are most abundant at –2 m MLLW (Donahue et al., 2009). Deeper in the subtidal, densities of *Carcinus* decrease to zero by –7 m below MLLW, *C. irroratus* densities are similar from –2 m to –10 m, while *C. borealis* densities increase from –2 m to –10 m (Novak, 2004). These differences in intertidal and subtidal distributions reflect the distribution of predation risk (Donahue et al., 2009). Gulls are important predators in the intertidal and shallow subtidal zones (Ellis et al., 2005) while lobsters and fishes are important subtidal predators (Ojeda and Dearborn, 1991). On

Appledore Island, predation on *C. irroratus* and *C. borealis* decreased in the subtidal while predation on *Carcinus* increased, indicating that *Carcinus* species are relatively more susceptible to predation by gulls and/or less susceptible to predation by lobsters and other subtidal predators (Donahue et al., 2009; Novak, 2004). In fact, *C. irroratus* and *Carcinus* are preferred over *C. borealis* as prey for lobsters (Jones and Shulman, 2008); *Carcinus* may be particularly susceptible to lobsters, which have both consumptive and non-consumptive effects on *Carcinus* (League-Pike and Shulman, 2009). High rates of gull predation on *C. borealis* result in increased populations of *Carcinus* in the intertidal zone (Ellis et al., 2007). Thus, gulls create a refuge for *Carcinus* in the intertidal zone by reducing densities of *C. borealis*, a potential predator and competitor, and by avoiding preying upon *Carcinus*.

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