



# Investigating the impact of introduced crabs on the distribution and morphology of littorinid snails: Implications for the survival of the snail *Littorina saxatilis*

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## ABSTRACT

Introduced species can have profound impacts on communities by displacing and consuming native organisms. The intertidal communities in the Gulf of Maine have been radically altered through a suite of invasions in the early 1800s, including the herbivorous snail *Littorina littorea* and the omnivorous European green crab *Carcinus maenas* leading to morphological and distributional changes in two native gastropod grazers (*Littorina saxatilis* and *Littorina obtusata*). Green crabs and native cancrid crabs occupy the mid to low intertidal zones, leaving the high intertidal zones relatively free from crab predation pressure. However, a more recent invasion in the 1980s by the intertidal omnivorous Asian shore crab *Hemigrapsus sanguineus*, has eliminated this predator-free zone in the high intertidal. This invasion is of particular concern to populations of *L. saxatilis*, which were relegated to the high intertidal through combined competition and predation pressure by *L. littorea* and *C. maenas*. In order to quantify the potential impact of *H. sanguineus* on native snails, we conducted both field and lab experiments, testing the susceptibility of different sized snails to predation by introduced crabs. Additionally, we measured the distribution, abundance, and morphology of intertidal snails and crabs. Smaller snails of all species were the most susceptible to predation, although susceptibility differed among snail species and predation capabilities differed among crab species. *L. saxatilis* was the most vulnerable snail species to predation, with 73 and 64% of the population susceptible to large *H. sanguineus* and small *C. maenas*, respectively, while >96% of the *L. littorea* population was resistant to predation. *L. saxatilis* has been relegated to the high intertidal where there is high abiotic stress and poor-quality food, but until the invasion of *H. sanguineus*, there was little predation risk. This added predation pressure may further threaten populations of *L. saxatilis*, especially as the upper intertidal becomes more hostile with increasing temperatures and possible species introductions.

## 1. Introduction

The Gulf of Maine is a low diversity system (Witman et al., 2004) historically influenced by top-down control from large predatory fishes (Jackson et al., 2001; Steneck et al., 2004). Declines in large predators, rapid warming, and shifting seasonality have facilitated sweeping changes in local communities (Pershing et al., 2015; Staudinger et al., 2019). In addition, the Gulf of Maine has a long history of species introductions, which alter community structure through competition and predation on native species (Carlton, 2003). Many benthic communities

are now dominated by introduced algae and invertebrates, which have changed the demersal invertebrate community (Dijkstra et al., 2017; Valentine et al., 2007). For example, the dominant herbivore in the intertidal, the snail *Littorina littorea* Linnaeus, 1758, exerts control over algal community assemblage by consuming seasonally abundant ephemeral algae and germlings of community dominants (Lubchenco, 1978).

Prior to European colonization, the rocky intertidal in the Gulf of Maine was dominated by two species of native littorinid snails, *Littorina saxatilis* Olivi, 1792 and *Littorina obtusata* Linnaeus, 1758

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(Blakeslee et al., 2008; Panova et al., 2011). *L. saxatilis* once occupied both the mid and low intertidal zones (Reid, 1996), but following several prominent species invasions, has shifted to occupying the high intertidal (Behrens Yamada and Mansour, 1987; Lubchenco and Menge, 1978). *L. saxatilis* primarily grazes algae and is capable of exerting top-down pressure on the community when not in the presence of more competitive snails (Eastwood et al., 2007). It forms distinct ecotypes within a small area, as it has direct development and limited dispersal capabilities as an adult (Johannesson, 2003). The other native littorinid, *L. obtusata*, is a fucoid algae specialist, living within and grazing on *Fucus* spp. Linnaeus and *Ascophyllum nodosum* (Linnaeus) Le Jolis (Watson and Norton, 1987). It primarily occupies the mid to low intertidal zones, taking refuge within the algae. Both of these native species saw significant declines in their population following the expansion of the invasive gastropod, *L. littorea* (Eastwood et al., 2007; Ganong, 1886).

Currently, the dominant littorinid snail in New England intertidal communities is the introduced periwinkle *L. littorea*, which was introduced to New England in the late 18th to early 19th century, likely coming over in rock ballast (Carlton, 1982). Although the cryptogenic status of *L. littorea* has been debated, molecular and historical investigations have confirmed its origin in Europe, likely colonizing North America through several invasions (Blakeslee et al., 2008; Brawley et al., 2009; Chapman et al., 2007). *L. littorea* is a generalist grazer, preferring periphyton, germlings, and algae without chemical or structural defenses (reviewed in Reid, 1996). It lives in both rocky and soft sediment habitats, occupying space from the high intertidal to subtidal zones (Brenchley and Carlton, 1983; Watson and Norton, 1985). *L. littorea* grazing controls the algal populations and sediment accumulation, and has had significant impacts on the community structure in the intertidal (Bertness, 1984; Lubchenco and Menge, 1978).

The invasion of *L. littorea* and the subsequent competition for food has relegated *L. saxatilis* to the high intertidal and supralittoral zone (Behrens Yamada and Mansour, 1987; Reid, 1996), where food resources are low and abiotic stressors such as desiccation, temperature variability, and freezing risk is high. *L. littorea* has been shown to have negative impacts on the growth of *L. saxatilis* (Behrens Yamada and Mansour, 1987; Eastwood et al., 2007; Watson and Norton, 1987) and reduces growth and foraging behavior in *L. obtusata* (Putnam and Peckol, 2018). Yet, *L. littorea* and *L. obtusata* seem to coexist in the field, likely a result of the wide habitat usage and diet of *L. littorea* (Putnam and Peckol, 2018). While *L. littorea* does not apparently experience negative competitive impacts from the native snails, it does experience density dependent intraspecific competition (Behrens Yamada and Mansour, 1987; Putnam and Peckol, 2018).

One of the main predators of littorinid snails in New England are introduced crabs (reviewed in Teck, 2006). Prior to European colonization, the prominent large predatory crustaceans in New England were two cancrinid crabs *Cancer borealis* Stimpson, 1859 and *Cancer irroratus* Say, 1817 and the American lobster *Homarus americanus* H. Milne Edwards, 1837. These three species forage throughout the intertidal, but are restricted by the tide; highest levels of intertidal predation occur within the low intertidal (Ellis et al., 2007). While these species are capable of consuming littorinid snails (Donahue et al., 2009; Jones and Shulman, 2008), snails were rarely found in field-collected gut contents (Donahue et al., 2009; Stehlik, 1993). Prior to invasions by primarily-intertidal crabs, the mid and high intertidal functioned as a refuge from crab predation. After the invasion of the European green crab *Carcinus maenas* Linnaeus, 1758 in the 18th or 19th century (Say, 1817), that refuge was removed. Soon after *C. maenas* invaded, it quickly became the dominant crustacean in the middle and lower intertidal (reviewed in Teck, 2006). *C. maenas* is a generalist, consuming mollusks, crustaceans, polychaetes, and algae (Ropes, 1968). In 1988, the Asian shore crab *Hemigrapsus sanguineus* De Haan, 1835 was introduced to the northwest Atlantic, and reached the Gulf of Maine by 2000 (Bourdeau and O'Connor, 2003), spreading as far North as Schoodic Peninsula, Maine (Delaney et al., 2008). Since its introduction, the abundance of

*H. sanguineus* has rapidly increased (Kraemer et al., 2007), and in some regions has displaced *C. maenas* as the dominant intertidal crustacean predator (Griffen et al., 2008). *H. sanguineus* can survive at all tidal heights including the high intertidal zone which likely served as a gastropod refuge from adult *C. maenas* (Eastwood et al., 2007).

The shift in decapod predation pressure through time could have large impacts on littorinid populations, which is likely to alter gastropod grazing pressure on algal communities. In this study, we investigate the relationships between both introduced crab species and the three littorinid snails in the Gulf of Maine. Densities and morphological measurements of crabs and snails at three sites across tidal heights and season on the coast of New Hampshire and southern Maine are reported. Using snail shell morphology measurements, we determine critical changes in shell investment as snails grow. Additionally, we examine the size dependent vulnerability of snails to crab predation through lab and field experiments in order to predict the impacts of invasive crab presence on native snail populations. This study aims to quantify and describe crab and gastropod presence in the intertidal and investigate the trophic relationships between these species.

## 2. Materials and methods

### 2.1. Study sites

Three sites along 6.7 km of the coast of the Gulf of Maine were sampled for littorinid and crab densities and morphological parameters: Seapoint Beach, Kittery Point, Maine (43.0909°N, 70.6600°W); Fort Stark, New Castle, New Hampshire (43.0584°N, 70.7114°W); and Odiorne Point, Rye, New Hampshire (43.0454°N, 70.7130°W). All sites were exposed rocky intertidal communities dominated by boulder and ledge habitat with neighboring areas of sandy beach and protected coves. Grain size ranged from 0.25 mm (fine sand) to larger than 2.5 mm (boulders) with most of the surface being covered in 0.1 to 1.0 m pebbles and cobbles. All sites exhibited distinct zonation typical of the Gulf of Maine (Lubchenco, 1980). The high intertidal zone was characterized by large cyanobacteria-covered boulders, the mid-intertidal zone was characterized by the brown fucoid algae *A. nodosum* and *Fucus* spp., the low intertidal zone was characterized by red algae, and the shallow subtidal was characterized by coralline algae and kelps, in addition to introduced algae (Dijkstra et al., 2017). Dominant introduced algae included *Neosiphonia harveyi* (Bailey) M.-S.Kim, H.-G.Choi, Guiry & G. W.Saunders, *Dasysiphonia japonica* (Yendo) H.-S.Kim, and *Bonnemaisonia hamifera* Hariot.

### 2.2. Field surveys

To determine the vertical distribution, size structure, and abundance of the three littorinid species (*Littorina littorea*, *Littorina obtusata*, and *Littorina saxatilis*) and the four most common decapod crab predators (*Carcinus maenas*, *Hemigrapsus sanguineus*, *Cancer borealis*, and *Cancer irroratus*), seasonal surveys were conducted at each site. Sampling was conducted in December 2011; March, June, September, and December 2012; and June 2016. During December 2011, only Seapoint Beach and Odiorne Point were sampled. Surveys were conducted within the shallow subtidal and three intertidal heights, defined by their algal composition (see section 2.1). During June 2016, the subtidal was not sampled. Tide pools were excluded from sampling, as they represent distinct communities (Lubchenco, 1978).

Quadrats were placed randomly along a 100 m transect line at each tidal height. To determine the density of littorinid populations, all snails were counted within ten 0.25 m<sup>2</sup> quadrats at each height. All *Littorina* spp. within a 0.0625 m<sup>2</sup> quadrat, nested within the larger 0.25 m<sup>2</sup> quadrat, were collected for morphological characterization. When logistically possible, we collected a minimum of ten individuals per species for each intertidal zone, which in some instances meant sampling more than ten quadrats to get the requisite number of individuals

for morphological characterization. Due to logistical limitations, only ten quadrats were collected in the shallow subtidal for each site and season. Shell length, aperture length, and shell thickness were measured with digital calipers for each snail. Shell length was measured to give an overall size of the snail, and allowed us to compare relative age within a species. Aperture length correlates with the size of the animal's foot (Etter, 1988), and the opening dictates the maximum cheliped size that can access the shell. Since many crabs feed by crushing the snail shell, shell thickness is indicative of how well defended the animal is. To determine the density and size structure of crabs, all *C. maenas*, *H. sanguineus*, *C. irroratus*, and *C. borealis* were collected within ten 1.0 m<sup>2</sup> quadrats at each height. All crabs were transported to the lab where width and length of the larger cheliped and carapace width were measured and sex was determined for mature crabs.

### 2.3. Laboratory feeding trials

To determine the potential susceptibility of smaller snails to crab predation, we conducted a laboratory no-choice experiment using both *C. maenas* and *H. sanguineus* and all three snail species in the summer of 2016. Snails and crabs were collected haphazardly from Fort Stark and held at 10 °C for three to five days. During this time, food was withheld from crabs. Individual crabs were placed in plastic 19 × 17 × 11 cm containers and maintained at 10 °C. During each trial, crabs were given 18 snails of one species, evenly distributed among nine size categories: 2–3, 3–4, 4–5, 5–6, 6–7, 7–8, 8–9, 9–10, and 10–12. Crabs were given 24 h to feed and then the number of snails consumed was recorded. Each crab was fed all three snail species during the course of the experiment in three separate trials. In between trials, crabs were fed mussels and then starved for three days to standardize hunger levels. The order of the snail species fed to each crab was randomized. These no-choice experiments were run with 73 *C. maenas* (20–55 mm, 39 mm average carapace width) and 124 *H. sanguineus* (15–30 mm, 23 mm average carapace width).

### 2.4. Field feeding trials

We conducted field experiments in August and September of 2012 at Fort Stark to determine the feeding preferences of *H. sanguineus* and *C. maenas*. Snails were enclosed in cages with one of three types of crab or no crab (control). The crab treatments were either one 35-mm carapace width *H. sanguineus*, one 20-mm carapace width *H. sanguineus*, or one 35-mm carapace width *C. maenas*. All crabs were male and had two fully-grown and intact claws. Crab sizes were informed by the initial surveys (see results below). 35-mm carapace width *H. sanguineus* are relatively large individuals within our survey area, 20-mm carapace width *H. sanguineus* are average sized individuals, and 35-mm carapace width *C. maenas* were used for comparison with the largest *H. sanguineus*. Eleven snails were placed within each cage, divided into 5 mm shell length size class ranges. We used three size classes for *L. obtusata* and *L. saxatilis* (2.5–5 mm, 5–10 mm, and 10–15 mm) and five size classes for *L. littorea* (2.5–5 mm, 5–10 mm, 10–15 mm, 15–20 mm, and 20–25 mm). Maximum size classes were determined by availability of snails and size class breaks were chosen to allow for comparison across a broad range of sizes.

All animals were haphazardly collected from Fort Stark within one week of deploying the cages and maintained in the laboratory at 10 °C in 32 ppt seawater until deployment. All snails had intact shells with no large chipping or scars. Cages were constructed from 1-cm square-opening polyvinyl chloride coated steel mesh with a 1 mm plastic mesh cage nested within. Each cage was 15 × 15 × 5 cm. Sets of four cages (one from each treatment) were attached together with hog rings to reduce the effect of spatial heterogeneity on crab behavior. At each of three intertidal heights two sets of cages were buried under small boulders to simulate natural habitat and shelter as well as to secure the cages. After 14 days, all cages were retrieved, and presence or absence of each snail was documented. All damage was scored by the same

investigator to ensure consistent scoring across all trials. Snails were scored as dead if only shell fragments were left or if the shell was empty. Three replicate deployments were conducted for a total of 18 replicates per treatment. However, during the third deployment, Hurricane Sandy swept away the two middle intertidal blocks. An additional four cages within sets of four were torn open, allowing for snails to escape the cages, and were therefore not used in analyses.

### 2.5. Statistical analysis

All statistical analyses were performed in R version 4.2.2 (R Core Team, 2022). Relationships and trends were considered statistically significant if the *p*-value was below 0.05. We acknowledge that this cutoff is arbitrary and *p*-values close to but above 0.05 may still signify ecologically-relevant relationships.

Relationships between snail shell morphology parameters were assessed with Davies' tests and change-point regression models (R package segmented 1.6–2, Muggeo, 2003). The Davies' test can determine if there is a non-constant relationship between two shell parameters. Change-point regression models allow for quantitative estimation of segmented relationships between two morphology parameters and indicate the change-point value (i.e., the point of inflection). When a segmented linear relationship was not found, a linear regression was performed to relate the two parameters. Segmented relationships were allowed to have one breakpoint and 50 bootstrap samples were used in the bootstrap restarting algorithm.

Relationships between snail shell morphology parameters (i.e., shell length, aperture length, and shell thickness) and tidal height, sample season, and their interaction were evaluated with linear mixed effects models (LMM, R package nlme 3.1–160, Pinheiro and Bates, 2022). Linear mixed effect models for crab morphology parameters (i.e., carapace width, cheliped length, and cheliped width) also had sex as an additional fixed factor and no interactive effects were modeled. For both groups, site and quadrat within site were modeled as random factors. Tidal heights which had <20 individuals of a species were excluded from that species analyses and if a species only occurred at one tidal height, height was dropped from the model.

The impact of season, height, and their interactive effect on snail and crab densities were evaluated with generalized linear mixed effect models with Poisson error distributions (GLMM, R package lme4 1.1–31, Bates et al., 2015). Models were tested for over- and underdispersion and where models were over- or underdispersed, negative binomial error distributions were used. Site was incorporated into the model as a random factor. Where models were nearly unidentifiable (unstable fitting of model parameters) interactive effects were not evaluated. Negative binomial linear mixed effect models perform poorly with inflated-zero data and so when a tidal height had a mean of <1 individual × m<sup>-2</sup>, that tidal height was dropped.

For both the laboratory and field predation experiment, the effect of crab treatment, snail species, and size of snail on survival of snails were evaluated with generalized linear models (GLM) with binomial error distributions. Height was included as a fixed factor for the field experiment model. The interactive effects between crab treatment, snail species, and size of snail were evaluated, but there was insufficient power to evaluate the interactions between the aforementioned factors and tidal height. Population-level vulnerability to predation by crab treatments was assessed by taking the sum of the products of the proportion of snails at a given shell length and the predicted proportion that would survive in an interaction with a crab derived from the binomial GLM. Size frequency distributions were pooled across seasons, tidal heights, and sites. Vulnerability calculations did not incorporate crab densities.

### 3. Results

#### 3.1. Density and morphometric surveys

Across sampling seasons, sites, and tidal heights, 5943 *Littorina littorea*, 1683 *Littorina obtusata*, and 1760 *Littorina saxatilis* were measured for shell morphology parameters. An additional 10,260 *L. littorea*, 3410 *L. obtusata*, and 1021 *L. saxatilis* were counted for density estimates. For crabs, 2189 *Hemigrapsus sanguineus*, 1132 *Carcinus maenas*, 130 *Cancer irroratus*, and 48 *Cancer borealis* were measured for carapace and cheliped morphology parameters and density estimates. Results from cheliped morphology analyses followed similar patterns as carapace analyses and are presented in the supplementary materials (Table S1-S8).

Crabs and snails had clear tidal height distribution patterns that

varied with season (Fig. 1). Density of all snail species and *H. sanguineus* had a significant interactive response to sampling season and tidal height (GLMM,  $X^2 \geq 19.1$ ,  $df = 3-9$ ,  $p < 0.01$ ), but each pattern was species specific. *C. maenas* had insufficient densities to evaluate the interactive effect of sampling season and tidal height but both factors separately had significant effects on *C. maenas* distribution (GLMM,  $X^2 \geq 60.3$ ,  $df = 2-3$ ,  $p < 0.01$ ). Both *Cancer* spp. had insufficient data for analyzing the effects of tidal height and season on density but densities across these factors are displayed in Fig. 1.

*L. littorea* was present in every tidal height and during every sampling season and was the most abundant snail at the sites we sampled. *L. littorea* was most abundant in the lower intertidal (mean of 216 snails  $\times m^{-2}$ ) and during June and December (85.0 and 81.1 snails  $\times m^{-2}$ , respectively) and least abundant in the upper intertidal (30.5 snails  $\times m^{-2}$ ) and during September (48.6 snails  $\times m^{-2}$ ). *L. littorea* was most

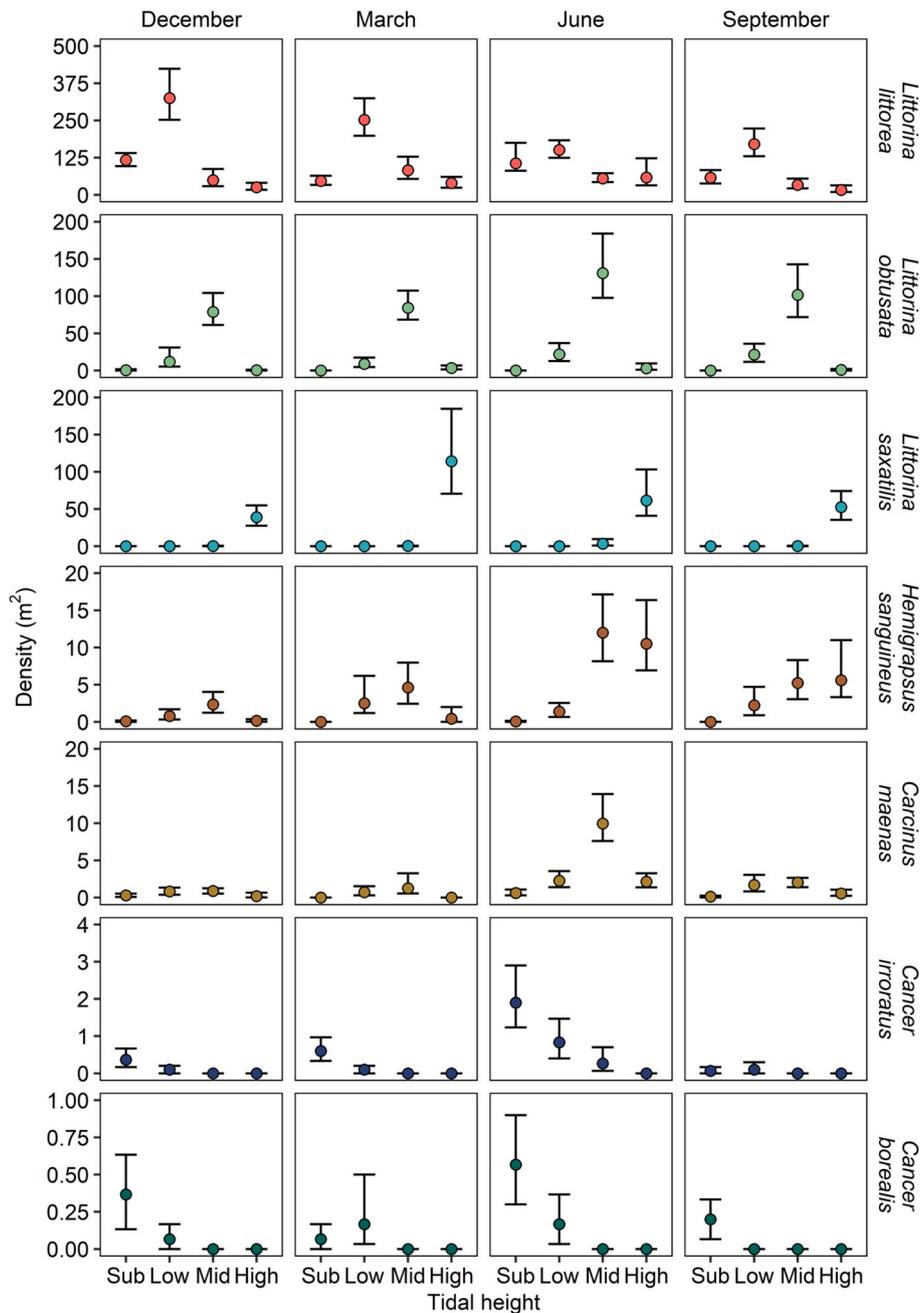


Fig. 1. Mean density of intertidal and shallow subtidal littorinid snails and crabs across tidal heights and sampling seasons. Error bars are 95% bootstrapped confidence intervals.

evenly distributed across tidal heights during the warmer months (June and September) and were more abundant in the lower intertidal during the colder months (December and March). *L. littorea* shell length, aperture length, and shell thickness had significant interactive responses to sampling season and tidal height (Fig. 2, LMM,  $F_{9, 618} \geq 4.1, p < 0.01$ ) with snails being largest during March (mean of 19.6 mm shell length) and in the subtidal (24.2 mm) and smallest during December (17.8 mm) and the upper intertidal (12.8 mm).

*L. obtusata* was primarily found in the lower and middle intertidal zones (Fig. 2), almost exclusively associated with fucoïd algae (e.g., *Ascophyllum nodosum* and *Fucus distichus* Linnaeus, 1767). Several individuals were found in the subtidal (6 individuals) and upper intertidal (85) and were either associated with particularly high elevation *Fucus* spp. or seemed to have been tossed into the location by wave action. *L. obtusata* was most abundant in the middle intertidal (mean of 97.5 snails  $\times$  m<sup>-2</sup>) and during June (18.8 snails  $\times$  m<sup>-2</sup>) and least abundant in the subtidal (0.2 snails  $\times$  m<sup>-2</sup>) and during December (6.1 snails  $\times$  m<sup>-2</sup>). *L. obtusata* aperture length had a significant interactive response to sampling season and tidal height (Fig. 2, LMM,  $F_{3, 257} = 3.1, p = 0.03$ ). Shell length did not have a significant interactive response to sampling season and tidal height (Fig. 2, LMM,  $F_{3, 257} = 2.4, p = 0.07$ ) nor the main effect of tidal height (Fig. 2, LMM,  $F_{1, 257} = 2.5, p = 0.11$ ), but was significantly related to sampling season (Fig. 2, LMM,  $F_{3, 257} = 6.7, p < 0.01$ ). Shell thickness also did not have a significant interactive response to sampling season and tidal height (Fig. 2, LMM,  $F_{3, 257} = 1.6, p = 0.19$ ), but did significantly respond to the main effect of tidal height (Fig. 2, LMM,  $F_{1, 257} = 15.7, p < 0.01$ ) and did not significantly respond to

sampling season (Fig. 2, LMM,  $F_{3, 257} = 0.8, p = 0.51$ ). *L. obtusata* were smallest in March (mean of 7.0 mm) and largest in June (8.6 mm).

*L. saxatilis* were almost exclusively found in the upper intertidal (mean of 60.6 snails  $\times$  m<sup>-2</sup>), taking refuge in moist gravel, under rock overhangs, and within rock crevices (Fig. 2). Across all sites and seasons, only 61 individuals were found in the middle intertidal and none were found in the lower intertidal or subtidal. *L. saxatilis* was most abundant in June (mean of 12.8 snails  $\times$  m<sup>-2</sup>) and least abundant in December (3.0 snails  $\times$  m<sup>-2</sup>). Only in the upper intertidal were sufficient *L. saxatilis* collected for shell morphology analyses, and therefore the effect of tidal height on shell parameters was not evaluated. Sampling season did not significantly affect shell and aperture length of *L. saxatilis* (Fig. 2, LMM,  $F_{3, 187} \leq 2.5, p \geq 0.06$ ), but did significantly affect shell thickness (Fig. 2, LMM,  $F_{3, 187} = 4.8, p < 0.01$ ).

*H. sanguineus* was the most abundant crab we found during our surveys and occurred at all sampled tidal heights (Fig. 3B), although few were found in the subtidal (5 individuals). They were most abundant in the middle intertidal (mean of 3.3 crabs  $\times$  m<sup>-2</sup>) and during June (3.8 crabs  $\times$  m<sup>-2</sup>) and least abundant in the subtidal (0.04 crabs  $\times$  m<sup>-2</sup>) and during December (0.6 crabs  $\times$  m<sup>-2</sup>). Carapace width and cheliped length and width were significantly related to season (Fig. 3A, LMM,  $F_{3, 135} \geq 8.9, p < 0.01$ ), height (Fig. 3B, LMM,  $F_{2, 135} \geq 3.8, p < 0.01$ ), and sex (Fig. 3C, LMM,  $F_{2, 1031} \geq 124, p < 0.01$ ). Crabs were largest in December (mean of 16.0 mm carapace width), in the lower and upper intertidal (15.1 mm), and males were the larger sex (18.4 mm).

*C. maenas* also occurred at all sampled tidal heights. They were most abundant in the middle intertidal (mean of 2.3 crabs  $\times$  m<sup>-2</sup>) and during

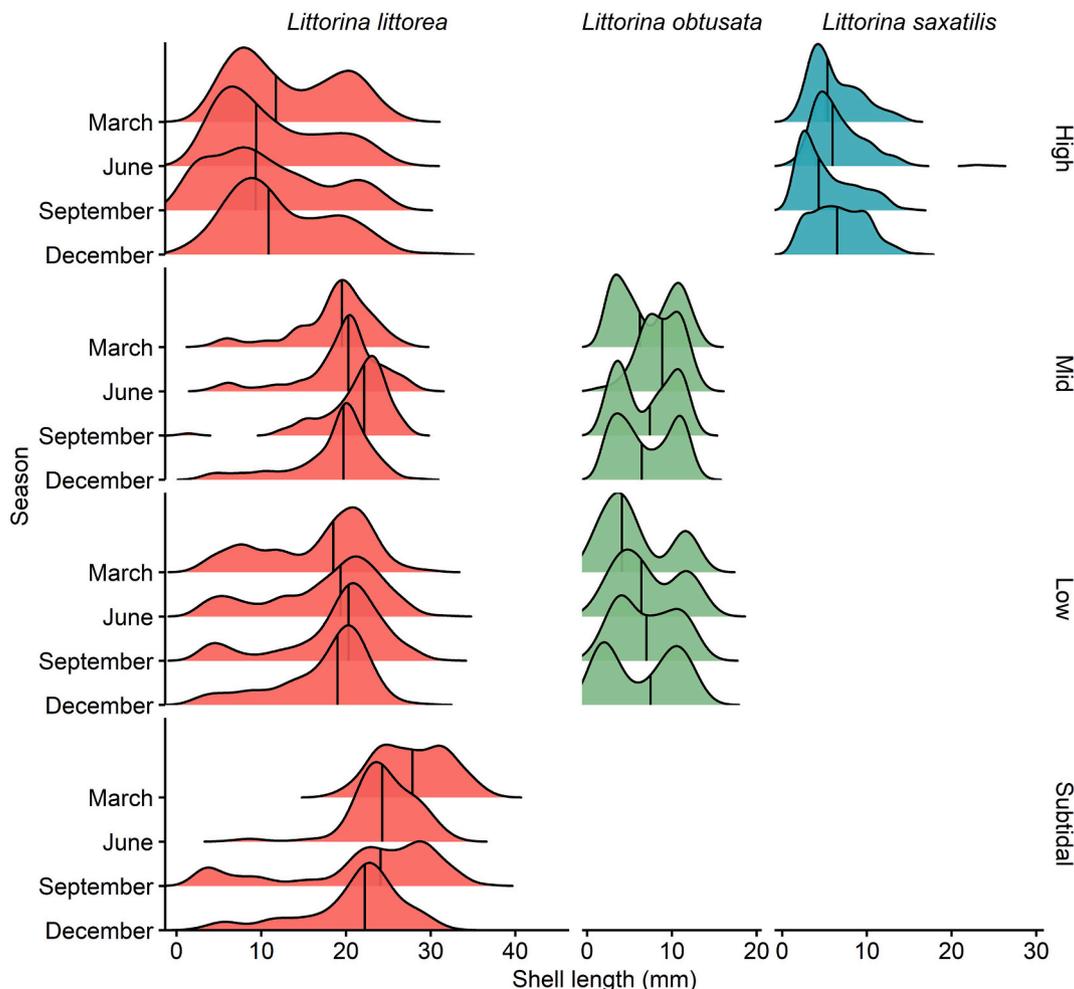
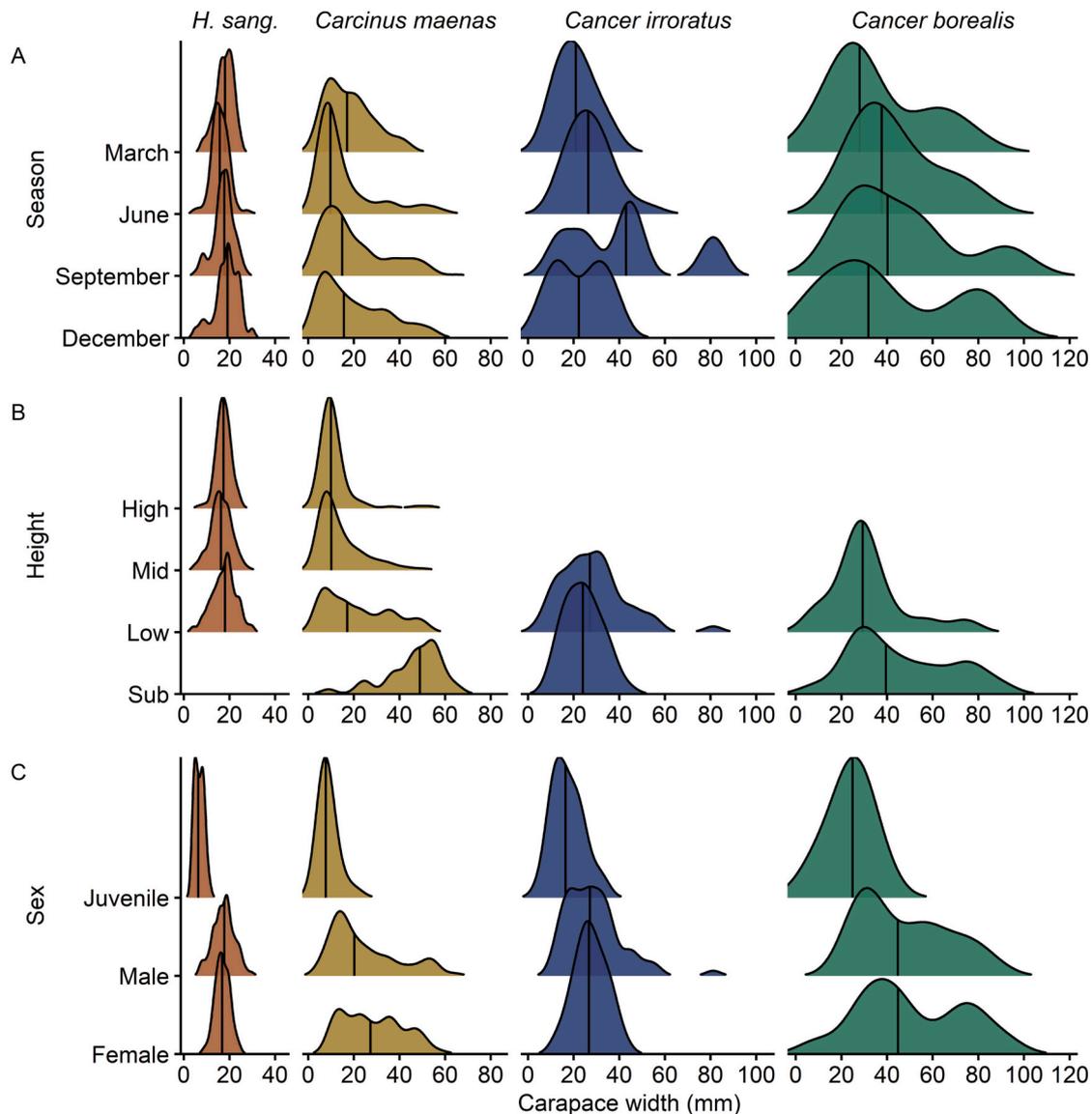


Fig. 2. Size-frequency distribution of littorinid snails across tidal heights and seasons. Solid vertical lines indicate median shell length.



**Fig. 3.** Size-frequency distribution of crabs across (A) seasons, (B) tidal heights and (C) sex. Solid vertical lines indicate median carapace width. Distributions are not displayed for tidal heights and seasons that had fewer than 10 crabs.

June ( $3.9 \text{ crabs} \times \text{m}^{-2}$ ) and least abundant in the subtidal ( $0.3 \text{ crabs} \times \text{m}^{-2}$ ) and during March ( $0.5 \text{ crabs} \times \text{m}^{-2}$ ). Carapace width and cheliped length and width were significantly related to season (Fig. 3A, LMM,  $F_{3, 177} \geq 2.7$ ,  $p < 0.05$ ), height (Fig. 3B, LMM,  $F_{2, 177} \geq 98.9$ ,  $p < 0.01$ ), and sex (Fig. 3C, LMM,  $F_{2, 351} \geq 138$ ,  $p < 0.01$ ). Crabs were largest in March (mean of 28.9 mm carapace width), in the subtidal (42.1 mm), and females were the larger sex (32.0 mm).

*C. borealis* was rare, occurring only in the subtidal and lower intertidal. They were most abundant in the subtidal (mean of  $0.3 \text{ crabs} \times \text{m}^{-2}$ ) and during June ( $0.2 \text{ crabs} \times \text{m}^{-2}$ ). Carapace width and cheliped measurements were significantly related to height (Fig. 3A, LMM,  $F_{1, 33} \geq 4.7$ ,  $p \leq 0.04$ ) and sex (Fig. 3C, LMM,  $F_{2, 10} \geq 9.7$ ,  $p < 0.01$ ), but not season (Fig. 3B, LMM,  $F_{3, 33} \leq 0.5$ ,  $p \geq 0.68$ ). Crabs were largest in the subtidal (mean of 46.6 mm carapace width) and females were the larger sex (50.2 mm).

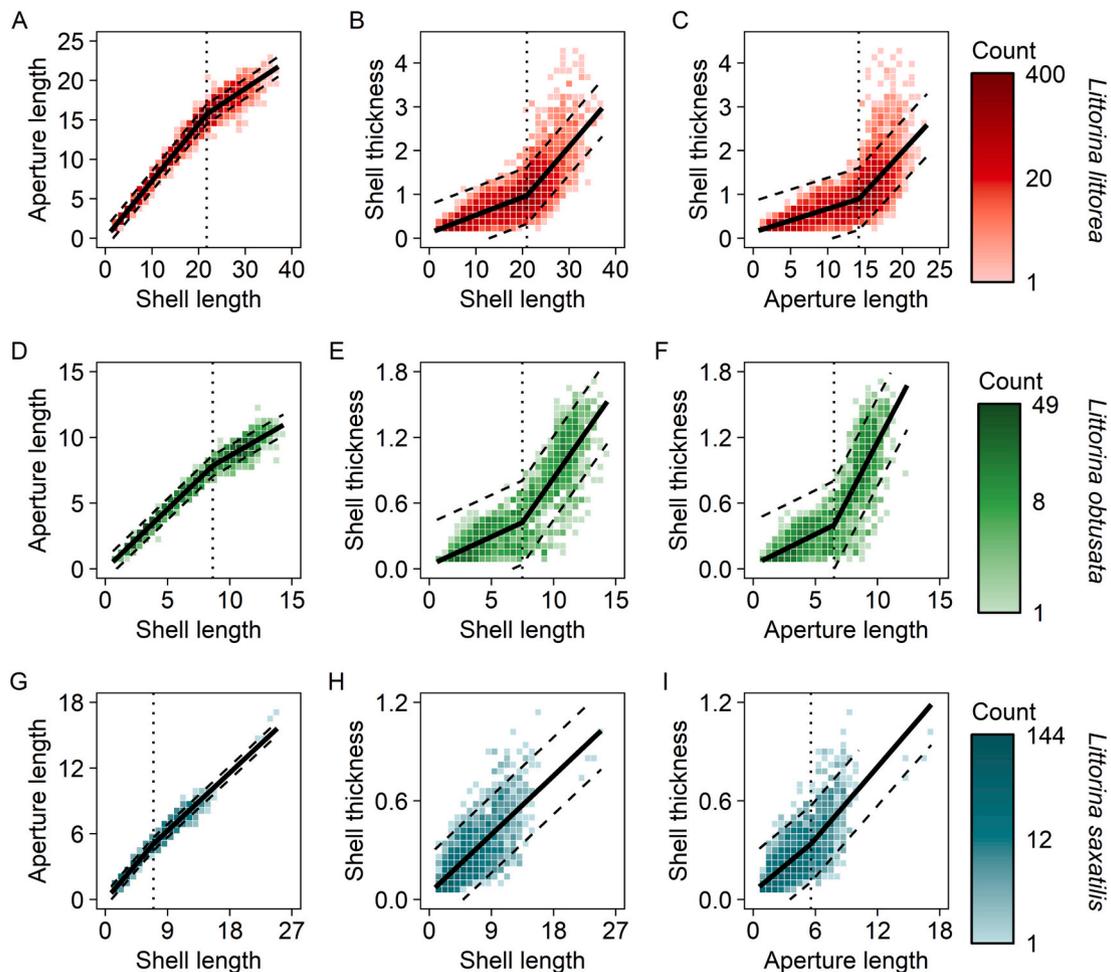
*C. irroratus* was more abundant than *C. borealis* and had a broader distribution across the intertidal, occurring in the middle intertidal in low numbers (9 individuals). Like *C. borealis*, *C. irroratus* was most abundant in the subtidal (mean of  $0.7 \text{ crabs} \times \text{m}^{-2}$ ) and during June ( $0.8 \text{ crabs} \times \text{m}^{-2}$ ). Carapace width and cheliped measurements were significantly related to season (Fig. 3A, LMM,  $F_{3, 62} \geq 6.2$ ,  $p < 0.01$ ) and

sex (Fig. 3C, LMM,  $F_{2, 63} \geq 7.9$ ,  $p < 0.01$ ), but not height (Fig. 3B, LMM,  $F_{1, 62} \leq 2.9$ ,  $p \geq 0.09$ ). Crabs were largest during September (mean of 38.4 mm carapace width) and females were the larger sex (31.8 mm).

Generally, regression models with segmented relationships fit better than linear models for nearly all species and combinations of shell metrics (Fig. 4, Table 1, Davies' Test,  $p < 0.01$ ). Only the relationship between *L. saxatilis* shell length and shell thickness fit better with a linear model (Fig. 2H, Table 1, Davies' Test,  $p = 0.55$ ). In both *L. littorea* and *L. obtusata*, investment in aperture lengthening halved at the change-point and thickening of the shell nearly tripled in *L. littorea* and more than tripled in *L. obtusata* (Table 1). While *L. saxatilis* had some significant change-points (i.e., between shell length and aperture length and between aperture length and shell thickness), they were less pronounced than either of the other littorinids (Table 1).

### 3.2. Predation experiments

In both the laboratory and field predation experiment, both crab species consumed all three species of snails. In the laboratory experiment, snail survival had a significant interactive response with crab species and snail species (GLM,  $F_{2, 3534} = 31.6$ ,  $p < 0.01$ ) and snail



**Fig. 4.** The relationship between (A, D) shell length and aperture length, (B, E) shell length and aperture thickness, and (C, F) aperture length and aperture thickness in the snails (A–C) *Littorina littorea*, (D–F) *Littorina obtusata*, and (G–I) *Littorina saxatilis*. Solid lines are change-point regression model fits, where significant change-points were detected, or linear regression fits with a 95% prediction interval (dashed lines). Dotted vertical lines indicate a significant change in slope.

**Table 1**

Coefficients and change-points for each regression model relating shell morphometrics for *Littorina littorea*, *Littorina obtusata*, and *Littorina saxatilis*. A second coefficient and the change-point are reported where a regression model with segmented relationships fit better than a linear model.

Species	Shell metric 1	Shell metric 2	Coefficient 1	Coefficient 2	Breakpoint (mm)
<i>L. littorea</i>	Shell length	Aperture length	0.72	–0.33	21.7
<i>L. littorea</i>	Shell length	Aperture thickness	0.041	0.083	20.9
<i>L. littorea</i>	Aperture length	Aperture thickness	0.054	0.13	14.2
<i>L. obtusata</i>	Shell length	Aperture length	0.91	–0.36	8.6
<i>L. obtusata</i>	Shell length	Aperture thickness	0.052	0.11	7.5
<i>L. obtusata</i>	Aperture length	Aperture thickness	0.056	0.16	6.5
<i>L. saxatilis</i>	Shell length	Aperture length	0.73	–0.14	7.3
<i>L. saxatilis</i>	Shell length	Aperture thickness	0.040		
<i>L. saxatilis</i>	Aperture length	Aperture thickness	0.052	0.021	5.6

species and snail shell length (GLM,  $F_{2, 3534} = 21.1$ ,  $p < 0.01$ ). All snails smaller than 10 mm in shell length were consumable by both species but *H. sanguineus* could not consume *L. obtusata* above 10 mm (Fig. 5). No snails died in the control treatment. In the field experiment, there was a significant interactive response to crab treatment, snail species, and snail shell length (GLM,  $F_{4, 475} = 2.6$ ,  $p = 0.04$ ) and to tidal height (GLM,  $F_{2, 475} = 3.6$ ,  $p = 0.03$ ). All crabs were capable of consuming all size-classes of *L. saxatilis*, but *L. obtusata* had a size-refuge from *H. sanguineus* above 10 mm and *L. littorea* had a size-refuge from both crab species (>10 mm for *C. maenas* and > 15 mm for *H. sanguineus*, Fig. 6). In control treatments, only three of 220 snails died (1.3%, one *L. obtusata* and two *L. littorea*). *L. saxatilis* had the highest proportion of

its population at risk of consumption by all species of crabs (Fig. 6, > 56%), whereas *L. littorea* only had up to 4% of its population at risk. *L. obtusata* was intermediate with 27–40% of their population at risk of consumption, depending on the decapod predator.

#### 4. Discussion

Distribution and morphology of native organisms can be altered by introduced species and this is typified by the historic invasions of *Littorina littorea* and *Carcinus maenas* (Eastwood et al., 2007; Trussell, 2000). Our study documents the extent of spatial and temporal overlap between littorinids and the two introduced intertidal crabs, *Hemigrapsus*

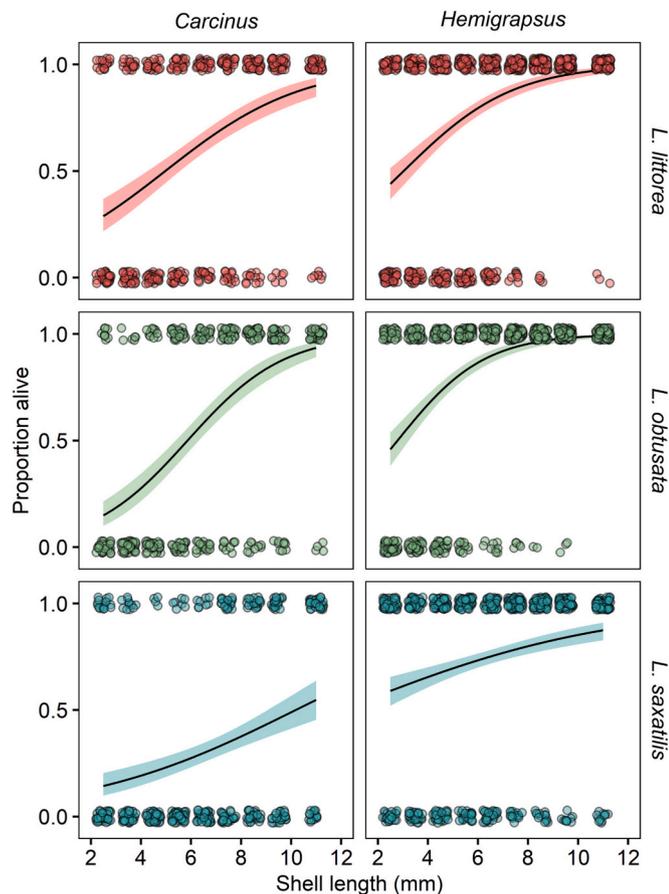


Fig. 5. The effect of crab treatment and snail shell length on survival of three littorinid snails in laboratory enclosure experiments. Points are individual responses to the crab treatment. The solid line indicates the binomial regression fit and the colored areas are the 95% confidence intervals of those models.

*sanguineus* and *C. maenas*, both capable of exerting top-down pressure on snails within the intertidal. Overall, the introduced crabs and *L. littorea* used a greater range of tidal heights than the native species, supporting the idea that introduced species use a broader range of resources than their native counterparts. Successful introduced species are more likely to be generalists than specialists, as species with broad tolerances are more likely to establish and spread in a novel environment and outcompete native species (Blackburn and Duncan, 2001). Our field data suggests that the predation pressure exerted by these crabs varies substantially depending on both the tidal height and season. Both invasive crabs were most abundant in the mid intertidal zones, while the largest *H. sanguineus* were present in the upper and low intertidal, and the largest *C. maenas* were observed in the low intertidal. Predation pressure is likely highest in the mid intertidal zone where crabs were most abundant.

Our findings suggest that *H. sanguineus* poses a significant threat to *Littorina saxatilis* through increased predation pressure in the high intertidal zone. Greater than 56% of *L. saxatilis* are consumable by both introduced crabs (Fig. 6) and, unlike *C. maenas*, adult *H. sanguineus* have substantial overlap with *L. saxatilis* in the high intertidal. Additionally, *L. saxatilis*, unlike its congeners, increases in shell thickness linearly as it grows, leading to a thinner shell than the other species in larger individuals. All three snail species have similar initial investment in shell thickness (0.04–0.05 mm shell thickness per 1 mm shell length), but *L. littorea* and *Littorina obtusata* both more than double their shell thickness investment after reaching a critical point (20.9 and 7.5 mm, respectively). This shift may have been selected for in response to the increased predation pressure both species have experienced in the

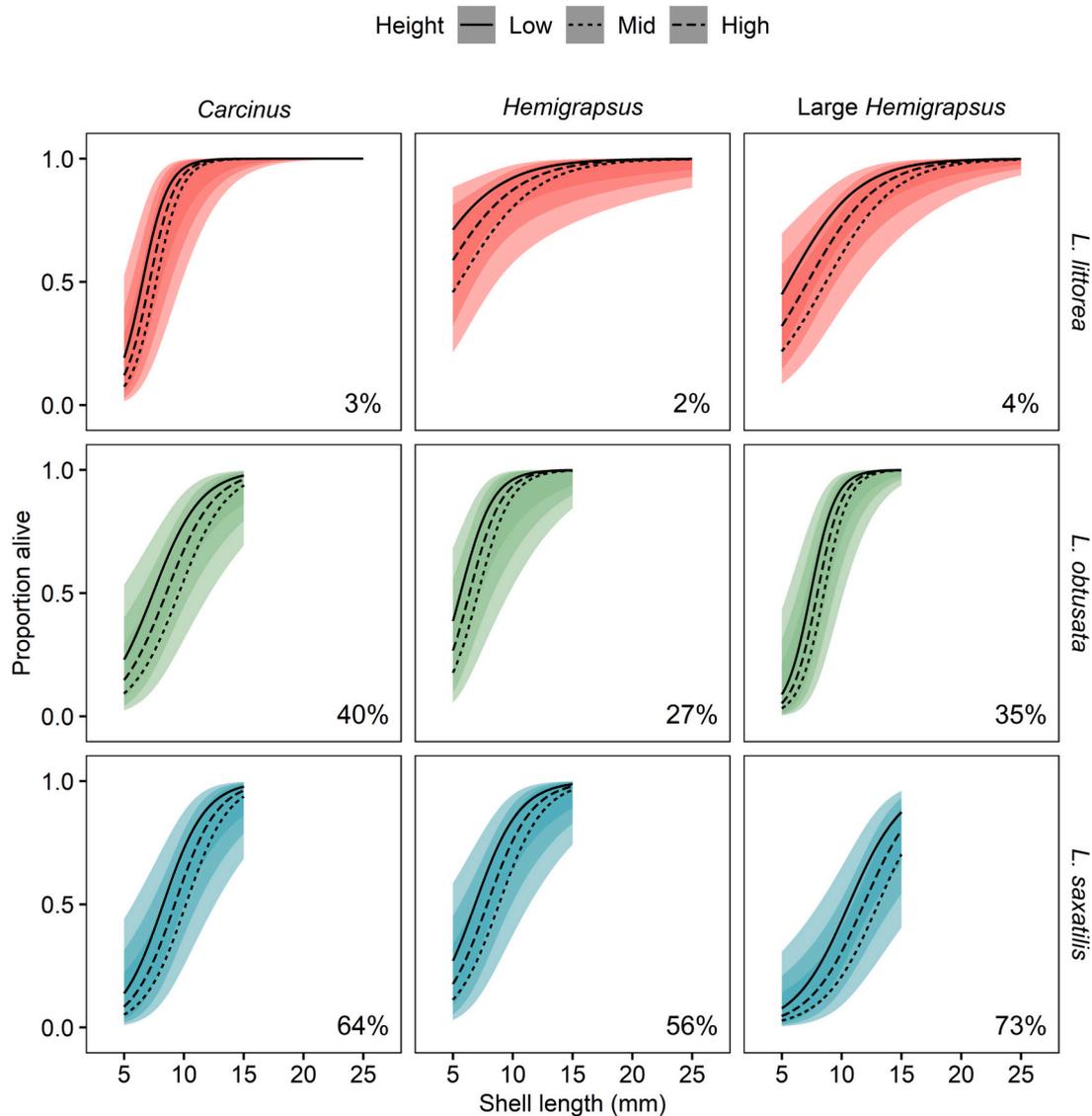
middle and lower intertidal and shallow subtidal environments where there are significantly more decapod predators. While the crabs tested in this study were unable to consume *L. littorea* above 15 mm, *C. maenas* and native decapod predators such as *Cancer borealis* are able to consume larger bodied snails, and may therefore contribute to this shift (Perez et al., 2009). Sustained predation pressure by crabs on a snail population often leads to shifts in shell morphology (reviewed in Reid, 1996). For example, the spire of *L. obtusata* has been reduced and shell thickness has increased in populations exposed to decapod predation (Trussell and Nicklin, 2002).

Snails were most susceptible to predation at small sizes across all three snail species. Predation susceptibility dropped substantially between 5 and 10 mm in shell length (Fig. 6). For *L. obtusata* and *L. saxatilis*, a large proportion of the population was below 10 mm in length (67% and 86%, respectively) and therefore most of the population is vulnerable to predation from both introduced crabs. *L. littorea* is larger bodied than the other two species and experiences a size-refuge for a substantial part of its life (Fig. 2). In addition, *L. littorea* also grows faster than *L. saxatilis* on a similar quality diet (Behrens Yamada and Mansour, 1987), thus moving more quickly out of the vulnerable size range. This high predation pressure at small size classes is concerning, as high mortality among juveniles may reduce the number of individuals reaching adulthood. As mortality rates are highest among the smallest size classes, the impacts on these populations may not be observed for several generations.

Due to competitive pressure from *L. littorea*, *L. saxatilis* has been relegated to the high intertidal zone (Behrens Yamada and Mansour, 1987; Pardo and Johnson, 2005), which was once relatively free of crab predators. In regions where there are no crab predators and *L. littorea* is absent, *L. saxatilis* can occupy the middle (Johannesson and Johannesson, 1990) to subtidal zones (Reid, 1996), and grows significantly larger in the lower intertidal (Behrens Yamada and Mansour, 1987; Pardo and Johnson, 2005). While *L. saxatilis* is more vulnerable to crab predation than the other snails, it may be the best able to locally adapt to novel pressures. *L. saxatilis* has direct-developing larvae (Johannesson, 2003) and high site-fidelity as an adult, moving only a few meters over the course of several months (Janson, 1983). Combined, these factors lead to distinct localized ecotypes (Johannesson, 2003; Reid, 1996), which allow morphology to differ drastically across small distances (Johannesson and Johannesson, 1990). These characteristics may allow *L. saxatilis* populations to adapt to the increased potential predation pressure more rapidly through behavioral or morphological adaptations than their more abundant congener *L. littorea*, which broadcast spawns and is therefore potentially diluted with naïve larvae every year.

The invasion of *H. sanguineus* is ongoing, and densities of these two predators may fluctuate in the future. Initially, the invasion of *H. sanguineus* had negative competitive impacts on populations of *C. maenas*, and abundances declined at several locations in the Gulf of Maine (Bloch et al., 2015; O'Connor, 2018). Populations of *H. sanguineus* can be up to six times higher than those of *C. maenas* (Griffen and Delaney, 2007), possibly as a result of their higher tolerance for members of their own species. Studies have shown that density dependent cannibalistic interactions are stronger for *C. maenas* than they are for *H. sanguineus* (Griffen and Delaney, 2007; Griffen et al., 2008), and predation on juvenile *C. maenas* by *H. sanguineus* is high (Bloch et al., 2019). While it was suggested that *H. sanguineus* may replace *C. maenas* in the intertidal (Tyrrell and Harris, 2000), studies conducted well after the initial invasion have shown variable responses in the population of *C. maenas*, with some populations in decline (Griffen et al., 2021), but many populations remaining stable through time (Bloch et al., 2019; O'Connor, 2018).

Both crabs are generalist omnivores (Elner, 1981; Ropes, 1968; Seeley, 1986) and consumption of snails in the field is likely to be lower than what was observed in our experiments. Recent surveys at Fort Stark and Odiorne Point indicate that crab predation has had varying effects. At Odiorne Point, *H. sanguineus* has negatively impacted snail



**Fig. 6.** The effect of crab treatment, snail shell length, and tidal height on survival of three littorinid snails in field enclosure experiments. The black lines indicate the binomial regression fits with line types (i.e., solid, dashed, and dotted) indicating different tidal heights. Colored areas are the 95% confidence intervals of the model with darker colors indicating overlap between tidal height confidence intervals. Percentage of the population vulnerable to predation is reported in the bottom right of each panel, combined across all tidal heights.

populations, while it has had no impact on populations at Fort Stark (Griffen et al., 2020; Griffen et al., 2021). It is clear that predation pressure will fluctuate based on predator density, tidal height, and season. Further monitoring of *H. sanguineus* populations and their trophic relationship with littorinid snails will be necessary as snails have remarkable impacts on algal composition (Lubchenco and Menge, 1978) and changes in predation pressure may result in trophic cascades.

We tested the capability of crab predators to consume different snail species and sizes, and the respective resistance of those snails to predation. It seems that, of the three littorinid species in this study, *L. saxatilis* is most at risk of being negatively affected by the presence of introduced intertidal crabs, due in part because of their small tidal height range, their reproductive strategy (i.e., no outside sources at a site because they brood their young), and their relatively thin shells. It has already been pushed into the less desirable high intertidal by competition with *L. littorea* (reviewed in Eastwood et al., 2007), where there are lower quality food sources, and environmental conditions are more extreme. There is also the potential for additional predators or competitors added through range expansions and new invasions, which are increasingly common in the Gulf of Maine (McMahan et al., 2020;

Overholtz et al., 2011). Additionally, abiotic conditions are becoming more extreme with the progression of climate change, which is likely to make the high intertidal a much harsher environment. While *L. saxatilis* possesses the ability to locally adapt, it is unclear whether it will be able to keep pace with its rapidly changing environment or if competition and predation will further marginalize populations.

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#### CRediT authorship contribution statement

**Christopher D. Wells:** Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Kaitlin S. Van Volkom:** Conceptualization, Methodology, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Sara Edquist:** Conceptualization, Methodology, Investigation, Data curation, Writing –

original draft, Writing – review & editing. **Sinead Marovelli**: Conceptualization, Methodology, Investigation, Writing – review & editing. **John Marovelli**: Conceptualization, Methodology, Investigation, Writing – review & editing.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Data availability

Data will be made available on request.

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### Appendix A. Supplementary data

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