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Interactions between the invasive European green crab, *Carcinus maenas* (L.), and juveniles of the soft-shell clam, *Mya arenaria* L., in eastern Maine, USA

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ABSTRACT

Invasive species pose a threat to biodiversity in numerous marine ecosystems, and may have severe economic effects on commercially important species. The European green crab, *Carcinus maenas*, is one of the most common invaders of marine ecosystems globally. Since its invasion into eastern Maine, USA, during the early 1950's, populations of the soft-shell clam, *Mya arenaria*, have declined greatly. This has triggered the establishment of shellfish hatcheries and the development of aquaculture techniques to enhance the wild fishery. This study investigated interactions between *C. maenas* and cultured juveniles of *M. arenaria* both in the field and laboratory. In the field (Holmes Bay, Cutler, Maine), clam (initial mean shell length [SL] ±95% CI: 15.8 ± 0.5 mm; n = 30) survival was: 1) 7× higher in predator deterrent treatments compared to open controls; 2) not improved by using rigid vs. flexible netting; and, 3) not improved by raising and supporting deterrent netting 5 cm above the sediment surface. Wild clam recruitment was 4x greater in protected vs. open experimental units. In laboratory trials using similar sized juvenile clams, green crabs consumed clams protected by predator deterrent netting, and in one case did so without leaving visible signs of chipping, crushing, or disarticulating the valves. Physical evidence, other than crushing, may be used to differentiate between clam death due to predation vs. suffocation, disease, or other sources of mortality.

1. Introduction

Predation has played a key role in limiting population growth of marine organisms in the evolutionary past (Sallan et al., 2011; Stanley, 2008), and continues to drive important direct and indirect effects on populations in modern marine ecosystems (Babcock et al., 1999; Freestone et al., 2011; Nakaoka, 2000). Studies examining in situ interactions between decapod predators and their infaunal bivalve prey (Irlandi, 1997; Kuhlmann and Hines, 2005; Seitz et al., 2001; Whitlow, 2010; Wong et al., 2010) have shown the importance of interactive factors such as prey and predator size, prey and predator behavior, bottom/habitat type, crab molt frequency, and large-scale environmental perturbations such as hypoxia (Seitz et al., 2003) and other stressors (Smee et al., 2010) to help explain bivalve mortality patterns.

Soft-shell clams, *Mya arenaria* L., are ubiquitous residents of the soft-bottom intertidal and shallow subtidal zone in the northeast (Beukema, 1976) and northwest Atlantic (Conde et al., 2010; Hunt, 2004), where they are also an important commercial species (Beal, 2002; Dow, 1977). *Mya* feeds by filtering phytoplankton from the water column through its long, fused siphons, and burrows deeply with age to avoid predation (Zaklan and Ydenberg, 1997). Behavioral responses such as increasing burial depth (Flynn and Smee, 2010; Whitlow, 2010) and reduced growth (Beal et al., 2001) occur in the presence of predators. Juveniles (<15 mm shell length, SL) of *M. arenaria* live at or near the sediment-water interface (LeBlanc and Miron, 2006), and during this early part of its life history crustaceans (Bowen and Hunt, 2009; Hunt and Mullineaux, 2002; Taylor and Eggleston, 2000) and other predators such as fish (Kelso, 1979; Steimle et al., 2000) may nip the siphons, or remove individuals completely from the sediments to consume them (Blundon and Kennedy, 1982; Smith et al., 1999). As *Mya* increases in size, it becomes prey to infaunal predators such as naticid gastropods (Edwards and Hubner, 1977), nemertean worms (Bourque et al., 2001), and other species that are adept at removing it from sediments and consuming it at the surface such as large decapod crustaceans (Floyd and Williams, 2004; Ropes, 1968; Seitz et al., 2001; Smith and Hines, 1991). *Mya* may reach a size-refuge (Commito, 1982) or spatial refuge (Skilleter, 1994) from some predators, although these may not be generalizable across the clam's geographic distribution (Beal, 2006a). In Maine, USA, and other New England states, cyclical declines in soft-shell clam populations since the mid-1900's have been largely associated with the dynamics of the invasive green crab, *Carcinus maenas* (Cohen et al., 1995; Whitlow, 2010).

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Short-term field experiments in eastern Maine over the past two decades with juveniles of *M. arenaria* have used flexible netting as a means to deter predators to enhance bivalve survival (Beal, 2006a,b; Beal and Kraus, 2002; Beal et al., 2001). Most trials have shown the importance of predation in regulating clam populations, with the use of exclusion netting explaining between 5 and 45% of the variation in clam survival; however, relatively high percentages of missing and/or dead clams with crushed valves also have been associated with predator exclusion treatments in these experiments (e.g., up to 34.6% see Beal, 2006b). The cause of missing and crushed clams from experimental units completely protected with netting, and with no predator (live or dead) present (or the presence of molts or molted appendages) in experimental units at the end of the field trial, has not been established unambiguously. Chipping of the ventral margin of dead clams of *M. arenaria* and other bivalves, or nearly complete crushed valves (articulated or disarticulated) has been used as the primary physical evidence related to decapod predation (Beal, 2006a,b; Boulding and Labarbera, 1986; Peterson, 1982) while empty valves that show no signs of chipping or crushing have been attributed either to natural death, disease such as neoplasia (Weinberg et al., 1997), death due to suffocation, or death from benthic, nemertean worms that leave no mark after consuming their prey (Bourque et al., 2002).

Here, alternative types of predator netting are tested in the field and laboratory on survival of juveniles of *Mya arenaria* to help explain the fate of missing and crushed individuals from previous exclusion studies, and examine interactions and effects of the presence of green crabs, *Carcinus maenas*, on clam survival through a series of laboratory experiments. Green crabs were used because they have been observed with increasing frequency in eastern Maine over the past decade: 1) in intertidal soft-bottoms (Beal, pers., obs.); and, 2) in experimental units filled with ambient sediments designed to exclude this and other predators (Beal, pers. obs.). In addition, *C. maenas* have become more common recently elsewhere in Maine within intertidal soft bottoms (ME DMR, 2013; Whitlow and Grabowski, 2012). The working hypothesis is that in previous field trials (described above), successful attacks by *C. maenas* on completely protected clams occurred when crabs rested on top of the flexible netting, weighing it down, and then used the tips of their chelae through the apertures (4.2 mm or 6.4 mm) to excavate bivalves from the sediment by grasping their siphons. Clams were then consumed either through the netting, or on the outside of the netting when crabs forced small pieces of shell and tissue through the netting apertures. Further, an additional hypothesis is that missing clams would have been crushed to an extent that any remaining umbos and shell fragments in experimental units at the end of the field trial would have been smaller than the aperture of the sieves (1–2 mm) used to wash the sediments from each unit (see Beal et al., 2001 for a description of these methods). If the prediction is correct, then treatments using rigid netting or flexible netting that is supported and raised sufficiently above the sediments of experimental units containing juveniles of soft-shell clams, or units partially filled with sediment and covered with netting, should not contain crushed or missing clams after sufficient time has elapsed for predators to access clams.

2. Methods

2.1. Field Experiment I. (15 July–29 October 2011; Duck Brook Flat, Cutler, Maine)

This experiment was conducted in unvegetated sediments near the lower mid-intertidal at Duck Brook Flat (DBF) in Holmes Bay, Cutler, Maine, USA (44° 41′ 39.04″ N, 67° 18′ 17.82″ W), from 15 July to 29 October 2011 (106 days; see Beal and Kraus, 2002 for a description of this site). Experimental units (plastic horticultural pots, 0.018 m^2 and ca. 15 cm deep), similar to those used by Beal et al. (2001), were used to test the interactive effects of netting type (a = 2) and exclusion treatment (b = 5; Table 1; Fig. 1) on soft-shell clam survival and growth. Each type of netting was fully crossed with each exclusion treatment yielding ten treatments. Predator exclusion netting was either rigid (extruded) or flexible with a 6.4 mm aperture (Industrial Netting; Minneapolis, MN; http://www.industrialnetting.com/). The five exclusion treatments were: 1) fully protected with netting that was supported ca. 5 cm from the sediment surface using four short pieces of metal wire rods fabricated from coat hangers (2.5 mm diameter; *P*redator *E*xclusion *N*etting *S*upported – PENS); 2) fully protected with netting that was unsupported (no metal rods; *P*redator *E*xclusion *N*etting *U*nsupported – PENU); 3) fully protected with unsupported netting, but with metal rods present to control for potential artifacts caused by the presence of the rods (*P*redator *E*xlusion *N*etting unsupported, but with *R*ods present – PENR); 4) open enclosure with a 1-cm rim of netting around the outside periphery to deter clam migration and with four short metal rods (*O*pen *E*nclosure with peripheral *M*esh *C*ollar – OEMC); and, 5) open enclosure without a peripheral collar, but with a piece of netting to serve as a roof control that allowed predators access to the experimental units, but with a circular piece of netting (ca. 15 cm diameter) supported by wire rods ca. 5 cm from the sediment surface (*O*pen *E*nclosure *R*oof *C*ontrol – OERC).

Metal rods used in eight of the ten treatments had hooked ends (Fig. 1), and were affixed to the units by heating up the straight end, piercing it horizontally through the unit about 1 cm below the rim, and then bending it in such a way to secure it to the pot. Four rods were evenly spaced along the circumference of the rim of each unit, and were measured beforehand to ensure a fixed distance between the rim of the pot and the top of the hooked end. Units fully protected with pieces (50 cm × 50 cm) of unsupported, flexible netting (Fig. 1-G) were similar to those used in past experiments at this site (Beal and Kraus, 2002). That is, the netting completely covered the top of the unit and was raised a small distance above the surface of the sediments (by pulling the netting upward after installing the unit in the sediments) to prevent the netting from interfering with clam feeding. It is possible, however, that the slackness in the netting associated with this treatment is enough to allow predators such as crabs to rest on the top of the netting, weighing it down sufficiently so that it might be possible for them to access clams through the apertures. To examine this hypothesis more closely, a second, fully protected treatment was used except the flexible netting was raised approximately 5 cm above the sediment and

Table 1
Description of each of the five levels of the exclusion factor from Field Experiment I (15 July to 29 October 2011) at Duck Brook Flat in Holmes Bay, Cutler, Maine, USA. Each exclusion type was crossed with both types of netting (Flexible or Rigid; 6.4 mm aperture). (n = 5; N = 50).

Exclusion Description	Abbreviation	Features			
		Netting Present	Predator Deterrent	Metal Rods	Netting Supported by Metal Rods
*P*redator *E*xclusion with *N*etting *U*nsupported	PENU	+	+	−	−
*P*redator *E*xclusion with *N*etting *S*upported 5 cm Off Bottom With Metal Rods	PENS	+	+	+	+
*P*redator *E*xclusion with *N*etting Unsupported & Metal *R*ods Present as a Control	PENR	+	+	+	−
*O*pen *E*nclosure with Peripheral *M*esh *C*ollar to Deter Clam Migration	OEMC	+	−	+	−
*O*pen *E*nclosure with Supported *R*oof *C*ontrol	OERC	+	−	+	+

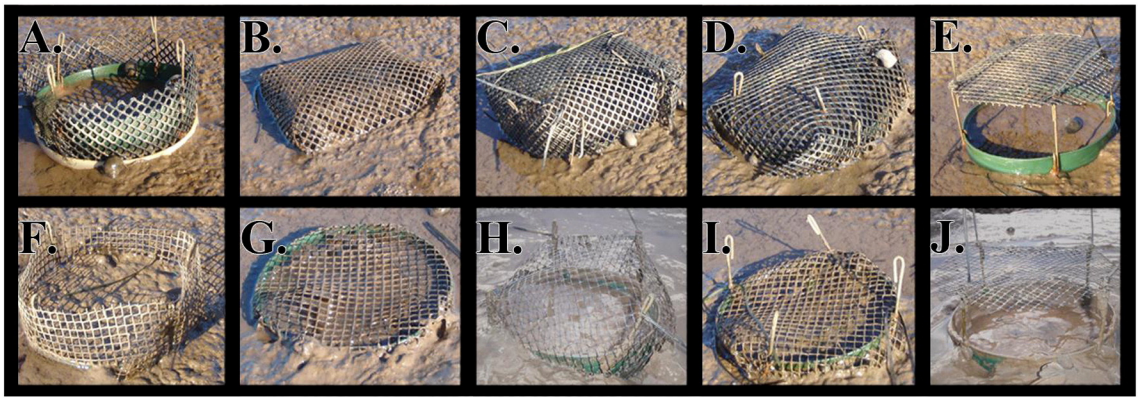

Fig. 1. Photos taken in the field showing each of the 10 treatments used in Field Experiment I at Duck Brook Flat (DBF) in Holmes Bay, Cutler, Maine, USA. The top row (A-E) shows each treatment with rigid netting, and the second row (F–J) shows each treatment with flexible netting (experimental units = 15 cm diameter; aperture size = 6.4 mm). (See Table 1 for a description of abbreviations used for each exclusion treatment.) Open enclosures (A & F: OEMC) had a rim, or collar, of netting around the periphery to deter clam migration, plus four metal wires affixed to the inside periphery at regular intervals. Full netting treatments (B & G: PENU), typical of normal exclusion treatments used in other field studies (e.g., Beal and Kraus, 2002); full netting treatments (C & H: PENS) with the top of the net supported ca. 5 cm from the sediment surface with metal wires to prevent netting from collapsing under the weight of crustacean predators; full netting treatments (D & I: PENR), similar to B & G, but that control for the presence of metal wires; and roof controls (E & J: OERC) that control for the possible effects of the netting roof (shading, reduced flow, increased sedimentation, etc.) while allowing predators access to clams in the units.

supported by securing it to four metal rods using cable ties (Fig. 1-H). Pieces of both flexible and extruded netting (26 cm × 2 cm) used for the fully open treatments were wrapped around the outer periphery of experimental units, and were held in place using heavy-duty rubber bands (Fig. 1-A & F). Pieces of extruded netting used for the three fully protected treatments (Fig. 1-B–D) were cut, shaped, and held together with nylon cable ties so that they would fit tightly and over each experimental unit once it was placed in the sediments. The circular pieces of extruded and flexible netting (Fig. 1-E & J) were affixed to the four metal rods in each unit using nylon cable ties.

On 15 July 2011, a 5 × 10 matrix was established, and each of the ten treatments assigned randomly to positions within each row (completely randomized block design; CRBD). Adjacent experimental units in both rows and columns were placed approximately 1 m apart to ensure independence of treatments. Experimental units were filled with ambient, muddy sediments, and then pushed into the sediments so that a small lip (ca. 0.15 cm) extended above the sediment surface. Next, six juveniles of *Mya arenaria* (mean shell length ±95% CI = 15.8 ± 0.5 mm; n = 30), produced (cultured) in 2010 at the Downeast Institute for Applied Marine Research & Education (DEI; Beals, ME) and overwintered according to Beal et al. (1995), were pushed gently into the top cm of sediment in each unit. This resulted in an initial stocking density of 330 individuals m^{-2}. Prior to the establishment of the experimental matrix, 10 benthic cores were taken from the experimental area using a coring device (area = 0.0182 m^2 to a depth of 15 cm) to establish ambient densities of wild clams and green crabs. Samples were transported to the University of Maine at Machias (UMM) where each was washed through a 2 mm sieve.

All experimental units were retrieved after 106 days on 29 October 2011, and taken to UMM where the contents of each was washed through a 2 mm sieve. All live, dead undamaged (DU), and dead chipped/crushed (DC) hatchery-reared individuals of *Mya arenaria*, *Carcinus maenas*, and juvenile wild recruits of *Mya arenaria* (SL ≤15 mm) were collected and enumerated. Any crushed valve without an umbo was disregarded and not collected. Missing clams also were noted. A growth rate was estimated for each live experimental clam by measuring its initial SL using a distinct disturbance line incorporated in both valves at the time when cultured clams are transferred to sediments (see Beal et al., 1999). Both initial SL and final SL were measured to the nearest 0.01 mm using digital calipers. A mean relative growth index ([Final SL – Initial SL]/Initial SL) was obtained for each experimental unit containing at least one live clam.

2.2. Field Experiment II. (3 July–28 October 2011; Duck Brook Flat, Cutler, Maine)

To enhance information about the ability of predators to prey on juveniles of soft-shell clams protected by flexible netting, a second field experiment was initiated on 3 July 2011 at DBF in unvegetated soft sediments near the mid intertidal (within ca. 50 m of Experiment I). The effect of two interactive factors on clam survival were tested: intraspecific clam density (a = 5; 3, 6, 12, 24, or 48 clams per unit representing densities of 165, 330, 660, 1320, and 2640 individuals m^{-2}, respectively), and predator exclusion (b = 2; flexible, unsupported exclusion netting similar to PENU [see above], but with 4.2 mm aperture vs. open enclosures similar to OEMC [see above], but without metal rods and with the periphery surrounded by a 1 cm piece of flexible netting [4.2 mm aperture] to deter clam migration). Experimental units (as described above) were filled with ambient sediments and arranged in a 5 × 10 matrix with 1-m spacing between rows and columns. Replicates of the ten treatments were randomly assigned a position within the matrix. Cultured juveniles of *M. arenaria* (mean SL ±95% CI = 13.0 ± 0.7 mm; n = 40), with the same origin and history as those used in Experiment I, were added to experimental units as described above. All units were collected from DBF after 117 days on 28 October 2011, and processed at UMM as described above.

2.3. Laboratory Experiment I (21 August to 11 September 2011; DEI, Beals, ME)

A laboratory experiment was conducted at the Marine Education Center at DEI on Great Wass Island, Beals, Maine, USA (44° 28′ 50.64″ N, 67° 35′ 54.97″ W) from 21 August to 11 September 2011 (22 days) to examine closely the behavior of green crabs preying on soft-shell clam juveniles held in treatments similar to those used in Field Experiment I (seawater temperature ranged from 13–15 °C). Six clams, produced at DEI in 2011 (mean shell length ±95% CI: 17.5 ± 0.7 mm, n = 49), were added to plastic horticultural pots (as described above) filled with a commercial sand (Sakrete® Natural Play Sand, Charlotte, North Carolina). Three pots were added to each of three 75-l aquaria (clear glass sides) and then sediment was added around each pot such that it completely encased each pot to its rim. One pot in each aquarium was covered with a piece of rigid or flexible netting (similar to PENU – Table 1) while the other pot was covered with a tight-fitting piece of flexible netting that would not bend or depress under the weight of a

crab. Unfiltered, ambient sea water flowed into each aquarium at all times during the 22-day trial period (13–15 °C). One male green crab (carapace width, CW = 60.2 mm, 64.9 mm, and 61.9 mm; each had recently completed ecdysis, and each had a hard carapace) was added to each aquarium at the beginning of the trial. Crabs were collected from the rocky intertidal adjacent to DEI the day before the trial. During the first eight days, crabs would sometimes climb out of the aquaria overnight. At that time, a wooden board was used to cover the top of each aquarium to ensure that crabs would remain confined to the aquarium.

Daily observations of each aquarium were made to estimate the number of live clams (by counting the number of visible siphons at the sediment surface) in each treatment, number of dead or crushed clams at the sediment surface, the position of the crab within the tank, and the percent of time each crab spent burrowed. At the end of the experiment, the contents of each pot was washed through a 1.8 mm sieve, and the number of live, dead undamaged (DU), and dead chipped/crushed (DC) clams recorded.

2.4. Laboratory Experiment II (3–9 January 2012; UMM, Machias, ME)

A second laboratory experiment was conducted in the aquaculture research laboratory at UMM from 3 to 9 January 2012. This experiment was designed to determine whether the physical presence of green crabs or chemical cues from this species would alter feeding activity of cultured juvenile soft-shell clams. To understand the fate of microalgae without any grazers and in the absence of light, prior to the beginning of the actual experiment (27 December 2011), four experimental units (diameter = 17 cm, depth = 15 cm) were filled with one liter of sand (as described above), a total of 1.5 l of seawater, and approximately 50,000 cells mL^{-1} of a microalgal monoculture (*Chaetoceros gracilis* [CCMP 1316]). Seawater used in the trial was collected at DEI, and filtered through a 1 μm filter bag. Each experimental unit received an independent supply of air. The first estimate of algal cell numbers in each experimental unit was conducted the next day, and again after a period of 6 days, on 2 January 2012, when the final count was recorded. All cell counts were completed using a haemocytometer. Some water had evaporated from the four units during the period of time; therefore, the volume of water left in each unit was measured and counts adjusted to obtain a density per 1.5 L. Sediment in each unit was checked for anoxia. None had an odor, and the sediment in each had not turned black indicating that the level of aeration was sufficient for a 6-day period in the experimental units.

Room temperature during the pre-trial period and throughout the second laboratory experiment was maintained between 15–17 °C, as this was approximately the temperature range in Laboratory Experiment I. During the pre-trial period and throughout Laboratory Experiment II, the room was kept in complete darkness, and lights were turned on only when data was being recorded. The experiment was initiated on 3 January 2012 and ran for 6 days. Sixteen experimental units (as in the pilot study, and filled to 2 L with filtered seawater – 34 ppt) were arranged into four blocks, and each of four treatments was assigned randomly to a position (2 × 2 matrix) within each block. Treatments were: 1) Control (C) – microalgae only (5×10^4 cells mL^{-1}; this treatment was similar to the pilot experiment); 2) Microalgae plus crushed green crab extract (CC) and six hatchery-reared juvenile soft-shell clams (mean SL ± 95% CI = 19.3 ± 0.6 mm, n = 51; produced at DEI during 2011); 3) Microalgae plus one live male crab (LC) and six hatchery-reared juvenile soft-shell clams; and, 4) Clam control (CL) – microalgae plus six hatchery-reared clams only. Crabs were obtained on 3 January 2012 from the rocky intertidal area adjacent to DEI, and each experimental unit was aerated independently. Because it was difficult to capture crabs at this time of year, crabs of both sexes were included in the trial; however, only males (CW range = 26.5–37.9 mm) were used in the LC treatment. Two of the four green crabs used in the CC treatment were females (CW = 27.7 mm and 38.6 mm). Clams were pushed gently into the sediment as in previous experiments. For experimental units associated with the CC treatment, each crab was crushed in a glass dish and ca. 10 ml of orange extract poured into a unit ca. 30 minutes after clams were established in the sediments. A small amount of seawater in each of the sixteen units was replaced on five of the seven days during the trial by mixing filtered seawater with aged freshwater kept in a HDPE carboy. To determine effects of treatment on the fate of algal cells, counts were recorded on Days 3 and 6 using a haemocytometer, and each measurement was an average of three counts from each treatment. At the end of the experiment, clams were collected by sieving the sediments from each experimental unit using a 1 mm sieve. Number of live, DU, and DC clams from each unit was recorded.

2.5. Laboratory Experiment III (27 June–17 July 2013; DEI, Beals, ME)

To further explore the ability of green crabs to consume juveniles of *Mya arenaria* protected with flexible netting, a third laboratory experiment was conducted. Plastic horticultural plant pots (as described above) were added in groups of three to each of five 75-l aquariums (T = 18–20° C). Sand (as described above) was added to each pot within each aquarium to create three treatments as follows: pot #1 – to the rim; pot #2 – within 1 cm of the rim; and pot #3 – within 8 cm of the rim. Next, sand was added to each aquarium so that the three experimental units were buried (on the outside of each unit) to their rim. Six clams (mean SL = 14.8 ± 0.4 mm, n = 30) were placed on the sediment surface of each unit and then a piece of flexible netting (6.4 mm aperture) with slack, similar to that used in Field Experiment I (i.e., PENU) and Laboratory Experiment I, was secured to each pot using a rubber band. One male individual of *Carcinus maenas* (CW = 69.9–71.7 mm) was added to each aquarium after clams had completely burrowed. Crabs were collected from the rocky shore adjacent to DEI, and were allowed 24 hr to acclimate to experimental temperatures. Seawater (32 ppt) in each aquarium was changed twice during the experimental interval, and clams were fed daily 100 ml of cultured T. *Isochrysis galbana*. The prediction from field trials was that if green crabs were able to consume soft-shell clams through the mesh netting, that clams would be consumed only in units filled to the rim with sand. At the end of the experiment, number of live and dead (DU, DC) clams in each experimental unit was noted.

2.6. Data analysis

For Field Experiment I, the relative efficiency of the CRBD (Underwood, 1997) against a completely randomized design (CRD) was lower for each dependent variable. Hence, blocking was ignored and the data analyzed as a CRD using analysis of variance (ANOVA), and the following linear model:

$$Y_{ijk} = \mu + A_i + B_j + AB_{ij} + e_{k(ij)}$$

Where:

- Y_{ijk} the dependent variable (mean percent survival, mean relative growth, mean number of recruits, and mean number of green crabs);
- A_i Netting type (j = 1–2, fixed);
- B_j Enclosure type (i = 1–5, fixed); and,
- e_k Experimental error (k = 1–5).

Relative growth (RG = [Final SL − Initial SL]/Initial SL) was used to assess growth rather than final SL or absolute growth because of the significant linear relationship between initial and final SL ($r^2 = 0.128$, $P < 0.0001$, n = 141), which was similar to previous studies (Beal, 2006b). An RG = 1 indicates a doubling of shell length. An arcsine transformation was performed on mean percent survival for the analysis of variance (ANOVA) to meet assumptions of variance homogeneity and

normality. No transformations were necessary for other dependent variables.

A series of mutually exclusive, single degree-of-freedom orthogonal contrasts was performed to more closely examine the nature of the predator exclusion treatments:

1) Predator Exclusion Netting vs. Controls (PENU, PENR, PENS vs. OEMC, OERC). This tests the overall importance of predation.
2) Predator Exclusion Netting (Unsupported and unsupported with metal rods present) vs. Predator Exclusion with supported Netting (PENU, PENR vs. PENS). This tests the importance of keeping netting above the sediment surface to ensure crabs and other predators cannot gain access to the clams through the netting.
3) Predator Exclusion Netting (Unsupported) vs. Predator Exclusion Netting (Unsupported, but with metal rods present (PENU vs. PENR). This tests whether the presence of the metal rods affects any of the dependent variables.
4) Migration control vs. Roof controls (OEMC vs. OERC). For the open enclosures, this tests whether the presence of a roof (but without a peripheral collar to deter migration) affects clam survival, growth, recruitment, or the presence of green crabs differently than in units without a roof but with a peripheral fence (collar).

Because one treatment associated with the relative growth data (roof control with flexible netting) had no survivors among the five replicates, and some experimental units from the remaining nine treatments contained no live clams, the planned contrasts were not orthogonal to each other. To control for the lack of independence among the planned contrasts, an adjusted type I error rate was used according to Winer et al. (1991): $\alpha' = 1 - (1-\alpha)^{1/n}$ (where n = number of contrasts; $\alpha' = 0.0127$).

The linear model used for the analysis of survival data from Field Experiment II, which were arcsine-transformed to meet assumptions of ANOVA, was identical to that used for Field Experiment I.

For Laboratory Experiment I, the frequency of the crab at one of four positions within each aquarium (1: beside treatment 1 (tight-fitting, flexible netting); 2: beside treatment 2 (slack-fitting, flexible netting); 3: beside treatment 3 (rigid netting); and, 4: between pots) was recorded, and a Fisher's Exact Test performed to determine if crab behavior differed between aquaria. To determine if siphonal activity was related to crab position within the aquaria, the number of visible siphon pairs in the pot next to the crab was recorded each day for each aquarium. This value was subtracted from the mean number of siphon pairs in the other two pots in the aquarium on a particular day. The mean difference should be zero under the null hypothesis that proximity of a crab to a particular pot does not affect siphon activity. A one-sample t-test on the mean difference was performed to test this null hypothesis.

Data from Laboratory Experiment II was analyzed as a CRD using ANOVA because of the lack of a significant block effect ($P > 0.75$). The linear model was the same as that used for Field Experiment I, where:

Y_{ijk} is the dependent variable (untransformed mean number of cells mL^{-1});
A_i Date (i = 1–2, fixed);
B_j Treatment (j = 1–4, fixed); and,
e_k Experimental error (k = 1–4).

A series of single degree-of-freedom orthogonal contrasts was used to examine more closely the treatment effect:

1) Crab vs. No Crab (LC & CC vs. C & CL);
2) Live Crab vs. Crushed Crab (LC vs. CC); and,
3) Control (without clams) vs. Control (with live clams) (C vs. CL).

Data from Laboratory Experiment III was analyzed as a randomized complete block design, with one replicate of each treatment per block (= aquarium). The dependent variable was number of dead, crushed (DC) clams per unit.

All analyses were conducted using SAS 9.2. Sample means are presented with their corresponding 95% confidence intervals.

3. Results

3.1. Field Experiment I. (15 July–29 October 2011; Duck Brook flat, Cutler, Maine)

Mean number of wild clams from the benthic cores taken on 15 July from the experimental area prior to establishing the trial was 10.9 ± 16.6 individuals m^{-2} (n = 10). Two clams (13.1 mm and 19.4 mm) occurred in two of the ten samples. None of the core samples contained a green crab or other large, potential crab predators (e.g., *Cancer irroratus*, B. Beal, pers. obs.).

3.1.1. Survival

Few missing and dead clams with crushed/chipped valves were observed from fully protected units (PENU, PENS, PENR) regardless of netting type (Table 2). Unlike previous field trials, combined losses due to missing and dead crushed/chipped valves from fully protected units with unsupported flexible netting (PENU) was only 3.3 ± 9.3% (a single clam in one of the five experimental units was found dead with distinct chipping along its ventral margin; Table 2). This was the only fully protected treatment where any dead clams with crushed or chipped valves was found; however, a single clam was missing from one of the five units covered with unsupported flexible netting and with the metal rods extending up through the netting (PENR) and in one unit with rigid netting supported 5 cm off the sediment surface by metal rods (PENS; Table 2). Mean percent of missing and crushed/chipped (DC) clams from the open enclosures (OEMC, OERC) ranged from 56.7% to 86.7%; concomitantly, the presence of netting explained nearly 71% of the total variation in mean survival (Table 3). No significant difference in mean survival was observed between treatments where rigid (48.0 ± 14.9%, n = 25) vs. flexible netting (46.0 ± 14.6%, n = 25) was used ($P = 0.4118$), and the pattern of survival across exclusion treatments was similar between netting types ($P = 0.9283$; Fig. 2). Among exclusion treatments, the orthogonal contrast that examined the importance of predation (fully protected units [PENU, PENS, PENR; 70.6 ± 8.3%, n = 30] vs. open controls [OEMC, OERC; 11.7 ± 8.0%, n = 20]) explained nearly 92% of the variation ($P < 0.0001$). The only other significant contrast was among the controls ($P = 0.0089$), where mean survival among units with roof controls (pooling netting type) was 1.7 ± 3.8% (n = 10) vs. 21.7 ± 13.8% (n = 10) for units with collars. None of the clams in the roof controls with flexible netting (OERC; Fig. 1–J) survived (Table 2), suggesting that the peripheral collars prevented clams from leaving the pots, collars reduced predator effectiveness, or predator effectiveness was enhanced somehow due to the presence of a roof.

3.1.2. Growth

Relative growth did not vary significantly either with exclusion type or netting (Table 4; Fig. 3). Mean final SL pooled across all treatments was 22.4 ± 0.7 mm (n = 38; Table 5), an absolute increase of 5.9 ± 0.7 mm.

3.1.3. Wild *Mya* recruits and *Carcinus maenas*

Wild recruits of *Mya* occurred in 36 of 50 (72%) experimental units (range = 1–17 individuals $unit^{-1}$, or 55–935 ind. m^{-2}). Mean number of recruits was ca. four times higher in units fully protected with netting (4.6 ± 1.4 ind., n = 30) compared to controls (1.1 ± 0.5 ind., n = 20; Fig. 4), and this difference was statistically significant ($P = 0.0003$; Table 6). In addition, significantly more wild recruits occurred in units with netting supported by metal rods (PENS: 6.2 ± 3.4 ind., n = 10) vs. those with unsupported netting (PENU, PENR: 3.8 ± 1.4, n = 20;

Table 2
Mean (±95% CI) percent alive (%A), dead with undamaged valves (%DU), dead with crushed or chipped valves (%DC), and missing (%M) of hatchery-reared juveniles of *Mya arenaria*, mean number of wild recruits of *Mya* (SL ≤15 mm), and mean number of green crabs, *Carcinus maenas* from experimental units (Area = 0.0182 m^2) associated with Field Experiment I at Duck Brook Flat, in Holmes Bay, Cutler, Maine (15 July to 29 October 2011). See Table 1 for a description of each level of the Exclusion factor, and Fig. 1 for a photo of each. (n = 5).

Netting	Exclusion	% A	% DU	% DC	% M	Recruits	Crabs
Flexible	PENU	66.7 (25.3)	30.0 (24.0)	3.3 (9.3)	0 (0)	3.4 (2.3)	0 (0)
	PENS	66.7 (20.7)	33.3 (20.7)	0 (0)	0 (0)	7.6 (6.5)	0 (0)
	PENR	80.0 (22.7)	16.7 (14.6)	0 (0)	3.3 (9.3)	4.0 (3.8)	0.2 (0.6)
	OEMC	16.7 (20.7)	16.7 (20.7)	13.3 (17.3)	53.3 (45.3)	1.2 (1.6)	0 (0)
	OERC	0 (0)	13.3 (17.3)	13.3 (17.3)	73.3 (23.6)	0 (0)	0 (0)
Rigid	PENU	63.3 (44.9)	36.7 (44.9)	0 (0)	0 (0)	4.6 (5.0)	0.6 (1.1)
	PENS	73.3 (27.8)	23.3 (31.4)	0 (0)	3.3 (9.3)	4.8 (5.4)	0.2 (0.6)
	PENR	73.3 (27.8)	26.7 (27.8)	0 (0)	0 (0)	3.0 (4.2)	0.4 (0.7)
	OEMC	26.7 (27.8)	16.7 (29.3)	16.7 (35.8)	40.0 (27.7)	2.4 (1.1)	0 (0)
	OERC	3.3 (9.3)	10.0 (27.8)	26.7 (18.5)	60.0 (31.4)	0.8 (1.4)	0 (0)

Table 6). Individuals of *C. maenas* (CW range = 6.7 mm to 13.7 mm) occurred in six units (10%), all of which were protected with netting (P = 0.0433; Table 6). Although five of the six units were protected with rigid vs. flexible netting, this result was not statistically significant (P = 0.0754; Table 6). A single crab was found in five units, and two crabs were found in one unit. None of the units with green crabs contained DC clams.

3.2. Field Experiment II (3 July–28 October 2011; Duck Brook Flat, Cutler, Maine)

The effect of stocking density on juvenile soft-shell clam survival was not statistically significant (P = 0.2913; Table 7); however, the netting treatment explained nearly 53% of the total variation in clam survival (P < 0.0001; mean clam survival in fully protected units = 66.5 ± 8.8% vs. 14.8 ± 10.1% in open units, n = 25), and this pattern was similar across all densities (P = 0.3628, Table 7). Clams were found dead with chipped/crushed valves or were completely missing from each of the five density treatments with predator netting (Table 8). A combined mean of 20% of individuals were missing or crushed from the highest density treatment. A total of 16 live green crabs was found in 10 of the 50 (20%) experimental units (units had 1, 2, or 5 crabs; 3 units were open enclosures, 7 units had protective netting). No significant effect due to the netting or density treatment on mean green crab number was observed (P > 0.09). Fifteen crabs had CW less than 9 mm (CW range = 3.8 mm to 8.7 mm; mean CW = 6.1 ± 1.0 mm), and none of the units with these crabs contained crushed clams. One male green crab (CW = 30.0 mm) was found in an open unit (initial density = 24 clams/unit). No live clams were observed in that unit and only three crushed valves were recovered, the remaining clams were missing. No significant effects due to density or netting treatment were observed on mean number of wild recruits of *M. arenaria* (P > 0.30; $\bar{x} = 1.4 \pm 0.45$ ind. $unit^{-1}$, or 74.7 ± 24.6 ind. m^{-2}; n = 50).

3.3. Laboratory Experiment I (21 August to 11 September 2011; DEI, Beals, ME)

Each crab settled close to one of the pots more than 50% of the time (i.e., >11 daily observations; Table 9); however, the pattern of crab behavior was not consistent between aquaria (P = 0.0006). Two crabs (in aquaria "A" and "B") behaved similarly, spending the majority of time (ca. 55%) adjacent to units protected with rigid netting, while the third crab spent the majority of time burrowed (ca. 77%) and adjacent to the pot with tight-fitting, flexible netting. On day eight (30 August), a dead, articulated shell with no tissue was observed in aquarium "C" (treatment = slack, flexible netting) on top of the sediment and underneath the netting. The clam had been chipped on its posterior ventral margin, in the area where siphons are located. In addition, the flexible netting was closer to the sediment than it had been on previous days, suggesting the crab had climbed on top of the netting, forcing it down toward the sediment surface during the time it preyed on the clam. On one occasion, a crab was found resting on top of rigid netting (3 September 2011; aquarium "A"). This pot had two visible pairs of siphons while the other two pots in the same tank had 4 visible pair of siphons. In general, however, number of visible pairs of siphons was not related to the position of the crab within the aquarium (T = 0.36, P = 0.717, n = 63). On 11 September, a dead clam with undamaged valves, and some tissue remaining, was found in a pot in tank A with rigid netting. All other clams were found alive.

3.4. Laboratory Experiment II (3–9 January 2012; UMM, Machias, ME)

Mean algal cell densities differed significantly among treatments (P < 0.0001; Table 10). Orthogonal contrasts demonstrated that treatments with either a crushed crab (CC) or a live crab (LC) had cell counts four times higher than those without crabs ($17.63 \pm 4.42 \times 10^4$ cells mL^{-1} vs. $4.81 \pm 1.52 \times 10^4$ cells mL^{-1}, n = 4) suggesting an effect on clam feeding. This result was consistent between sampling dates (P = 0.3294; Table 10; Fig. 5). Mean algal cell densities from both crab treatments

Table 3
Analysis of variance on the arcsine-transformed mean percent survival of hatchery-reared juveniles of *Mya arenaria* from Field Experiment I at Duck Brook Flat, in Holmes Bay, Cutler, Maine (15 July to 29 October 2011). Two factors (Plastic netting [a = 2; Rigid or Flexible; aperture = 6.4 mm] and Exclusion [b = 5; see Table 1 for a description of each level of the Exclusion factor]) were orthogonal to each other. The 4 single degree-of-freedom orthogonal contrasts for the Exclusion factor are presented. P-values in boldface represent statistically significant hypothesis tests (α = 0.05). (n = 5).

Source	*df*	*SS*	*MS*	*F*	*Pr > F*
Exclusion	4	29291.68	7322.92	25.41	**<0.0001**
Predator Exclusion (PENU, PENS, PENR) vs. Open Controls (OEMC, OERC)	1	26815.90	26815.90	93.04	**<0.0001**
Predator Exclusion Netting Unsupported (PENU, PENR) vs. Supported (PENS)	1	24.65	24.65	0.09	0.7715
Predator Exclusion Netting Unsupported (with vs. without metal rods: PENU vs. PENR)	1	272.95	272.95	0.95	0.3363
Open Enclosures (with collars vs. roof controls: OEMC vs. OERC)	1	2178.18	2178.18	7.56	**0.0089**
Netting (Rigid vs. Flexible)	1	198.28	198.28	0.69	0.4118
Exclusion × Netting	4	248.43	62.11	62.11	0.9283
Error	40	11529.24	288.23		
Total	49	41267.63			

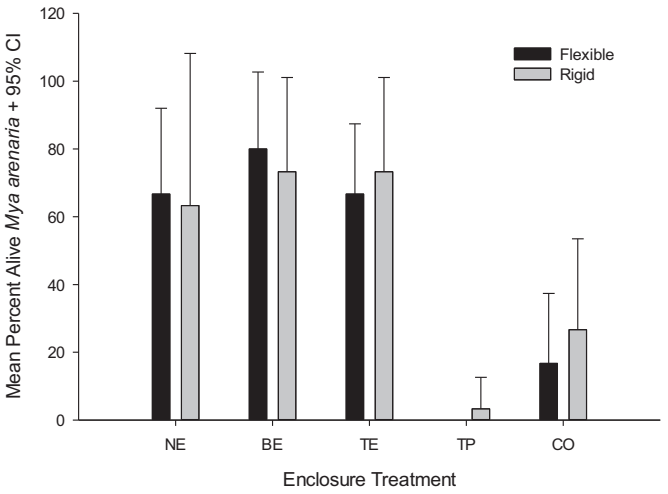

Fig. 2. Untransformed mean percent survival (+95% CI) from Field Experiment I conducted at DBF (15 July to 29 October 2011). (See Table 1 for a description of each level of the Exclusion treatment, and Fig. 1 for a photo of each treatment). (n = 5).

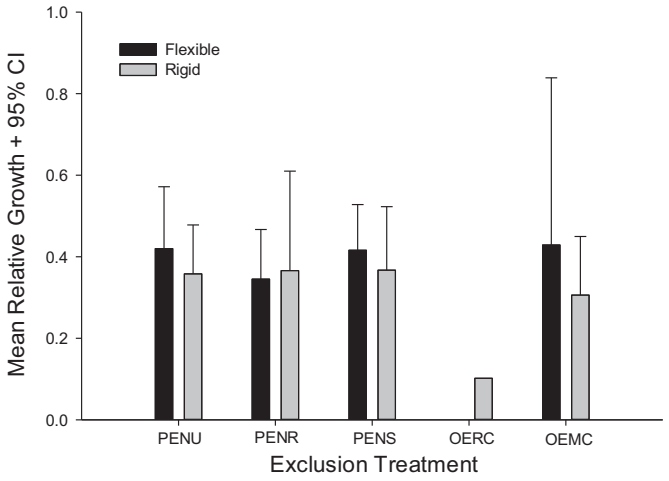

Fig. 3. Untransformed mean relative growth (+95% CI) from the field experiment conducted at DBF (15 July to 29 October 2011). (See Table 1 for a description of each level of the Exclusion treatment, and Table 5 for the number of replicates associated with each bar.).

(CC vs. LC, P = 0.3573) and both controls (C vs. CL, P = 0.2607) were not significantly different (Table 10).

At the end of the experiment, clam survival in controls (CC & CL) was approximately 94% (3 of 48 animals were found dead, with undamaged valves; Table 11). As with Laboratory Experiment I, the three DU clams from the two treatments without crabs were found below the sediment surface, had blackened shells with a distinct odor typical of H_2S, and most of the decomposed tissue remained within the valves. Of the four units containing clams and live crabs (LC), all clams were found alive in one unit (that crab had burrowed into the sediments and was missing a chela), and all clams were dead in the other three units; however, clam fate varied greatly between units. Animals in two of the LC units were all found dead within 24 hours after the experiment was initiated with chipped or crushed valves whereas those in the other unit had no discernible valve damage and were scattered on the surface of the sand within 24 hours. None of the valves (crushed or undamaged) in these three LC units had any attached flesh (i.e., shell and shell fragments were clean) indicating that crabs had consumed the soft tissue of each clam.

3.5. Laboratory Experiment III (27 June–17 July 2013; DEI, Beals, ME)

Crabs preyed on clams only in experimental units that were completely filled with sediments (P = 0.0067; Table 12). All dead clams (n = 5) were recovered as crushed valves with only the umbos recognizable, and remaining relatively intact.

4. Discussion

Field and laboratory studies presented here indicate how vulnerable juveniles of the soft-shell clam are to crustacean attack, especially green crabs, *Carcinus maenas*, supporting results from previous investigations from the northeast U.S. and Atlantic Canada (Beal et al., 2001; Elner, 1981; Floyd and Williams, 2004; Hunt, 2004; Pickering and Quijón, 2011; Whitlow, 2010). Field studies examining the role of predation on the fate of juveniles (<15 mm SL) of the soft-shell clam, *Mya arenaria* (Beal, 2006a,b; Beal et al., 2001) have noted dead chipped and crushed clams as well as completely missing individuals in treatments fully protected by netting. Similar observations have been made for juveniles of other infaunal bivalves such as *Mercenaria mercenaria* and/or *Chione cancellata* (Beal, 1983; Nakaoka, 2000; Peterson, 1982), *Katelysia scalarina* and *K. rhytiphora* (Peterson and Black, 1993), and when investigators used netting in mariculture research programs (Beal and Kraus, 2002; Cigarría and Fernández, 2000; Serdar et al., 2007; Spencer et al., 1992). Several hypotheses may explain the apparent mystery of crushed and missing clams from fully protected experimental units in the field. 1) Chipped or crushed clams could result from unintentional, improper handling of small bivalves by investigators when initiating the field studies, or at the end of the field trial during sample processing; 2) Small predators could have been added accidentally to experimental

Table 4
Analysis of variance on the untransformed mean relative growth of live hatchery-reared juveniles of *Mya arenaria* from Field Experiment I at Duck Brook Flat, in Holmes Bay, Cutler, Maine (15 July to 29 October 2011). (See Table 1 for levels of these factors, and Table 3 for a description of each single degree-of-freedom a priori contrast associated with the Exclusion factor.) Because no survivors occurred in one of the treatments (OERC-Flexible; See Table 2), a priori contrasts were not orthogonal; therefore, an adjusted type I error rate was used ($\alpha' = 0.0127$). (n ranged from 1 to 5; therefore, Type III sums of squares were used in the analysis – see Shaw and Mitchell-Olds, 1993).

Source	*df*	*SS*	*MS*	*F*	*Pr > F*
Exclusion	4	0.0674	0.0169	1.05	0.3985
Fully Netted vs. Controls	1	0.0476	0.0476	2.97	0.0957
Unsupported vs. Supported Netting	1	0.0025	0.0025	0.15	0.6986
Unsupported (with vs. without metal rods)	1	0.0058	0.0058	0.36	0.5540
Collar vs. Roof Control	1	0.0617	0.0617	3.85	0.0594
Netting (Rigid vs. Flexible)	1	0.2522	0.2522	1.57	0.2200
Exclusion × Netting	3	0.0220	0.0073	0.46	0.7140
Error	29	0.4653			
Total	37	0.5910			

Table 5
Mean relative growth index and final SL of hatchery-reared *Mya arenaria* (±95% CI) from experimental units associated with Field Experiment I at Duck Brook Flat, in Holmes Bay, Cutler, Maine (15 July to 29 October 2011). n = number of experimental units containing live clams. (Mean initial SL ±95% CI = 15.8 ± 0.5 mm; N = 30.) See Table 1 for a description of each level of the Exclusion factor, and Fig. 1 for a photo of each.

Netting	Exclusion	n	Relative Growth	Final SL
Flexible	PENU	5	0.420 (0.152)	22.97 (2.24)
	PENS	5	0.416 (0.112)	23.12 (3.84)
	PENR	5	0.345 (0.122)	22.36 (1.64)
	OEMC	3	0.429 (0.410)	24.33 (2.50)
	OERC	0	-	-
Rigid	PENU	5	0.358 (0.120)	20.41 (3.29)
	PENS	5	0.367 (0.156)	22.19 (2.04)
	PENR	5	0.366 (0.244)	22.39 (2.94)
	OEMC	4	0.306 (0.144)	22.49 (4.58)
	OERC	1	0.102 (0.000)	19.85 (0.00)

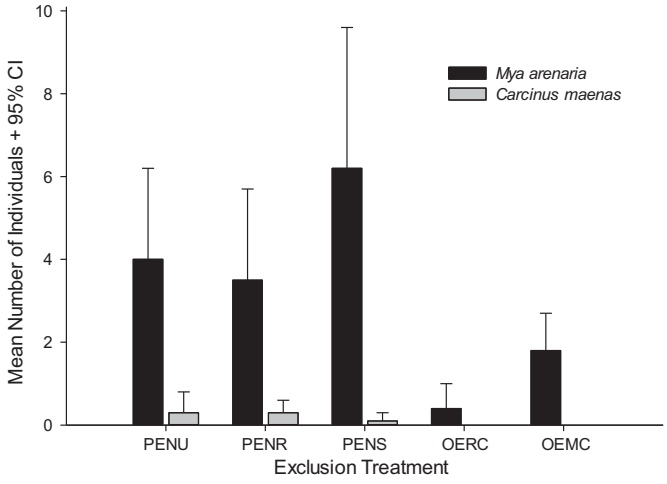

Fig. 4. Mean number of wild recruits of *Mya arenaria* (SL ≤ 15 mm) and *Carcinus maenas* in experimental units from Field Experiment I conducted at DBF (15 July to 29 October 2011). (See Table 1 for a description of each level of the Exclusion treatment.) (n = 5).

units at the beginning of the study when ambient sediments were used to fill units, and then became entrapped inside. With time, and successful molting or growth, these predators could have attained sizes large enough to consume clams in an experimental unit; 3) Small predators could have crawled or recruited through the mesh aperture into the experimental unit sometime during the field trial, then grown to a size where they became entrapped and, with continued growth, consumed the clams at some larger size; 4) The flexibility of some types of plastic netting, combined with the mass of larger crabs, depressed the netting to the sediment surface of the experimental unit permitting the crustaceans an opportunity to insert the tips of their chelae through the net aperture and encounter the siphons or posterior ventral shell margin of the clams, pulling them to the sediment surface then crushing them through the netting, or using a mandibular chipping technique as described by Morton and Harper (2008).

4.1. Green crab behavior in the field and laboratory

Although direct observation of mortality events did not take place in the field, several lines of evidence suggest that individuals of *Carcinus maenas* were primarily responsible for the loss of juveniles of *Mya arenaria*. For example, at the end of Field Experiment I & II, 10% and 20% of the experimental units contained green crabs, respectively. No other large decapods (e.g., *Cancer irroratus* – Beal, 2006a; *Homarus americanus*) were found in or around experimental units at the end of the field trials in October 2011. In addition, green crab populations along the Maine coast have increased dramatically since 2009 (ME DMR, 2013; Whitlow and Grabowski, 2012; B. Beal, pers. obs.).

Table 7
Analysis of variance on the arcsine-transformed mean percent survival of hatchery-reared juveniles of *Mya arenaria* from Field Experiment II at Duck Brook Flat, in Holmes Bay, Cutler, Maine (3 July to 28 October 2011). P-values in boldface represent statistically significant hypothesis tests (α = 0.05). (n = 5).

Source	*df*	*SS*	*MS*	*F*	*Pr* > *F*
Intraspecific Density	4	1904.15	476.04	1.29	0.2913
Predator Exclusion	1	20644.74	20644.74	55.82	<**0.0001**
Density × Exclusion	4	1649.84	412.46	1.12	0.3628
Error	40	14793.73	369.85		
Total	49	38992.46			

Crushed clams collected from experimental units in both the field and laboratory were typical of crustacean damage (Beal, 2006a) rather than from accidental damage. Valves of *Mya* that have been crushed by *C. maenas*, or other crustacean predators such as *C. irroratus*, have a distinctive chipping or crushing pattern (Boulding, 1984). Sometimes one valve is left nearly intact, while a fraction of the other remains attached by the hinge ligament (this was the predominant damage type observed in Laboratory Experiment II). In other instances, both valves are crushed nearly completely leaving only the umbo region that is held together by the hinge ligament (this damage type occurred most often in the open controls [OEMC, OERC] in Field Experiment I and in Laboratory Experiment III). Previous field studies with juveniles of *M. arenaria* have shown that live crabs can enter experimental units (either through the apertures as early post-larvae or from accidental inclusion when ambient sediments are placed into units at the beginning of the trial) resulting in mass clam mortality (Beal et al., 2001). This scenario occurred in a single experimental unit from Field Experiment II when a live *C. maenas* (CW = 30 mm) was discovered along with no live clams, three disarticulated, crushed valves, and 22 of 24 individuals missing.

Although few clams were found dead with crushed/chipped valves or missing in the fully protected units from either field experiment (Tables 2 & 8), the three laboratory trials provide some resolution about how *C. maenas* may prey on juveniles of *Mya* in field enclosures with predator deterrent netting present. In Laboratory Experiment I, a single clam was discovered dead with chipped valves in the area where the siphons protrude near the posterior ventral margin. That observation, and the fact that the flexible netting on that experimental unit was closer to the sediment surface than it had been on previous days, suggests that by sitting or resting on top of the netting, crabs may depress the flexible netting enough to allow them to prey on clams underneath. Although the actual predation event was not observed, we infer that crab behavior is similar to that outlined in hypothesis #4 (described above).

In Laboratory Experiment II, crabs ate voraciously, consuming all clams in two of the four LC units, leaving all valves chipped or crushed (DC); however, in another unit with a crab, all clams were found dead with undamaged valves (DU; Table 11). The occurrence of dead clams with undamaged valves in field settings has been associated with

Table 6
Analysis of variance on the untransformed mean number of wild recruits (SL ≤ 15 mm) of *Mya arenaria* and mean number of green crabs, *Carcinus maenas*, from Field Experiment I at Duck Brook Flat, in Holmes Bay, Cutler, Maine (15 July to 29 October 2011). P-values in boldface represent statistically significant hypothesis tests (α = 0.05). (n = 5).

		Wild *Mya arenaria* recruits				*Carcinus maenas*			
Source	*df*	*SS*	*MS*	*F*	*Pr* > *F*	*SS*	*MS*	*F*	*Pr* > *F*
Exclusion	4	195.28	48.8200	5.38	**0.0015**	0.92	0.23	1.53	0.2110
Fully Netted vs. Controls	1	144.21	144.21	15.88	**0.0003**	0.65	0.65	4.36	**0.0433**
Unsupported vs. Supported Netting	1	40.02	40.02	4.41	**0.0421**	0.27	0.27	1.78	0.1900
Unsupported (with vs. without metal rods)	1	1.25	1.25	0.14	0.7126	0.00	0.00	0.00	1.0000
Collar vs. Roof Control	1	9.80	9.80	1.08	0.3051	0.00	0.00	0.00	1.0000
Netting (Rigid vs. Flexible)	1	0.18	0.18	0.02	0.8887	0.50	0.50	3.33	0.0754
Exclusion × Netting	4	30.72	7.68	0.85	0.5046	0.60	0.15	1.00	0.4189
Error	40	363.20	9.08			6.00	0.15		
Total	49	589.38				8.02			

Table 8
Fate of juveniles of *Mya arenaria* in Field Experiment II at Duck Brook Flat, Cutler, Maine (3 July to 28 October 2011). Exclusion ("−" refers to open enclosures with a 1 cm strip of flexible netting [4.2 mm aperture] surrounding the periphery of each experimental unit [Area = 0.0182 m^2] to deter clam migration; "+" refers to experimental units fully covered with a piece of flexible netting [4.2 mm aperture] to deter predation). Means (±95% CI) are given for each fate category – %A, %DU, %DC, and %M, and these abbreviations are described in Table 2. (n = 5).

Density (m^{-2})	Exclusion	% A	% DU	% DC	% M
165	−	40.0 (53.9)	20.0 (37.0)	33.3 (50.7)	6.7 (18.5)
330	−	13.3 (17.3)	43.3 (27.8)	23.3 (18.5)	20.0 (26.9)
660	−	8.3 (14.6)	33.3 (30.2)	16.7 (20.7)	41.7 (36.6)
1,320	−	11.7 (19.1)	12.5 (10.3)	20.0 (12.4)	55.8 (25.5)
2,640	−	0.8 (1.4)	11.7 (16.0)	6.7 (8.5)	80.8 (11.3)
165	+	60.0 (34.6)	33.3 (29.3)	0 (0)	6.7 (18.5)
330	+	76.7 (18.5)	20.0 (17.3)	3.3 (9.3)	0 (0)
660	+	68.3 (34.6)	28.3(34.0)	1.7 (4.6)	1.7 (4.6)
1,320	+	70.0 (25.7)	20.8 (22.8)	0.8 (2.3)	8.3 (15.1)
2,640	+	57.5 (19.4)	22.5 (15.8)	2.9 (5.7)	17.1 (26.5)

Table 10
Analysis of variance on the untransformed mean number of microalgal cells × 10^4 mL^{-1} from Laboratory Experiment II (3–9 January 2012). All treatments included microalgae initially established at 5 × 10^4 cells mL^{-1} U^{-1}: 1) control (C): no soft-shell clam juveniles, no crab; 2) crushed crab (CC): clams present, crab effluent; 3) live crab (LC): clams and crab present; and, 4) clam control (CL): clams present, no crab. Cell counts were taken on days 3 (6 January) and 6 (9 January). Single degree-of-freedom orthogonal contrasts are presented for the treatment factor. P-values in boldface represent statistically significant hypothesis tests (α = 0.05). (n = 4).

Source	*df*	*SS*	*MS*	*F*	*Pr > F*
Date	1	132.0313	132.0313	3.84	0.0616
Treatment	3	1389.0938	463.0313	13.48	<**0.0001**
LC & CC vs. C & CL	1	1313.2813	1313.2813	38.24	<**0.0001**
LC vs. CC	1	30.2500	30.2500	0.88	0.3573
C vs. CL	1	45.5625	45.5625	1.33	0.2607
Date X Treatment	3	124.0938	41.3646	1.20	0.3294
Error	24	824.2500	34.3438		
Total	31	2469.4688			

non-predatory activity such as disease, mishandling, starvation (Beal, 2006b; Micheli, 1997; Peterson, 1982), or from predators other than decapods that typically leave no shell damage (Bourque et al., 2002; Cadée, 1994; Cha, 1994). If the probability of mishandling juveniles in the experiment was 0.5 (clams either were mishandled or they were not), then the probability that all six in one unit would have been mishandled would be 0.0313 (2-tailed Binomial test). Similarly, disease seems unlikely, or more clams in the controls would have met the same fate. For example, 3 of 48 clams in the control (CC, CL) units died during the six-day trial. If clams had died due to disease, then a reasonable estimate of the proportion of diseased clams at the beginning of the trial would be 3/48, or 0.0625. The probability that all six clams in the LC unit died due to disease would be <0.0001 (2-tailed Binomial test). In addition, clams likely did not starve because there was ample food for them to eat (Fig. 5). Since the six DU clams were all within a unit containing a crab, all clams were scattered on the surface and not discolored (as opposed to being burrowed in the sediment with both valves discolored black, as was the fate of the three DU clams from the control units), and no tissue was present in the valves, it would appear that the crab somehow consumed the clams without leaving any discernible shell damage. Because green crabs are known to crush juvenile, infaunal bivalves (Ejdung et al., 2009; Ropes, 1968; this study), this result is surprising. Perhaps some individuals of *C. maenas* are able to consume juveniles of *Mya* as individuals of the brachyuran crab, *Hemigrapsus sanguineus* (25–40 mm CW), is known to consume larger *M. arenaria* (ca. 45 mm SL) (Brousseau et al., 2001). In that study, predation did not involve shell crushing or chipping. Instead, crabs used their chela to pull tissue from the gaping siphonal (posterior) end of the clam, leaving the prey shells intact. *C. maenas* has been observed preying on blue mussels, *Mytilus edulis*, without inflicting shell damage, a method termed "boring" by Elner (1978). Other decapod crustaceans have been noted for their ability to prey on bivalves without inflicting shell damage (Lau, 1987). For most species of crabs, a critical bivalve prey size exists below which predation occurs (Seed and Hughes, 1995); however, in species with a mantle gape, as in *Mya arenaria*, crabs may be able to cut the mantle tissue between the valves, sever at least one adductor muscle and then begin to consume the tissues without damaging the shells. If *C. maenas* is able to prey on some juveniles of *Mya* without leaving evidence of its attack in the shells, then predation rates by this exotic predator on soft-shell clams may be higher than reported elsewhere (e.g., Beal, 2006a,b; Hunt and Mullineaux, 2002; Whitlow, 2010; Whitlow et al., 2003).

Results from Laboratory Experiment III provide the most conclusive evidence for the ability of green crabs to prey on juveniles of *M. arenaria* that are purportedly protected with flexible, plastic netting (aperture = 6.4 mm) in our experimental units. Individual clams consumed by *C. maenas* occurred only in the treatment where crabs could access clams through the netting (High Sand; Table 12). In that laboratory trial, slack, flexible netting protected all clams, but because sediment depth inside two of the three experimental units per aquarium was apparently lower than the depth to which the netting could stretch, clams in those units were safe compared to animals housed in units filled with sediments. Beal and Kraus (2002) placed groups of similar size experimental units containing cultured juveniles of *M. arenaria* in ambient sediments at DBF, and surrounded them with wooden boxes pushed into the sediments so that various types

Table 9
Percent frequency of the daily position of the green crab relative to experimental units (15 cm plastic pots) from 21 August to 11 September 2011 (22 days; Laboratory Experiment I). Each unit per aquarium was randomly assigned to one of three treatments: 1) tight-fitting, flexible netting (i.e., without slack); 2) flexible netting with slack; and, 3) rigid netting. Treatments 2 & 3 were similar to Exclusion treatment PENU in Field Experiment I (see Table 1). Percent of time crabs were burrowed also is presented.

Aquarium	Carapace Width (mm)	Percent Frequency of Crabs Among Treatments				% Time Burrowed
		Trt 1	Trt 2	Trt 3	Between pots	
A	60.2	22.7	9.1	54.5	13.7	0
B	64.9	22.7	9.1	54.5	13.7	45.5
C	61.9	72.7	13.7	4.5	9.1	77.3

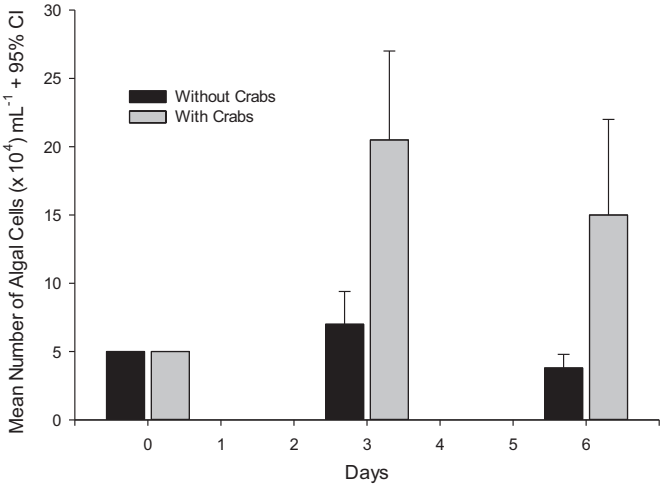

Fig. 5. Mean number of microalgal cells × 10^4 mL^{-1} (*Chaetoceros gracilis*) from Laboratory Experiment II (3–9 January 2012). Experimental units were stocked initially with 5.0 X 10^4 cells. Data from crushed crab (CC) and live crab (LC) treatments ("With Crabs"), and data from control (C) and clam control (CL) treatments ("Without Crabs") were pooled due to the lack of a significant difference between means (see Table 10) (n = 4).

Table 11
Mean number alive, dead uncrushed, dead crushed of juveniles of soft-shell clams and final salinity from Laboratory Experiment II (3–9 January 2012). C = control; CC = crushed crab; LC = live crab; CL = clam control.

		Carcinus maenas		*Mya arenaria*			
Block	Treatment	CW (mm)	Sex	Number Alive	Number DU	Number DC	Final Salinity (ppt)
1	C	-	-	-	-	-	38
	CC	31.6	M	6	0	0	39
	LC	37.9	M	0	0	6	39
	CL	-	-	6	0	0	39
2	C	-	-	-	-	-	36
	CC	38.6	F	6	0	0	38
	LC	32.9	M	6*	0	0	36
	CL	-	-	6	0	0	36
3	C	-	-	-	-	-	34
	CC	27.7	F	6	0	0	40
	LC	33.8	M	0	6**	0	40
	CL	-	-	5	1	0	35
4	C	-	-	-	-	-	35
	CC	25.6	M	5	1	0	35
	LC	26.5	M	0	0	6***	39
	CL	-	-	5	1	0	39

* The crab was found burrowed, and was missing its right chelae.
** These shells were articulated, had no signs of chipping, and had no tissue. They were found on top of the sediment with their shells open less than 24 hours after the experiment was initiated.
*** Of these six dead chipped clams, the valves of two were articulated, and two other clams were missing half of one valve, but with the umbo intact.

of netting could be stretched tightly around the box to protect the clams. A gap of several cm existed between the netting and the units, and only a small percentage (<6 %) of clams were recovered dead with crushed valves after 174 days in the field (April to October, 1991). Similar results were observed by Spencer et al. (1992) who examined the effectiveness of different types of protective netting on survival of *Tapes philippinarum* in boxes on intertidal beaches near Conwy in Wales, UK.

4.2. Soft-shell clam responses to predators in the field and laboratory

Results from both field experiments underscore the relative importance of predation, especially by decapods, in controlling populations of juvenile soft-shell clams as others have shown (e.g., Beal, 2006b; Beal et al., 2001; Floyd and Williams, 2004; Glude, 1955; Jensen and Jensen, 1985; Smith et al., 1955; Welch, 1968; Whitlow et al., 2003). Combining field data from percent dead crushed/chipped and missing categories (Tables 2 & 8) from open enclosures demonstrated that losses between 56.7–86.7% occurred in Field Experiment I, and up to 87.5% in Field Experiment II. Missing clams are presumed dead (Beal, 2006a), and together with animals identified as DC, these data demonstrate that the relative intensity of predation on small *Mya* at DBF is much higher than observed in the early 1990's over a similar time period and in open enclosures (see Table 6 in Beal and Kraus, 2002). Because green crab population numbers respond directly to seawater temperatures (Welch, 1968), predation rates on soft-shell clams may have increased recently due to increases in crab numbers in response to gradual warming of seawater in eastern Maine (Mills et al., 2013).

Number of 0-year class individuals of *Mya* (wild recruits) responded significantly to predator deterrent netting in Field Experiment I (Table 6), but not in Field Experiment II. Examining all experimental units stocked initially with six clams in Experiment II (N = 10), wild recruit density was approximately 4.5x greater in the protected (1.8 ± 1.8 ind. unit^{-1}, n = 5) vs. control (0.4 ± 0.7 ind. unit^{-1}, n = 5) treatment (P = 0.083). Enhancement of 0-year class individuals of *Mya* in predator exclusion treatments in eastern Maine has been shown to be variable in previous studies. For example, Beal and Kraus (2002) observed significantly higher (3x) wild recruit densities in protected vs. control treatments at one intertidal site in eastern Maine but not at DBF. Beal et al. (2001) found no enhancement of wild recruits due to predator exclusion along a tidal gradient at an intertidal site approximately 20 km west of DBF; however, predator deterrence led to a 3-fold enhancement in numbers of *Mya* recruits at three of four intertidal sites in far eastern Maine during 2003 (Beal, 2006b). In predator exclusion studies conducted elsewhere, *Mya* responded with increased recruitment in cages that protected small individuals from horseshoe crab attack in Delaware Bay, New Jersey (Bottom, 1984), from green crabs and fish in Barnstable Harbor, Massachusetts (Hunt and Mullineaux, 2002), and from *C. maenas* and *Crangon crangon* in the European Wadden Sea, especially after mild winters (Strasser, 2002).

Laboratory Experiment II examined the feeding behavior of clams with crabs present, with crab cues present, and in controls without crabs or cues. Mean algal cell densities increased by 4x in treatments with crabs or cues compared to the controls; however, there was no significant difference between controls with and without clams (P = 0.26; Table 10). The power of this test was quite low (<0.50). Nonetheless, at the end of the trial, mean algal cell density mL^{-1} in the control without clams was $4.88 \pm 3.07 \times 10^4$ (n = 4), which was not significantly different than the initial stocking density of 5.0×10^4 cells mL^{-1} (one-sample t-test [2-tailed], p = 0.905). Conversely, final mean density in the control with clams was $3.25 \pm 0.79 \times 10^4$ mL^{-1} (n = 4), and this was significantly different from the initial stocking density (P = 0.006). This suggests that clams in the units with only the microalgae consumed the cultured phytoplankton over the 6-day trial, but clams in the live crab treatment (LC) that survived (one of four units; Table 11) and clams in the units with the crab cues (CC) did not feed at all, or consumed less phytoplankton than conspecifics in the CL treatment. Without the benefit of a crushed crab control (no clams plus crab due), another explanation is that excess nutrients (e.g., nitrogen and its metabolites) associated with the LC and CC treatments enhanced algal growth, and live clams in those treatments actually fed on algae at rates similar to clams in the CL treatment. In other lab trials, soft-shell clams increased their burial depth when activity simulating the red rock crab, *Cancer productus*, occurred (Zaklan and Ydenberg, 1997). In the field, Whitlow et al. (2003) were able to induce a similar behavior when adults of *Mya* burrowed ca. 12% deeper in plots that included green crabs vs. plots where crabs were excluded. Similar results were observed by Whitlow (2010) in the laboratory; however, no differences in shell growth were detected between treatments with and without crabs or their cues. Beal et al. (2001) found that shell growth of juveniles

Table 12
Number of live and dead crushed juveniles of *Mya arenaria* ($\bar{x}_{SL} = 14.8 \pm 0.4$ mm, n = 30) in Laboratory Experiment III (27 June–17 July 2013). All individuals of *C. maenas* were male. Each experimental unit in an aquarium was completely covered with a piece of plastic, flexible netting (aperture = 6.4 mm). ANOVA detected a significant treatment effect (P = 0.0067) on the number of dead crushed clams per unit. Treatments: Low = experimental unit (15 cm diameter × 15 cm deep plastic horticultural pot) filled half-way with sand; Medium = unit filled with sand to within 1 cm of the rim; High = unit filled completely with sand to the rim.

Aquarium	*Crab CW (mm)*	Treatment	Number of crushed clams
I	70.6	Low	0
		Medium	0
		High	0
II	70.3	Low	0
		Medium	0
		High	1
III	71.7	Low	0
		Medium	0
		High	2
IV	70.5	Low	0
		Medium	0
		High	1
V	69.9	Low	0
		Medium	0
		High	1

of *Mya* was 6.6% lower during April to December in experimental field units in eastern Maine intertidal flat when predators (moon snails, *Lunatia heros*, or green crabs) were unintentionally included in exclosure units than when they were not. The data presented here, in combination with other independent trials and observations, suggest that green crabs can induce both direct and indirect responses in soft-shell clam behavior that may be size- or age-dependent. Hard clams, *Mercenaria mercenaria*, behaved similarly in the lab (i.e., reduced feeding in the presence of predators – knobbed whelks, *Busycon carica*; blue crabs, *Callinectes sapidus*) (Smee and Weissburg, 2006). In field enclosures, long-term exposure to predators (whelks) resulted in depressed hard clam growth rates compared to controls (Nakaoka, 2000). Together, these studies and the laboratory trial presented here, suggest that these bivalves can alter their behavior by reducing their chemical presence in an attempt to decrease their susceptibility to mobile predators that use sensory cues from prey while foraging.

5. Conclusion

The invasive green crab, *Carcinus maenas*, is an ecosystem engineer that alters the function and organization of marine habitats (intertidal rocky shores – see Trussell et al., 2003; *Spartina* marshes – see McDonald et al., 2006; Ropes, 1968; eelgrass beds – see Davis et al., 1998; Garbary and Miller, 2006; intertidal mudflats – see Grosholz et al., 2000; and subtidal locations – see Elner, 1981; Donahue et al., 2009), reduces biodiversity and alters food webs (Garbary et al., 2014; Pejchar and Mooney, 2009). Green crabs are omnivores (Baeta et al., 2006; Griffen, 2014), and their diet reflects their size and habitat (Elner and Hughes, 1978; Grosholz and Ruiz, 1996; Mascaro and Seed, 2001; Rangeley and Thomas, 1987; Sungail et al., 2013), but they prefer bivalve molluscs (Elner, 1981; Grosholz and Ruiz, 1995; Ropes, 1968). In eastern Maine, USA, green crabs are a major threat to both wild and cultured populations of *Mya arenaria* (Beal and Kraus, 2002; Beal et al., 2001). Green crabs attack juveniles of *M. arenaria* in the field and laboratory using a variety of tactics that can result in typical shell damage ranging from ventral margin chipping to complete breakage of both valves leaving only the umbos intact. In addition, some crabs apparently can consume soft-shell clams without inflicting any damage to the shell. Whether this occurs by severing the mantle tissue that gapes between valves of this infaunal bivalve or by other means is unclear, but suggests that previous investigations assessing the relationship between green crabs and their soft-shell clam prey (Beal, 2006a; Floyd and Williams, 2004; Flynn and Smee, 2010) may have underestimated the effect this predator plays in the early life-history of this bivalve.

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