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SPATIAL VARIABILITY IN RECRUITMENT OF AN INFAUNAL BIVALVE: EXPERIMENTAL EFFECTS OF PREDATOR EXCLUSION ON THE SOFTSHELL CLAM (*MYA ARENARIA* L.) ALONG THREE TIDAL ESTUARIES IN SOUTHERN MAINE, USA

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ABSTRACT The infaunal, suspension-feeding softshell clam (*Mya arenaria* L.) is a conspicuous member of the intertidal macrofauna in numerous northern temperate and boreal soft-bottom communities. Recruitment variability can affect the magnitude and scope of various ecosystem services provided by *M. arenaria*, including its role as a source of food and energy for organisms at higher trophic levels. Manipulative field experiments were conducted in the intertidal zone in 2014 and 2015 at three tidal estuaries in southern Maine, to investigate the importance of post-settlement processes in determining the strength of the annual 0-y class cohort across predator-exclusion treatments within and between tidal heights. Four short-term (4–5 mo), small-scale studies over both years in the Webhannet River (Wells, ME) and Fore River (Portland, ME), the two southernmost estuaries, demonstrated that clam recruits were up to 118× more abundant when predators were deterred versus controls. In a 7-mo study conducted in the Harraseeket River (HR; Freeport, ME) during 2014, recruits of *Mya* attained densities 899× greater in large-scale plots designed to exclude large (>6 mm) predators than in ambient, adjacent sediments where predators were undeterred. A novel, epibenthic settlement trap (0.15 m^2), initially containing no sediments and designed to deter both infaunal and epibenthic predators larger than 1.9 mm, was used to examine spatial variability in clam recruitment over a 6-mo period in 2015 in the HR. Traps showed a 60-fold difference in mean number of clam recruits between sides of the river only 600 m apart. Collectively, results suggest that post-settlement mortality rates of 0-y class individuals of *Mya* exceed 99% at these locations, severely limiting ecosystem services they would otherwise provide, and that these early losses are primarily responsible for explaining distribution and abundance patterns of ≥1-y class individuals.

KEY WORDS: *Mya arenaria*, post-settlement mortality, spatial variability, predator exclusion, field experiment

INTRODUCTION

Suspension-feeding bivalves play an important role in marine ecosystems serving both biotic and abiotic functions. For example, oysters, clams, mussels, cockles, and scallops couple benthic-pelagic processes affecting the exchange of dissolved nutrients and gases across the sediment–water interface (Doering et al. 1987, Michaud et al. 2006, Komorita et al. 2010) and exerting top-down grazer control on phytoplankton (Thrush et al. 2006, Donadi et al. 2013). These consumers also alter water quality via clearance rates and biodeposition of feces and pseudofeces that can affect production of marine plants (Peterson & Heck 1999, Castorani et al. 2015), macroalgae (Kotta et al. 2009), and the distribution and abundance of members of the benthic community (Commito & Boncavage 1989, Kenaya 2014). As secondary producers, bivalves play an essential role as a source of food and energy for other invertebrates (Richards et al. 1999, Polyakov et al. 2007), wading birds and ducks (Degraer et al. 2007), fish (Kelso 1979, Irlandi, 1994), and large mammals (Carlton & Hodder 2003).

These and other ecosystem services derived from suspension-feeding bivalves can be ephemeral in space or time depending on the intensity and success of the settlement (Larsen & Guillemette 2000, LeBlanc & Miron 2006) and post-settlement processes that affect standing stocks of juveniles and adults (Dekker & Beukema 2007, Dethier et al. 2012). For example, benthic primary production and sandflat nutrient fluxes vary as a positive function of density of a shallow-burrowing suspension-feeding bivalve because of the cumulative effects of excretion (Sandwell et al. 2009), and individual clearance rates of the same species decrease with increasing densities (Jones et al. 2011). Whereas the importance of abiotic factors on post-settlement success of bivalve populations has been noted (de Montadouin & Bachelet 1996, Green et al. 2009), early post-settlement mortality due to predation (Hunt & Mullineaux 2002, Strasser 2002, Andresen & van der Meer 2010) may be one of the most important factors affecting the structure of bivalve populations (but see Gerasimova et al. 2015, Seitz et al. 2016). In addition, investigations have shown strong correlations between abiotic (e.g., temperature) and biotic (e.g., predation) conditions that help to explain some of the temporal variation in bivalve recruitment in temperate estuaries and coastal wetlands (Strasser et al. 2003, Beukema & Dekker 2014).

The softshell clam, *Mya arenaria* L., is an infaunal, suspension-feeding bivalve that occurs intertidally and in shallow subtidal soft sediments in the Northwest Atlantic from Labrador, Canada, to Cape Hatteras, NC (Abbott 1974). Over this range, reproduction and subsequent larval settlement is seasonal, occurring approximately twice annually south of Gloucester, MA, and once annually throughout the northern part of its range (Ropes & Stickney 1965, Brousseau 1978). Larvae settle at shell lengths (SL) between 200 and 250 microns (Stickney 1964), and growth of intertidal juveniles varies with tidal height as animals attain larger sizes more quickly near the low versus upper intertidal (Beal et al. 2001). Settlement

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intensity and subsequent recruitment varies both with biotic and abiotic factors (Emerson & Grant 1991, Dunn et al. 1999), and losses from the beginning to the end of the settlement season can be >99.9%. High mortality rates can result in annual cohorts that contribute little to population size or ecosystem services, even when rates of settlement are relatively high (Hunt et al. 2003).

In the state of Maine, softshell clams are ubiquitous members of the soft-bottom intertidal and shallow subtidal community (Newell & Hidu 1986), where they form the basis of a coast-wide commercial fishery for human consumption (Hanna 1998) that depends annually on successful natural recruitment to repopulate harvested beds. Whereas no long-term fishery-independent data set following the densities of adults or juveniles exists for this species, during the last four decades, commercial landings of softshell clams across the state have decreased by nearly 75% (Beal et al. 2016). Whereas a number of factors may be responsible for declines of standing stocks of adult clams (e.g., disease, overfishing, pollution, ocean acidification, and recruitment limitation), previous work in the northern Gulf of Maine and southern Bay of Fundy—far eastern Maine—has shown that predation by the invasive green crab, *Carcinus maenas* (L.), and the naticid gastropod, *Euspira heros* (Say), is likely responsible for regulating populations of 0-y class individuals (Commito 1982, Beal & Kraus 2002, Beal 2006a, 2006b, Tan & Beal 2015). Within the past decade, commercial clam landings in southern Maine (southern Gulf of Maine) have declined by approximately 70% (Maine Department of Marine Resources 2017); however, few field investigations have been conducted in this region to examine mechanisms to help explain the decline (Whitlow 2010, Green et al. 2013). Whereas post-settlement processes have been shown to play a significant role in structuring many benthic invertebrate populations (Ólafsson et al. 1994), it is unclear for intertidal populations of *Mya arenaria* in southern Maine whether low settlement rates due to pre-settlement factors that limit larval supply or poor survival conditions at the time of settlement (Miller & Waldbusser 2016) is more or less important than processes acting after settlement.

To disentangle which factors may be important drivers regulating clam numbers in the southern Gulf of Maine, recruitment dynamics of *Mya arenaria* was investigated in three tidal estuaries in southern Maine during 2014 and 2015. Several types of exclusion netting were used to deter both epibenthic and infaunal predation on post-settled, 0-y class individuals of *Mya* in six short-term, manipulative field experiments (April/May to October/November) over two field seasons. The logic for determining relative importance of pre- versus post-settlement processes was straightforward: predator-exclusion treatments and controls should have similar densities of juvenile clams if pre-settlement or at-settlement processes were important in regulating populations of juveniles and adult clams. Conversely, post-settlement processes, specifically predation or disturbance due to predation, should be important if exclusion treatments contain higher numbers of juveniles compared with controls (*sensu* Munroe & McKinley 2007).

The specific hypotheses tested were informed by results from previous studies of *Mya arenaria* recruitment and ecology of juvenile clams in eastern Maine (Beal et al. 2001, Beal & Kraus 2002, Beal 2006a) and the southern Bay of Fundy (Beal 2006b), as well as recent observations in southern Maine concerning population densities of green crabs that are known softshell clam predators (Glude 1955, Ropes 1968, Welch 1968, Whitlow 2010). Populations of *Carcinus maenas* have increased rapidly in Maine over the past 5 y, especially along the southern Maine coast (McClenachan et al. 2015) coinciding with recent mild winters in this region (Fernandez et al. 2015), and a period of warming seawater temperatures in the Gulf of Maine (Pershing et al. 2015). Previous field trials examined the effects of predator size on *Mya* recruitment by manipulating the aperture size of exclusion netting (Beal & Kraus 2002). Recruitment was enhanced nearly 3× when predators were deterred by netting with aperture sizes ranging from 4.2 to 12.7 mm versus open controls, and nearly 2× as many 0-y class individuals occurred in experimental units (EU) that deterred predators with netting ≥6.4 mm versus the smallest aperture exclusion netting. In addition, epibenthic predators such as crabs and fish were more important than infaunal predators (*sensu* Ambrose 1984) in controlling densities of *Mya* recruits. Beal and Kraus (2002) also examined the effectiveness of different types of netting [flexible versus extruded (= rigid)] used to deter predators on clam recruitment, and found that for equal aperture sizes, netting type did not have a significant effect on recruit density. Predators may also affect mean SL and size–frequency distribution of post-settled clams. For example, Beal et al. (2001) discovered that clam juveniles in EU that deterred predators were 5% larger than clams in open enclosures. In a caging experiment, Hunt and Mullineaux (2002) found that excluding predators resulted in larger mean SL and concomitant dramatic differences in size–frequency distribution of recruits of *Mya* compared with clams outside the cages. Similarly, predation has been shown to alter size distributions of 0-y class individuals of other bivalve species (Richards et al. 1999). Hence, the first four hypotheses are as follows: (1) predation—post-settlement predation, rather than pre-settlement factors (*sensu* Bowen & Hunt 2009), is largely responsible for limiting densities of 0-y class individuals of *Mya*, and mean SL of clam recruits will be smaller in control versus protected treatments. In addition, size–frequency distributions of recruits in EU that do not deter or restrict predator access should have a smaller range, with fewer and smaller classes, compared with the frequency distribution of recruits in exclusion treatments; (2) predator size—recruitment density and mean SL are both positive functions of predator size; (3) deterrent type—predators are equally deterred from preying on post-settled clam recruits regardless of the type of exclusion netting; and, (4) infaunal predation—epifaunal predators will play a disproportionately greater role as mortality agents of clam recruits compared with predatory infauna. In addition, Beal (2006b) found 3–8× more recruits of *Mya* in upper versus lower intertidal EU in each of two embayments, increasing intraspecific density of clam juveniles had no effect on recruitment (i.e., no gregarious recruitment behavior was observed), and that significant spatial variation in density of recruits occurred at scales that spanned four orders of magnitude from 5 to 10,000 m. Whereas mean SL of recruits was not measured by Beal (2006b) or by Beal et al. (2001), cultured juveniles of *Mya* (ca. 12 mm SL) grew more rapidly (25%–35%) at lower versus upper tidal heights over 6–8 mo. Thus, hypotheses 5–7 are: (5) tidal height—recruitment will vary positively with tidal height, increasing density with increasing tidal height, mean SL of recruits of *Mya* will be greater at lower versus upper tidal heights, and size–frequency distributions of recruits also will reflect differences due to tidal height; (6)

spatial variation—within a tidal height, recruitment variation will vary significantly across scales ranging from 20 to 300 m; and (7) intraspecific density—increasing intraspecific densities of juvenile (1 y) clams will not affect densities of 0-y class recruits (see LeBlanc & Miron 2006, Bowen & Hunt 2009).

MATERIALS AND METHODS

Study Sites

Field trials were conducted in three tidal estuaries in southern Maine (Fig. 1) to assess the importance of pre- versus post-recruitment processes of *Mya arenaria*. Sites were chosen based on previous studies on softshell clam ecology conducted in or near the vicinity of each (Whitlow 2010, Whitlow & Grabowski 2012), and all three were in areas where commercial clam beds had once occurred but where no harvesting had occurred within the past 5 y because of the lack of commercial densities of adult clams >50-mm SL (D.-M. Nault personal communication, Maine Department of Marine Resources, B. Beal personal observation). Experiments were conducted in the upper (1.0 m tide level) and lower intertidal (0.0 m tide level) in the Webhannet River (WR, Wells, ME; 43°19′38.5752″N, 70°33′55.4868″W; Fig. 1A; see MacKenzie & Dionne (2008)) for a description of the prominent vegetation in this salt-marsh dominated system) and Fore River (FR, Portland, ME; 43°39′7.6392″N, 70°17′57.3072″W; Fig. 1B; see Morgan et al. (2015)) in 2014, and only in the upper intertidal at both locations in 2015. Experiments were conducted in the lower intertidal in the Harraseeket River (HR, Freeport, ME; 49°

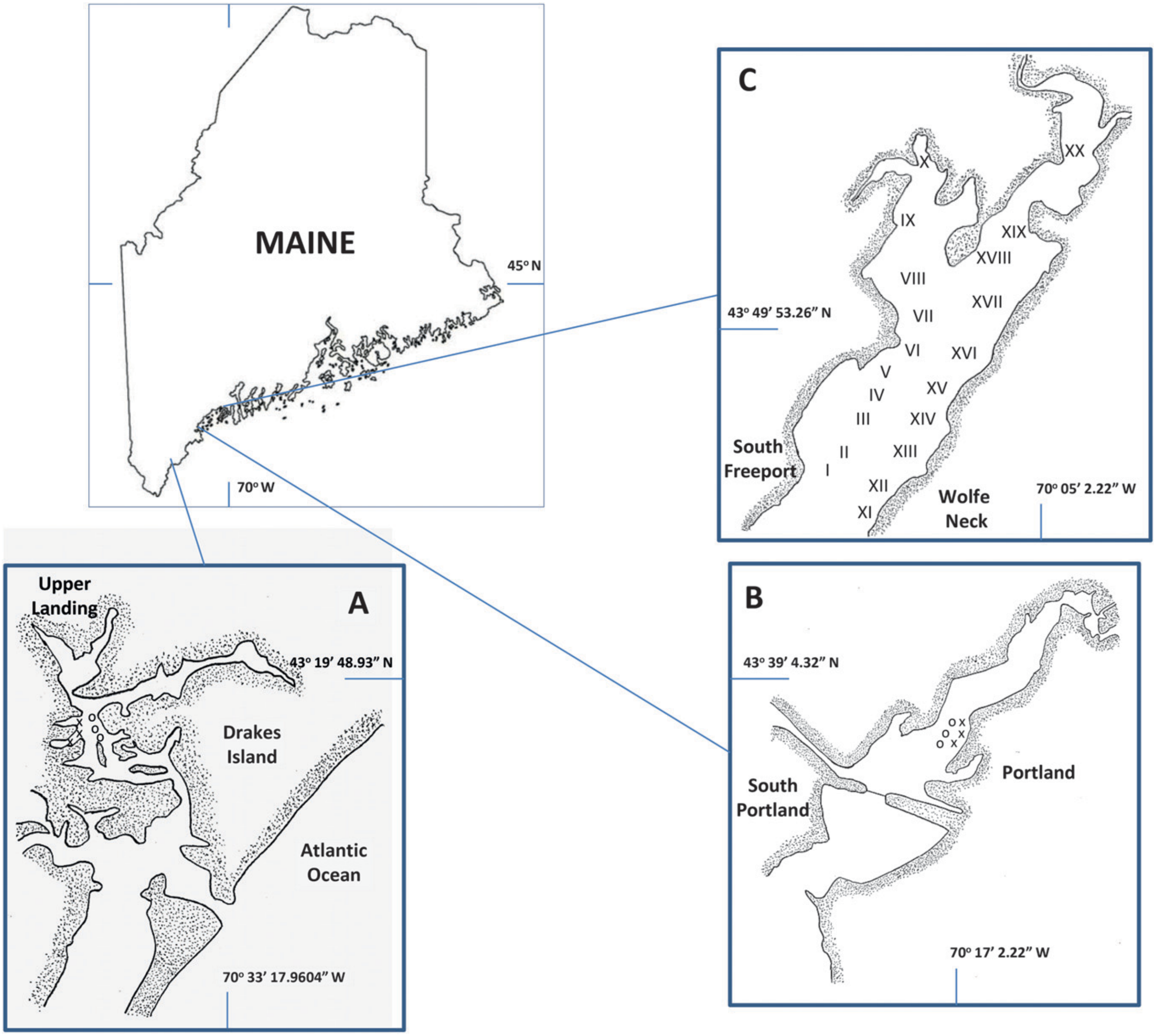

Figure 1. Study sites. (A) WR, Wells, ME. x's denote upper intertidal blocks (2014 and 2015) and o's denote lower intertidal blocks (2014). (B) FR, Portland, ME. x's and o's denote upper and lower intertidal blocks as in (A). (C) HR, Freeport, ME. Roman numerals denote lower intertidal sites where epibenthic recruitment boxes (see Materials and methods) were deployed in 2015 (west side of river = sites I–X; east side of river = sites XI–XX). In 2014, study sites were located on the west side at site III (CC) and the east side at site XIII (AR).

49′26.2704″N, 70°6′9.0252″W; Fig. 1C) during both 2014 and 2015. Sediments in the upper intertidal at these sites were composed of a muddy sand (*sensu* Folk 1980), whereas those in the lower intertidal were more unconsolidated softer mud. Tides (semidiurnal) varied in amplitude between 2 and 3 m at each site depending on lunar cycle. Seawater temperatures ranged from 5°C to 23°C during April/May to October/November when field trials were conducted, with peaks occurring in mid-August. Measurements were taken by the Wells Estuarine Research Reserve near the mouth of the inlet at WR (https://www.wellsreserve.org/research/environmental-monitoring), approximately 22 km southeast of the FR site (Station 44,007, National Data Buoy Center; http://www.ndbc.noaa.gov/station_page.php?station=44007), and at site XIII in HR (Fig. 1) using a HOBO temperature data logger (B. Beal unpublished).

Experiment I. (Hypotheses #1–6): Effects of Tidal Height, Predation, and Spatial Variation (2014—Webhannet and FR)

Interactive effects of tidal height, predation, and spatial variation on softshell clam recruits were examined using comparative field experiments deployed in the upper and lower intertidal at WR (May 12 to October 10) and FR (May 13 to October 11). A series of plastic horticultural pots (EU = 15 cm diameter × 15 cm deep with eight 1-cm diameter drainage holes in the bottom—as described in Beal et al. 2001) was arrayed at each site and tidal height in three 2 × 5 matrices (= blocks; 1 m spacing between rows and columns) 20 m apart. Pots were dug into the soft sediments with hands or trowels to a depth of 14.5 cm, and then filled with ambient sediments. As part of a complementary study to examine the fate of juveniles of *Mya arenaria* along a tidal gradient, 12 cultured individuals of *M. arenaria* [mean SL ± 95% confidence interval (CI) = 12.95 ± 0.20 mm, $n = 451$] were added to each EU and gently pushed 4–6 mm below the sediment surface using fingers. Two replicates of each of five predator-exclusion treatments (a control and four netting treatments; Table 1) were randomly assigned positions within each block at each site and tidal height. Fate and growth of the cultured animals is reported elsewhere (Munroe et al. 2015). Here, abundance and size of wild, 0-y class recruits, animals ≤25-mm SL that typically lack a distinct disturbance line near the umbo indicating a slowing of growth over the winter (*sensu* Beal & Kraus 2002), are reported. No wild softshell clams were found in samples of ambient sediments ($A = 0.0182$ m^2 to 15 cm deep; $n = 5$) at either tidal height at WR and at lower tidal height at FR. A single clam (4.2 mm SL) was found in samples from the upper intertidal height at FR. In addition, no individuals of *Carcinus maenas* or the infaunal nemertean predator, *Cerebratulus lacteus* (Leidy), occurred in any samples. After 151 days, EU were removed from the sediments, and the contents of each washed through a 1-mm sieve. It was possible to distinguish cultured clams from wild, 0-y class recruits because of a distinct disturbance line that forms in the valves of cultured clams on placing them in sediments whereas 0-y class individuals typically have no similar distinctive disturbance lines (Beal et al. 1999). Recruits from each EU were enumerated and the SL of each measured to the nearest 0.01 mm with digital calipers. When the number of recruits per EU exceeded 50, a random sample of 20 individuals was taken, and the individuals measured (as described previously). The random sample was obtained by placing all recruits into a bulk pile using fingers, then removing 50 of these animals from the pile and placing them on a piece of paper with numbers from 1 to 50. Each clam was placed on a number, and then a random number table used to choose the 20 animals to be measured. All live green crabs from each EU were enumerated, and the carapace width (CW) of each was measured to the nearest 0.01 mm using digital calipers. The presence of *C. lacteus* also was noted.

A mixed-model nested analysis of variance (ANOVA) was performed on the square root–transformed mean number of 0-y class recruits per EU (to homogenize variances) for each site.

The following linear model was used to analyze clam recruitment data for each site separately:

TABLE 1.

Description of the five predator-exclusion treatments used in the field Exps. I and II (2014 and 2015) in the Webhannet and FR ("unit" refers to a plastic horticultural pot 15 cm in diameter × 15 cm deep with eight 1 cm diameter drainage holes in the bottom).

Predator-exclusion treatment	Description
(1) Control	Open unit with narrow (1 cm wide × 50 cm long) piece of flexible netting* (aperture = 4.2 mm; 17.64 mm^2) around periphery to keep clams from moving outside of unit. Predators are not excluded from this treatment (Tan & Beal 2015).
(2) Flexible netting	Unit covered with a 30 cm × 30 cm piece of flexible netting (4.2 mm aperture) to deter predators larger than 5.9 mm.
(3) Flexible netting and extruded netting	Top of unit covered with a 16 cm × 16 cm piece of extruded netting† (aperture = 6.4 mm; 40.96 mm^2) that was held in place by a piece of 4.2 mm flexible netting (as in Treatment #2) that covered the unit. Double-layered protection to deter predators >5.9 mm.
(4) PetScreen	Unit covered with a piece of PS‡ (rectangular aperture measuring 1.7 mm × 0.9 mm; 1.53 mm^2) to deter predators >1.9 mm.
(5) PetScreentop and bottom	Unit covered with a piece of PS. In addition, a circular piece (15 cm diameter) of the same material was inserted into the bottom of the unit before the addition of sediments. This combination prohibited large nemerteans (e.g., *Cerebratulus lacteus*) and other predatory infauna from entering the unit from the bottom (via drainage holes) or the top.

* Polypropylene (OV7100; Industrial Netting; http://www.industrialnetting.com/ov7100.html).

† Polyethylene (XV1170); Industrial Netting; http://www.industrialnetting.com/xv1170.html).

‡ PetScreen (http://www.phifer.com/consumerdiy/product/62/petscreen-pet-resistant-screen).

$$Y_{ijkl} = \mu + A_i + B_j + AB_{ij} + C(A)_{k(i)} + BC(A)_{jk(i)} + e_{l(ijk)},$$

where

Y_{ijkl} = dependent variable (square root–transformed mean number of 0-y class individuals per unit);

μ = theoretical mean;

A_i = tidal height ($a = 2$; upper versus lower; factor is fixed);

B_j = predator exclusion ($b = 5$; see Table 1; factor is fixed);

C_k = block ($c = 3$; factor is random); and

e_l = experimental error ($n = 2$; difference from unit-to-unit within a given combination of tidal height, predator exclusion, and block).

Four preplanned, single degree-of-freedom orthogonal contrasts (*sensu* Neter et al. 1990) were used to better understand differences in mean number and sizes of *Mya* recruits among predator-exclusion treatments (Table 1). (1) Effects of predators examines the importance of post-settlement predation in controlling recruit density and size (mean SL) by comparing the mean of both variables in open control (unnetted) EU versus the mean of all protected EU; tests for the effects of predators regulating density and size of 0-y class individuals of *Mya arenaria* (Hypothesis #1). (2) Predator size examines the effects of predator size on density of recruits by comparing the mean density of recruits and mean recruit SL from the two treatments in which the smaller aperture netting (PetScreen, PS) is used to exclude both small and large predators (≥1.92 mm—distance of the diagonal) versus the mean of the two treatments in which the larger aperture netting is use to exclude larger predators (≥5.94 mm—distance along the diagonal); tests whether densities of clam recruits and their mean SL varies with predator size (Hypothesis #2). (3) Predator access to prey examines predator effectiveness/behavior across distinct types of predator-exclusion netting by comparing mean recruit density in EU with versus without rigid mesh netting (Hypothesis #3). (4) Infaunal predation examines the relative importance of excluding the nemertean, *Cerebratulus lacteus*, and other potential infaunal predators from both the top and bottom of EU versus excluding infauna from entering only through the top of EU (Hypothesis #4). Hypothesis #5 (tidal height) was tested by examining whether differences exist in mean density and mean SL of recruits from each tidal height, and Hypothesis #6 (spatial variation) was tested by examining the added variation in mean recruit density pooled across treatments from block-to-block within a tidal height.

To avoid excessive type I errors, an adjusted alpha [$\alpha' = 1 - (1 - \alpha)^{1/n}$, where $\alpha = 0.05$ and n = number of contrasts] was used as a decision rule (Winer et al. 1991). Underwood (1997) was consulted to determine appropriate mean square estimates for each source of variation.

Site-specific 2 × 4 *G*-tests of independence were used to examine whether tidal height (upper versus lower) affected size–frequency distributions (size classes = I: ≤10 mm; II: 10.1–15.0 mm; III: 15.1–20.0 mm; and IV: >20 mm SL) of softshell clam recruits pooled across exclusion treatments.

Experiment II. (Hypotheses #1–4 and 6): Effects of Spatial Variability and Predation (2015—Upper Intertidal—Webhannet and FR)

Effects of spatial variation and predation on abundance of 0-y class softshell clams were examined together using a comparative field experiment deployed in the upper intertidal at WR and FR (Fig. 1A, B) on May 25 and 26, respectively. Two locations (about 100 m apart) were chosen at each site, and within each location three 2 × 5 blocks ca. 20 m apart (two replicates of each of the same five treatments from Exp. I—Table 1) established with 1-m spacing between rows and columns. At both sites, location 1 was closest to the upper part of the estuary. Sediments at WR were more unconsolidated and muddy at location 1 versus 2. No obvious difference in sediment compaction was observed between the two locations at FR. Plastic horticultural pots (as described previously) were used to examine the effect of excluding predators on the fate and growth of cultured clams and abundance of 0-y class recruits of *Mya arenaria*. After 144 days, EU from each block at each site (WR—October 16; FR—October 17) were removed from the sediments, and the contents of each washed through a 1-mm sieve. In addition, the number and size of *Carcinus maenas* and number of the nemertean, *Cerebratulus lacteus*, from EU were recorded.

A mixed-model nested ANOVA was performed on the square root–transformed mean number of 0-y class recruits per unit (to homogenize variances) for each site separately. The following linear model was used to analyze clam recruitment data for each site separately:

$$Y_{ijkl} = \mu + A_i + B(A)_{j(i)} + C_k + AC_{ik} + CB(A)_{jk(i)} + e_{l(ijk)},$$

where

Y_{ijkl} = dependent variable (square root-transformed mean number and size of wild recruits per unit);

μ = theoretical mean;

A_i = location ($a = 2$; upper versus lower part of estuary separated by 100 m; factor is fixed);

B_j = block ($b = 3$; factor is random);

C_k = predator exclusion ($c = 5$; see Table 1; factor is fixed); and

e_l = experimental error (unit-to-unit variation within a given predator treatment, block, and location; $n = 2$).

Preplanned, single degree-of-freedom orthogonal contrasts were used to focus on differences in mean number and size of recruits among predator-exclusion treatments (as described previously). A series of orthogonal 2 × 4 *G*-tests of independence was used to explore differences in size–frequency distributions of clam recruits across predator-exclusion treatments. Shell lengths were divided into four size classes (<5.0, 5.1–10.0, 10.1–15.0, and >15.1 mm).

Experiment III. (Hypotheses #6–7): Effects of Intraspecific Density and Spatial Variability (2014—HR)

Interactive effects of intraspecific softshell clam density and spatial variability on number of 0-y class softshell clams were examined at a site in the lower intertidal on the east and west sides of HR approximately 600 m apart [Fig. 1C; sites III (Collins Cove [CC]) and XIII (Across-the-River, AR)] from April 19–21 to November 8–10 (201–205 days). Cultured softshell clam juveniles ($\bar{x}_{\mathrm{SL}} = 12.95 \pm 0.20$ mm and $n = 451$) were broadcast onto the mudflat surface into 22.3 m^2 plots (3.7 m × 6.03 m) and immediately covered with a piece (28.6 m^2) of flexible predator-exclusion netting (4.2 mm aperture; Table 1). Nets were secured by forcing 15–20 cm of the perimeter of each into the sediments by walking on the net edge (*sensu* Beal et al. 2016). A series of Styrofoam floats (10 cm diameter × 7.6 cm wide) arrayed in a quincunx pattern were affixed to the underside of each net to prevent netting from interfering with clam feeding during tidal inundation. To examine whether effects of intraspecific clam density on clam recruitment vary spatially, predator nets at each site were grouped in ten blocks of four (5 m separating each net that was arrayed perpendicular to the low-water mark; 10 m separating each block) with two netted plots per block stocked with cultured clams at a density of 160 individuals m^{-2} and two at 320 ind. m^{-2}. To determine whether an additional level of predator exclusion would enhance clam recruitment, a cylindrical green crab trap (14-guage vinyl-coated wire—1.27 cm apertures; 0.9 m long × 0.46 m diameter with 10 cm diameter entrances at both ends) was deployed adjacent (within 3 m) to five randomly selected blocks at each site. Traps, baited with fresh, crushed adults of *Mya arenaria*, were fished twice weekly and remained next to a specific block of nets from May 5 to October 1 when crab density became <5 individuals per trap. All crabs caught in each trap were removed from the site and disposed of in a nearby landfill.

Initial ambient densities of wild softshell clams at CC and AR were 30.4 ± 17.2 and 4.5 ± 6.5 ind. m^{-2}, respectively ($n = 25$ benthic cores, surface area = 0.0182 m^2, 15 cm deep and SL ranged from 6.3 to 13.9 mm). No *Carcinus maenas* or *Cerebratulus lacteus* were recovered in any cores. In November, two benthic cores were taken within each protected plot at both sites ($n = 80$ per site), and two similar cores were taken adjacent to nets (ca. 4 m away) in each block at each site ($n = 20$ per site). Samples were processed and clams enumerated and measured from each (as described previously). Only the fate of wild, 0-y class recruits is presented here. When the number of 0-y class clams exceeded 50 per sample (e.g., 55 of 80 samples from AR, or 68.8%), a random sample of 20 individuals (as described previously) was taken and measured to estimate mean SL and size–frequency distribution.

A mixed-model nested ANOVA was performed on the square root–transformed number of softshell clam recruits per core (to homogenize variances) for each site separately. The following linear model was used:

$$Y_{ijkl} = \mu + A_i + B_j + AB_{ij} + C_k + AC_{ik} + BC_{jk} + ABC_{ijk} + D(ABC)_{l(ijk)} + e_{m(ijkl)},$$

where

Y_{ijkl} = dependent variable (number of 0-y class individuals per core);

μ = theoretical mean;

A_i = block ($a = 5$; I, II, III, IV, and V; factor is random);

B_j = crab Trap ($b = 2$; present versus absent; factor is fixed);

C_k = intraspecific clam density ($c = 2$; 180 versus 360 ind. m^{-2}; factor is fixed);

D_l = plot ($d = 2$; I versus II; factor is random); and

e_m = experimental error ($n = 2$; difference from core-to-core within a given combination of plot, stocking density, crab trap, and block).

Experiment IV. (Hypotheses #2 and 6): Effects of Spatial Variability and Predator Size (2015—HR)

Interactive effects of spatial variation and predator size on abundance of 0-y class softshell clam recruits were investigated on both the east and west side of HR at 10 lower intertidal locations (ca. 200–300 m apart; Fig. 1C). Six empty wooden recruitment boxes (EU = large settlement traps; 57 cm × 26.5 cm × 7.6 cm = 0.15 m^2) were placed on the surface of the flat in a 2 × 3 array with 1 m spacing between rows and columns at each location from April 9 to 12 (N = 120). Units were covered on both the top and bottom with predator-exclusion netting, and anchored to the sediment surface by passing a notched wooden lath (50 cm) through a nylon twine loop at each short end. Both laths were then pounded into the sediments to a depth of 45–47 cm with hammers. Four of the six boxes per location were covered on the top and bottom with PS designed to exclude all but the smallest predators because the aperture size would allow organisms ≤1.9 mm to enter into a box. Because this technique was novel, it was unclear whether sediment was necessary for postlarvae to settle in the recruitment box. Therefore, once established on the mudflat surface, approximately 1 L of play sand (http://www.homedepot.com/p/Quikrete-50-lb-Play-Sand-111351/100318476) was added to two of the PS-covered boxes to serve as a preliminary substrate for settling fauna. Sand was poured carefully through the screening so that it would be distributed as evenly as possible on the inside bottom of the boxes. The two remaining boxes excluded predators >9.1 mm and were covered on the top and bottom with an extruded, polyethylene mesh (6.4 mm aperture; Table 1). It was hypothesized that epibenthic recruitment boxes would act as sediment and settlement traps for marine invertebrates with planktonic larvae, including softshell clams. Also, it was surmised that small, mobile predatory fauna (e.g., crabs and worms) that may have settled the previous fall and overwintered at sizes smaller than the aperture size of the mesh could enter the EU at the beginning of the trial, especially those with the larger aperture netting.

Ambient clams were sampled from benthic cores (as previously given) at seven and five of the 10 sites on the west ($\bar{x}$ = 56.7 ± 30.2 ind. m^{-2}, $n = 50$) and east ($\bar{x}$ = 12.3 ± 10.6 ind. m^{-2}, $n = 50$) side of HR in April 2015, respectively, and ranged in SL from 2.0 to 8.1 mm. No individuals of *Carcinus maenas* or *Cerebratulus lacteus* were observed in any cores. Recruitment boxes were removed from each site from November 3 to 6 (205–211 days in the field), and the contents of each washed through a 1-mm sieve. All organisms and other material were placed into uniquely tagged plastic bags and frozen until processing (2–3 mo later). On thawing, softshell clams from each box were enumerated directly (for densities <500 individuals per box; N = 112) and indirectly (i.e., estimated; N = 8) for densities exceeding 500 animals. For indirect estimates, total mass of material from a box was measured to the nearest 0.1 g using an electronic balance. Next, three random subsamples (4–8 g) were taken by creating a bulk pile, scooping a subsample with a spoon, and then enumerating the number of softshell clams in each. Mean number of clams per gram was calculated, and then that value multiplied by the total mass. For example, material from a recruitment box from site XV (east side) had a mass of 690.3 g. The three subsamples of 7.2, 5.5, and 4.7 g contained 65, 46, and 41 softshell clams, respectively (subsample mean = 8.7 ind. g^{-1}). Assuming a linear relationship between subsample mass and clam number, the estimated number of clams from that box would be 6009 (8.70 ind. g^{-1} × 690.3 g). The SL (to the nearest 0.01 mm using digital calipers) of as many as 20 individuals of *Mya arenaria* per box was recorded. Where number of clams in a box was >20 individuals, a representative subsample of clams was taken from a bulk pile and individuals measured as described previously.

Because a wide range of clam SL was observed (see Results), if the smallest and/or largest *Mya* recruit was not among the 20 individuals from a particular EU, the SL of those individuals also was recorded.

Presence/absence of *Cerebratulus lacteus* as well as the number, CW, and mass (to the nearest 0.1 g) of *Carcinus maenas* was noted from each recruitment box. Ambient density of 0-y class individuals of *Mya* was estimated at each location on each side of HR during November by taking five benthic cores 2 m away from the 2 × 3 matrix ($n = 100$). Core samples were processed as described previously.

Neither were the data (number of clams per EU) normal nor the variances homogenous; therefore, a Box-Cox transformation (PROC TRANSREG; SAS/STAT 14.2) was used, resulting in a lambda (λ) value of 0 [equivalent to a $\log(Y + 1)$ transformation]. A mixed-model ANOVA was performed on the transformed data. The following linear model was used:

$$Y_{ijkl} = \mu + A_i + B(A)_{j(i)} + C_k + AC_{ik} + CB(A)_{jk(i)} + e_{l(ijk)},$$

where

Y_{ijkl} = dependent variable (number of wild recruits per box);

μ = theoretical mean;

A_i = side of river ($a = 2$; east versus west; factor is fixed);

B_j = location nested within each side of the river ($b = 10$; locations 200–300 m apart; factor is fixed);

C_k = predator exclusion ($c = 3$; factor is fixed); and

e_1 = experimental error (box-to-box variation within a given predator-exclusion treatment, location, and side of river; $n = 2$).

The rationale for including location within each side of the river as a fixed effect was 2-fold because it was purposefully decided to: (1) place recruitment boxes on each side of the river from near the head to the mouth; and (2) space the locations on each side of the river approximately equidistant (Fig. 1C). Two *a priori* contrasts were used to examine more closely the effects of predator-exclusion treatments and inclusion of an initial settlement substrate on softshell clam recruitment (adjusted type I error rate $\alpha' = 0.0253$): (1) predator size examines whether the size of the predator influences recruitment density by comparing mean number of recruits in boxes covered on the top and bottom with PS versus extruded netting (Hypothesis #2); and sediment tests whether differences in recruitment are due to the presence of an initial settlement substrate by comparing the mean number of recruits in PS boxes with or without 1 L of sand on the bottom.

A 2 × 8 *G*-test of independence was used to examine spatial variation in the number of recruits per EU between the sides of HR. The eight levels of recruit number per EU were: 0–10; 11–20; 21–30; 31–50; 51–100; 101–250; 251–1,000; and >1,000. To examine whether size–frequencies of the smallest and largest softshell clam recruits per EU varied between predator-exclusion treatments (PS versus extruded netting) pooled across the sides of the river and location within each side, 2 × 5 *G*-tests of independence were used (five levels of the smallest recruit size were: ≤2, 2.1–3.0, 3.1–4.0, 4.1–5.0, and >5 mm; five levels of the largest recruit size were: ≤10, 10.1–15.0, 15.1–20.0, 20.1–25.0, and >25 mm). In addition, 2 × 5 *G*-tests of independence were used to determine if the size–frequency distribution of green crabs varied from sides of HR or among predator-exclusion treatments (CW size classes were: 0–10, 10.1–15.0, 15.1–20.0, 20.1–25.0, and >25.1 mm).

All reported means are untransformed with their 95% CI. Statistical analyses were performed using SAS 9.4 TS Level 1M3.

RESULTS

Experiment I (Hypotheses #1–6): Effects of Tidal Height, Predation, and Spatial Variation (2014—Webhannet and FR)

Deterring predators enhanced mean recruit density by 23–95× more than that in control EU that did not restrict predators, and

TABLE 2.

Experiment I. Mixed-model nested ANOVA on the square root–transformed mean number of 0-y class individuals (recruits) of the softshell clam, *Mya arenaria*, per EU from the WR, Wells, ME (May 12 to October 10, 2014), and FR, Portland, ME (May 13 to October 11, 2014) (tidal height and treatment are fixed factors; block is a random factor). Preplanned contrasts appear indented and directly beneath the treatment and tidal height × treatment source of variation. Boldface *P* values indicate statistical significance. *n* = variable depending on the number of recovered EU (see Table 3). α′ = 0.0127 for all preplanned contrasts.

	WR			FR		
Source of variation	df	MS	Pr > *F*	df	MS	Pr > *F*
Tidal height	1	148.70	**0.0112**	1	236.97	**0.0006**
Treatment	4	61.33	**0.0028**	4	106.68	**0.0001**
Predation	1	110.44	**0.0034**	1	137.80	**0.0014**
Predator size	1	73.44	**0.0122**	1	238.32	**0.0001**
Deterrent type	1	6.41	0.4100	1	7.15	0.3921
Infaunal predation	1	6.06	0.4228	1	43.44	0.0455
Tidal height × treatment	4	36.74	**0.0204**	4	51.88	**0.0051**
Upper vs. low × predation	1	35.52	0.0656	1	48.24	0.0363
Upper vs. low × predator size	1	87.75	**0.0072**	1	122.45	**0.0022**
Upper vs. low × deterrent type	1	14.96	0.2159	1	26.51	0.1096
Upper vs. low × infaunal predation	1	8.74	0.3390	1	10.33	0.3060
Block (tidal height)	4	1.73	0.1821	4	2.50	0.8550
Treatment × block (tidal height)	14	2.06	0.0681	16	9.24	–
Experimental error	20	4.31	–	30	7.56	–
Total	47	16.77	–	59	21.29	–

approximately 10× more recruits occurred in lower versus upper EU; however, the effect of predator exclusion was disproportionate across tidal heights at both study sites (Table 2). Mean recruit density in the upper intertidal EU at WR was nearly 40× greater in EU that restricted predator access versus control EU, whereas in the low intertidal this difference was approximately 118×. Recruits at FR were 6× and 30× more abundant in predator-exclusion versus control treatments at the upper and lower intertidal, respectively. At both sites among exclusion treatments at the lower tidal height, mean number of recruits was 6–7× greater in units that excluded the smallest versus largest predators, but no similar differences were noted in the upper intertidal blocks (Fig. 2A, B; Table 3). Milky ribbon worms, *Cerebratulus lacteus*, were found only at WR, occurring in 4 EU with flexible netting (one in the upper and three in the lower intertidal). No significant effect because of infaunal predators on recruit density was observed at either WR or FR, and no significant spatial variation in recruit density was observed between blocks at each tidal height (Table 2).

Mean recruit SL did not vary significantly between tidal heights at either site ($P_{\text{Webhannet}} = 0.7223$, $\bar{x}_{\text{SL}} = 12.2 \pm 1.4$ mm, $n = 37$; $P_{\text{Fore}} = 0.0787$, $\bar{x}_{\text{SL}} = 9.8 \pm 1.2$ mm, and $n = 53$). At both sites, recruits in open EU, and those that excluded smaller predators (i.e., with PS), were approximately 20% smaller, on average, than those in EU protected with flexible netting, and recruits were 50%–66% larger in EU that deterred the larger versus smaller predators (Fig. 3). The size–frequency distribution of clam recruits varied significantly between tidal heights at both sites (Figs. 4 and 5). Proportionately more clams <10-mm SL occurred in lower (ca. 41%) versus upper (ca. 29%) intertidal EU at WR (2 × 4 *G*-test; $P = 0.0264$), whereas the opposite trend occurred at FR ($P < 0.0001$).

Individuals of *Carcinus maenas* occurred in 29 of 48 EU (60%) at WR (N = 62), and 17 of 60 EU (28%) at FR (N = 30). No other crab species was observed at either site. At WR, mean density per EU was 1.3 ± 0.4 ind. ($n = 48$), and there was no significant tidal-height ($P = 0.0617$) or predator treatment effect ($P = 0.6500$). Mean CW of crabs varied significantly by tidal height ($P = 0.013$; $\bar{x}_{\text{Upper}} = 9.4 \pm 2.4$ mm, $n = 22$; $\bar{x}_{\text{Lower}} = 7.8 \pm 3.5$ mm, and $n = 7$) but not by predator-exclusion treatment ($P = 0.706$). Mean density per EU at FR was 0.5 ± 0.4 ind. ($n = 60$), and mean CW was 10.7 ± 2.5 mm ($n = 30$). No significant difference in mean number or mean CW occurred for either predator-exclusion treatment or tidal height ($P > 0.40$). The distribution of green crab CW at both sites (Fig. 6) did not differ significantly across tidal heights (size classes were: 0–10; 10.1–20.0, and ≥20.1 mm; $G_{\text{WR}} = 2.8$, df = 2, $P = 0.2461$; $G_{\text{FR}} = 1.1$, $P = 0.5678$), and no significant correlation was observed between crab number per EU and number of *Mya* recruits per EU at either site ($r_{\text{WR}} = 0.242$, $P = 0.0972$; $r_{\text{FR}} = 0.334$, $P = 0.0713$).

Experiment II. (Hypotheses #1–4 and 6): Effects of Spatial Variability and Predation (2015—Upper Intertidal—Webhannet and FR)

Deterring predators resulted in a significant enhancement of *Mya* recruits compared with unprotected controls at WR (21×) and FR (3×) (Table 4; Fig. 7A, B), but the effects varied spatially. For example, at WR in location 2 (closer to the lower estuary), EU that deterred both infaunal and epifaunal predators had 7× more recruits than EU that did not deter infaunal predators (Table 5), but the same pattern did not exist in location 1 where recruit density was similar between these two treatments ($P = 0.0119$; Table 4; Fig. 7A). At FR, where approximately 80% more recruits were recovered from EU closer to the lower estuary ($P = 0.0383$; Table 4), the proportional difference in mean number of recruits between exclusion treatments and controls varied significantly between locations 1 and 2 (2× versus 4×, respectively; $P = 0.0286$; Table 4; Fig. 7B).

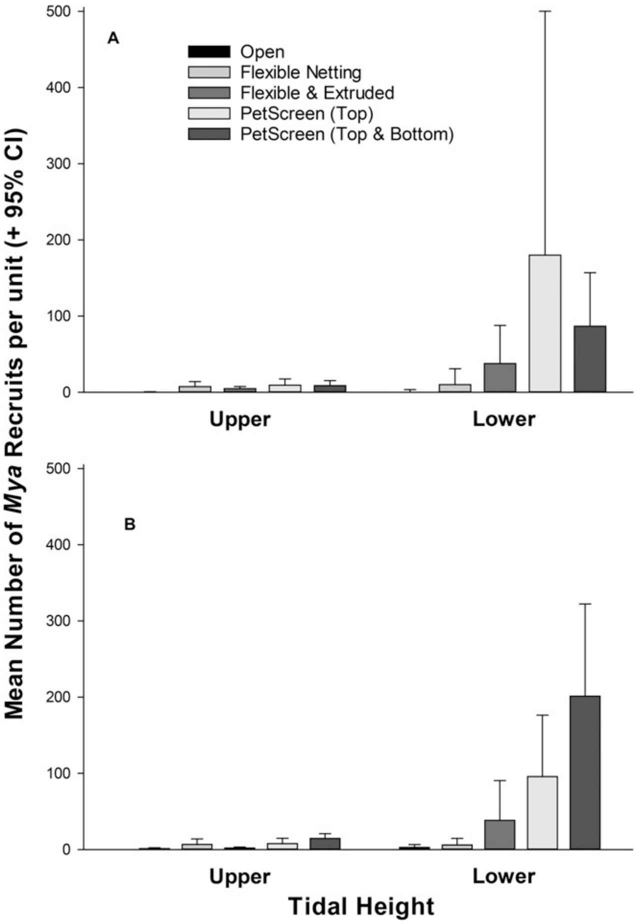

Figure 2. Experiment I. Mean (+95% CI) number of 0-y class recruits of *Mya arenaria* per EU (area = 0.0182 m^2) at the (A) WR, and (B) FR study site on October 10 and 11, 2014, respectively (see Table 2 for ANOVA results and Table 3 for number of replicate units per treatment).

Recruit SL ranged from 2.1 to 25.3 mm and 2.0 to 20.2 mm at WR and FR, respectively. Mean SL varied significantly across treatments at both study sites ($P \leq 0.0330$; Table 6). Clams in EU protected from predators were 65% and 30% larger, on average, than in open controls at WR and FR, respectively (Fig. 8A, B), but the result at WR was not statistically significant (Table 6). Mean SL at WR was 62% greater in treatments that excluded large versus small predators ($P = 0.0012$, Table 6). Analysis of size–frequencies (Table 7A) demonstrated that 52% versus 15% of recruits were ≤10 mm in treatments excluding smaller versus larger predators, respectively. In addition, significantly fewer recruits >15.1-mm SL were observed in EU that excluded infaunal predators compared with those that did not (Table 7A). At FR, where mean recruit density was 3× greater than at WR (17.6 ± 3.3 ind. per EU, $n = 60$), size–frequency analyses (Table 7B) demonstrated that proportionately more recruits ≤10-mm SL occurred in

TABLE 3.

Experiment I. Mean number (±95% CI) of 0-y class recruits of *Mya arenaria* at the WR (October 10, 2014) and FR (October 11, 2014) sites across tidal heights and predator-exclusion treatments (see Table1) after 151 days. Unit refers to a plastic horticultural pot (surface area = 0.0182 m^2) (12 of 60 units were not recovered from the WR site because of losses associated with storm events).

Site	Tidal height	Treatment	*n*	Per unit	Per m^2
Webhannet	Upper	Open (control)	5	0.2 (0.6)	10.9 (30.4)
		Flexible netting	6	7.5 (6.5)	411.2 (354.2)
		Flexible and extruded	6	4.8 (2.8)	264.9 (156.2)
		PetScreen top only	6	9.3 (8.3)	511.7 (456.9)
		PetScreen top and bottom	6	8.7 (6.7)	475.1 (366.9)
	Lower	Open (control)	3	0.7 (2.9)	36.5 (157.2)
		Flexible netting	4	10.0 (21.0)	548.2 (1,152.9)
		Flexible and extruded	4	37.8 (50.0)	2,069.9 (2,741.5)
		PetScreen top only	4	180.0 (320.2)	9,868.4 (17,556.9)
		PetScreen top and bottom	4	86.8 (70.3)	4,756.0 (3,848.6)
Fore	Upper	Open (control)	6	1.2 (1.2)	63.9 (67.3)
		Flexible netting	6	6.7 (7.2)	365.5 (396.4)
		Flexible and extruded	6	2.0 (1.3)	109.6 (72.8)
		PetScreen top only	6	7.7 (7.1)	420.3 (398.7)
		PetScreen top and bottom	6	14.5 (6.3)	794.9 (346.7)
	Lower	Open (control)	6	2.8 (3.8)	155.3 (210.4)
		Flexible netting	6	6.0 (8.6)	328.9 (468.8)
		Flexible and extruded	6	38.3 (52.2)	2,101.6 (2,860.9)
		PetScreen top only	6	95.7 (80.7)	5,244.9 (4,422.3)
		PetScreen top and bottom	6	201.2 (121.0)	11,028.9 (6,635.2)

open controls versus protected EU (Fig. 9), whereas a greater proportion of clams >10-mm SL occurred in EU excluding the larger versus small predators. Clam size–frequency distribution varied by deterrent type at FR (Table 7B) where clams were generally smaller in EU with flexible netting (70% were ≤10 mm SL) than in EU with both flexible and extruded netting (58% were ≤10 mm SL; Fig. 9).

The green crab was the only crustacean predator found in EU at both sites in October ($N_{\text{Webhannet}} = 50$, $N_{\text{Fore}} = 21$). Crabs at WR occurred in 21 of 30 (70%) EU at location 1 and 11 of 30 (37%) at location 2 ($\bar{x} = 0.83 \pm 0.27$ ind. per EU, $n = 60$), whereas at FR a single green crab was found in 10 (33%) and 11 (37%) of EU at locations 1 and 2, respectively ($\bar{x} = 0.35 \pm 0.16$ ind. per EU, $n = 60$). Approximately twice as many crabs were found in treatments designed to exclude predators ($\bar{x} = 0.9 \pm 0.30$ ind. per EU, $n = 48$) versus control EU ($\bar{x} = 0.5 \pm 0.61$ ind. per EU, $n = 12$) at WR where mean CW per EU was 11.7 ± 2.52 mm. Crabs occurred only in protected EU at FR ($\bar{x}_{\text{CW}} = 9.3 \pm 3.50$ ind. per EU). Size–frequency distribution of crabs varied significantly across treatments at WR ($P = 0.0011$, Fisher's exact test) as individuals >10-mm CW were more likely to occur in EU protected with the larger aperture netting. No similar pattern occurred at FR ($P = 0.7439$); however, the effect of predator exclusion on mean CW varied spatially ($P = 0.0120$; Fig. 10). No significant correlation was observed between crab number per EU and number of *Mya* recruits at either site ($r_{\text{WR}} = 0.271$, $P = 0.0718$; $r_{\text{FR}} = 0.102$, $P = 0.4932$).

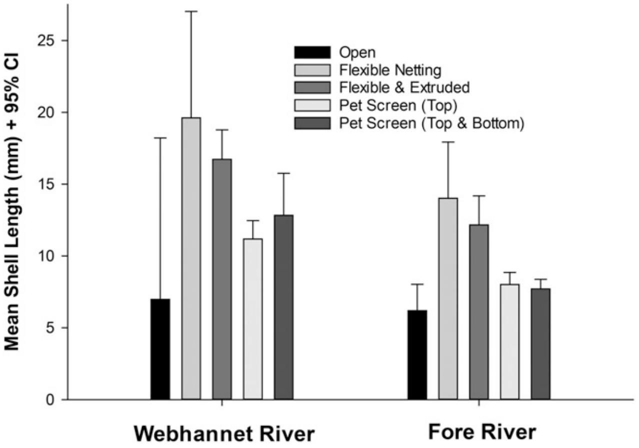

Figure 3. Experiment I. Mean (+95% CI) SL of recruits of *Mya arenaria* in EU recovered from the Webhannet and FR (pooled across tidal heights) on October 10 and 11, 2014, respectively. See Table 3 for the number of EU in each treatment (of 12) containing wild recruits.

Experiment III. (Hypotheses #6–7): Effects of Intraspecific Density and Spatial Variability (2014—HR)

Approximately two-thirds of netted plots at CC had been compromised by November (some were ripped, whereas the corners of many plots had come out of the sediments and were lying on the sediment surface allowing crabs, fish, and other mobile fauna unfettered access to the plots), and clam recruits were observed in only 17 of 80 core samples (ca. 21%) from the plots. Of samples containing *Mya arenaria* recruits, 15 came from intact netted plots (two-tailed binomial test given Ho: $P = 0.5$, $P = 0.0023$). Overall mean recruit density was 48.7 ± 12.7 ind. m^{-2} ($n = 80$), and no significant fixed effects (stocking density, trapping, and their interaction; $P > 0.18$) or added variation because of random factors (blocks, plots, and all component interaction terms; $P > 0.40$) were detected. Clams ranged from 1.7 to 38.3 mm, with 98% of individuals less than

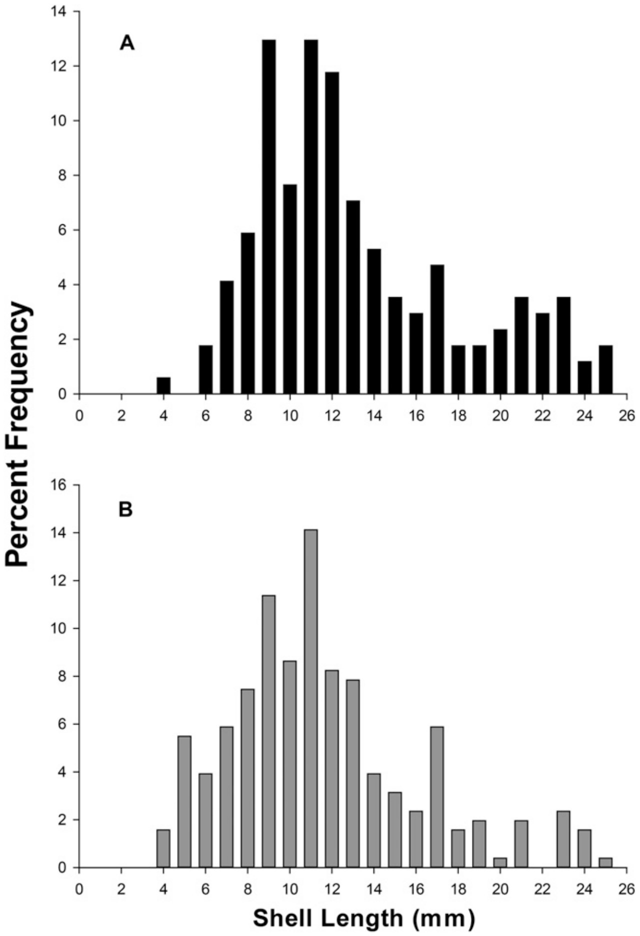

Figure 4. Experiment I. Size–frequency distribution of 0-y class individuals of *Mya arenaria* from the WR study site on October 10, 2014. (A) Upper intertidal [$n = 170$; recruits occurred in 22 of 29 (75.8%) units recovered]; (B) lower intertidal [$n = 255$; recruits occurred in 15 of 22 (68.2%) units recovered]. A 2 × 4 G-test (tidal height × size class; $P = 0.0264$) indicated that a disproportionate number of clams occurred in the smallest size class at the lower versus upper intertidal.

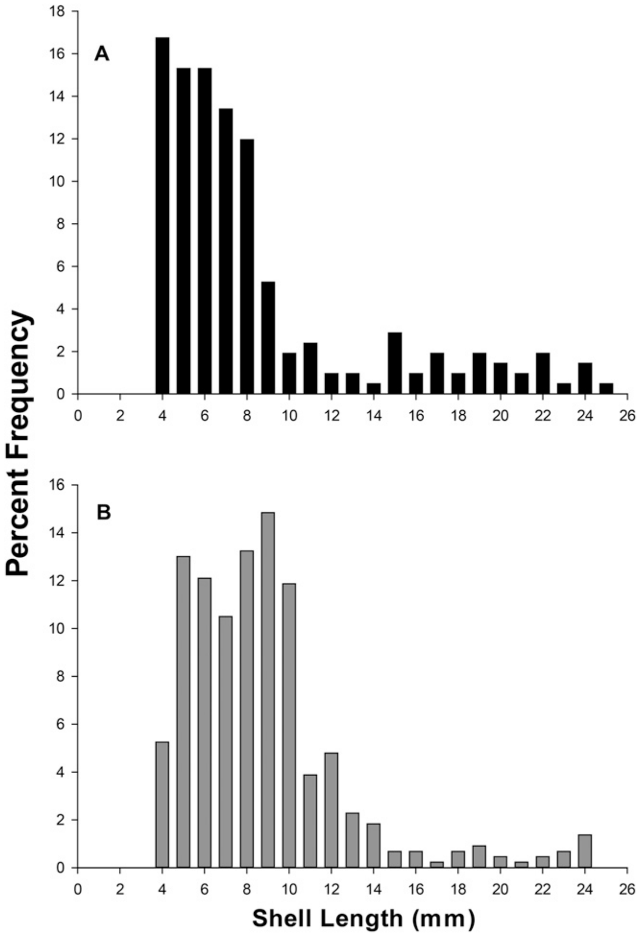

Figure 5. Experiment I. Size–frequency distribution of 0-y class individuals of *Mya arenaria* from the FR study site on October 11, 2014. (A) Upper intertidal [$n = 209$; recruits occurred in 26 of 30 (86.7%) units]; (B) lower intertidal ($n = 438$; recruits occurred in 27 of 30 (90.0%) units]. A 2 × 4 G-test (tidal height × size class; $P < 0.0001$) indicated that a larger proportion of clams occurred in the smallest size class at the upper versus lower intertidal.

12 mm and 94% less than 5 mm (Fig. 11A). Individuals of *Carcinus maenas* occurred in 25% of benthic cores from netted plots (density = 18.5 ± 7.9 ind. m^{-2}; mean CW = 7.1 ± 0.9 mm, $n = 27$; min. and max. CW = 3.4 mm and 14.6 mm, respectively). Mean density of *M. arenaria* in cores adjacent to netted plots was 10.9 ± 13.4 ind. m^{-2} ($n = 20$; four clams were observed from the cores—SL range = 4.1–13.9 mm), which was significantly lower than the mean of cores taken within the netted plots ($T_{\text{obs}} = 4.12$, df = 98, $P < 0.0001$).

Conversely, at AR in November all nets were intact and all edges buried as originally intended. Recruits of *Mya* were observed in 79 of 80 cores (98.8%) from the netted plots (4 of 80 cores contained >1,000 animals, and 48 cores contained >100 animals). Mean density was 14,830.0 ± 3,597.3 ind. m^{-2}, and only one source of variation (intraspecific density of 1-y cultured clams) was statistically significant ($P = 0.0123$; Table 8). Approximately 85% more 0-y class individuals were sampled from cores under nets with the higher intraspecific clam density ($\bar{x}_{160/\text{m}^2} = 10,432.5 \pm 3,954.2\,\text{ind. m}^{-2}$ versus $\bar{x}_{320/\text{m}^2} = 19,247.5 \pm 5,857.2\,\text{ind. m}^{-2}$; $n = 40$). Shell lengths of recruits ranged from 1.4 to 37.4 mm, with 69% of individuals less than 12 mm and 23% less than 5 mm (Fig. 11B). A total of 6 *Mya* recruits occurred in 4 of the 20 cores from samples taken away from the predator-exclusion plots, (16.5 ± 16.9 ind. m^{-2}; SL range = 3.2–7.9 mm). Ambient recruit density was significantly less than densities from plots that deterred epibenthic predators [$T_{\text{obs}} = 8.19$, df = 98 (Satterthwaite method), $P < 0.0001$]. Green crabs occurred in 6 of 80 cores (7.5%; density = 4.1 ± 3.2 ind. m^{-2}; CW ranged from 4.4 to 17.2 mm).

Experiment IV. (Hypotheses #2 and 6): Effects of Spatial Variability and Predator Size (2015—HR)

Juveniles of 13 bivalve, 2 polychaete, 5 gastropod, and 2 crustacean species were observed in the EU in November (Table 9). Only results for *Mya arenaria* and *Carcinus maenas* are presented here. Recruits of *M. arenaria* were observed in 112 of the 120 EU (only 2 EU from the east and 6 EU from the west side of HR, respectively, lacked recruits). Approximately 77% of EU on the west side of HR contained ≤50 recruits, whereas 57% of EU on the east side contained >50 recruits ($G = 30.8$,

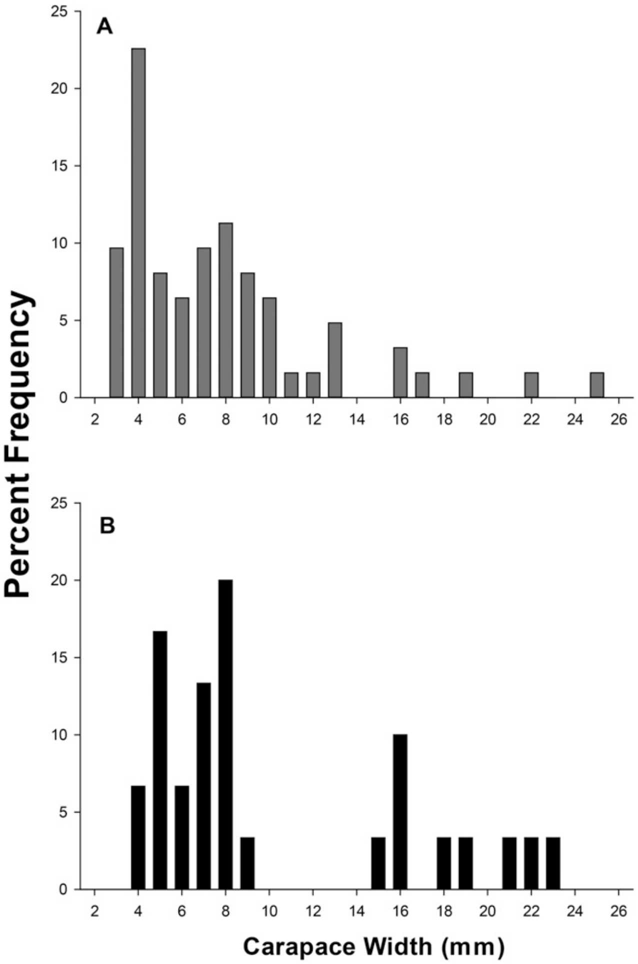

Figure 6. Experiment I. Size–frequency distribution of green crabs pooled across tidalheight and predator-exclusion treatment at the: (A) WR study site (October 10, 2014; N = 62), and (B) FR (October 11, 2014; N = 30).

TABLE 4.

Experiment II. Mixed model nested ANOVA on the square root-transformed mean number of 0-y class individuals (recruits) of the softshell clam, *Mya arenaria*, per EU from the WR, Wells, ME (May 25 to October 16, 2015), and FR, Portland, ME (May 26 to October 17, 2015) (location and treatment are fixed factors; block is a random factor). Location refers to two upper intertidal sites within each estuary (Fig. 1A, B). Treatment refers to predator-exclusion treatments (Table 1). Preplanned contrasts appear indented and directly beneath the treatment and location × treatment source of variation. Boldface *P* values indicate statistical significance. α′ = 0.0127 for all preplanned contrasts (*n* = 2).

		WR		FR	
Source of variation	df	MS	Pr > *F*	MS	Pr > *F*
Location	1	3.35	0.4143	23.97	**0.0383**
Block (location)	4	4.04	0.1246	2.59	0.2818
Treatment	4	16.39	**0.0002**	10.49	**0.0016**
Predation	1	25.45	**0.0008**	32.89	**0.0002**
Predator size	1	22.02	**0.0015**	1.92	0.2686
Deterrent type	1	6.72	0.0501	6.74	0.0473
Infaunal predation	1	11.39	0.0140	0.44	0.5891
Location × treatment	4	19.21	**0.0411**	2.42	0.2088
Location × predation	1	1.22	0.3813	8.44	**0.0286**
Location × predator size	1	2.29	0.2333	0.04	0.8689
Location × deterrent type	1	3.64	0.1388	0.07	0.8345
Location × infaunal predation	1	12.06	**0.0119**	1.12	0.3934
Treatment × block (location)	16	1.49	0.7438	1.46	0.7253
Experimental error	30	2.05	–	1.95	–
Total	59	3.22	–	2.84	–

df = 7, $P < 0.0001$; Fig. 12). Similarly, mean number of recruits per EU was nearly 10× higher on the east (318.4 ± 225.8, $n = 60$) versus west side of HR (33.5 ± 9.7; $P < 0.0001$, Table 10). EU that deterred small versus large predators had significantly higher mean number of recruits per EU (232.2 ± 170.4, $n = 80$ versus 63.3 ± 37.5, $n = 40$; $P < 0.0001$, Table 10), and this pattern was similar on both sides of HR ($P = 0.4052$, Table 10; Fig. 13). Addition of a substrate (play sand) to half of the EU with PS did not affect mean recruit abundance ($P = 0.7539$, Table 10). Significant differences in mean recruit number occurred between locations on both sides of HR ($P < 0.0001$), but variability associated with this source of variation was about 90% greater on the east versus west side (Table 10; Fig. 14). For example, mean number of individuals per EU varied from 9.2 ± 13.0 to 81.0 ± 57.4 ($n = 6$) on the west side of HR and from 25.5 ± 23.8 to 1,843.5 ± 2,390.8 on the east side ($n = 6$; Fig. 14). Effects of the three treatments ($PS_{no\ sand}$, PS_{sand}, and extruded netting) on mean recruit abundance did not vary significantly between the ten locations on the west but did on the east side of the river ($P = 0.0004$, Table 10). No significant differences in mean recruit abundance were observed among treatments at 3 of 10 east-side locations (XVI, XVII, XIX; Fig. 1C), whereas mean abundance was significantly higher in EU with PS versus extruded netting in the remaining locations.

Ambient densities (ind. m^{-2}) of 0-y class recruits in November in the vicinity of the 6 EU at each location ranged from 0 (six and five locations on the west and east side of HR, respectively) to 10.9 ± 30.4 (at two locations on the west side) and 32.9 ± 36.3 (at one location on the east side), with an overall mean across all locations of 6.2 ± 4.2 ($n = 100$).

Of 1,802 recruits measured from representative subsamples across all EU, clam SL ranged from 1.2 to 38.8 mm. Mean SL varied significantly with four of the five sources of variation (Table 11). Recruits were 18% larger on the west (11.8 ± 1.0 mm, $n = 54$) versus east (10.0 ± 0.8 mm, $n = 58$) side of HR. No significant difference in mean SL of recruits was detected between EU with versus without the primary sand substrate ($P = 0.5184$, Table 11; $\bar{x}_{PS(combined)} = 11.3 \pm 0.8$ mm, $n = 78$); however, recruits protected from the smaller predators were 15% larger than clams in EU covered with the netting that excluded larger predators (9.8 ± 1.3 mm, $n = 34$). Significant differences in mean SL occurred between locations on both sides of the river ($P < 0.0001$, Table 11), with a tendency for clams to increase in size from upper (head) to lower (mouth) river sites (Fig. 15). No significant relationship existed between mean SL and number of recruits ($r = 0.04$, $F = 0.13$, df = 1, 110, $P = 0.7188$).

Mean SL of the smallest recruits measured from each EU varied significantly between the east (2.8 ± 0.4 mm, $n = 58$) and

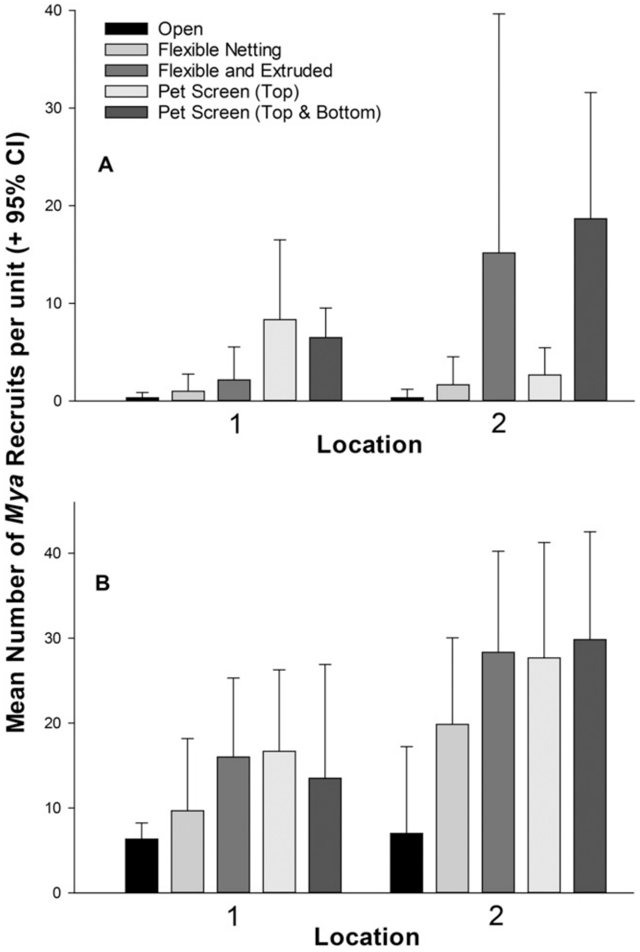

Figure 7. Experiment II. Mean (+95% CI) number of 0-y class recruits of *Mya arenaria* per EU (area = 0.0182 m^2) at two upper intertidal locations in the (A) WR and (B) FR study site on October 16 and 17, 2015, respectively. See Table 4 for ANOVA results for both sites (n = 6).

west side of HR (4.2 ± 0.8 mm, $n = 54$; $P = 0.0063$). The size–frequency distribution of the smallest recruits (Fig. 16) did not vary significantly with treatment (3 × 5 G-test of independence; $G = 11.3$, df = 8, $P = 0.2722$), but did so with the side of river such that clams <5-mm SL were observed more frequently in the east versus west side EU (2 × 5 G-test of independent; $G = 22.8$, df = 4, $P = 0.0001$). Largest recruits per EU varied from 1.8- to 38.8-mm SL (Fig. 17). No significant difference in mean SL occurred between the sides of the river ($P = 0.2136$; $\bar{x}_{\mathrm{SL}} = 22.2 \pm 1.4$ mm, $n = 112$), but did across treatments with recruits 25% larger in EU that deterred the smaller (23.7 ± 1.7 mm, $n = 78$) versus larger predators (18.8 ± 2.3 mm, $n = 34$). When EU were pooled across both sides of HR and location within sides, a 2 × 5 G-test of independence demonstrated that proportionately more clams < 20-mm SL occurred in EU that excluded the larger versus smaller predators ($G = 11.9$, df = 4, $P = 0.0177$).

The nemertean worm, *Cerebratulus lacteus*, was not observed in any of the EU; however, 96 green crabs (the only crustacean predator encountered; size range = 1.8- to 46.6-mm CW) occurred in 58 EU (N = 30 and 28 from the east and west side of HR, respectively). Mean number per EU did not vary significantly between side of river ($P = 0.4490$), but did by treatment ($P < 0.0001$). *A priori* contrasts indicated no significant difference in crab density among EU protected from the smaller predators with PS ($\bar{x}_{\mathrm{NoSand}} = 0.48 \pm 0.23$ ind., $\bar{x}_{\mathrm{Sand}} = 0.28 \pm 0.18$ ind., $n = 40$; $P = 0.2182$). Mean crab density was more than 4× greater in EU covered with the larger aperture extruded netting (1.65 ± 0.41 ind. per EU, $n = 40$), and this was significantly different from the pooled mean of the two other exclusion treatments ($P < 0.0001$). Higher crab densities (ind. per EU) generally were observed at sites on both sides of the river nearest the mouth [$P < 0.0001$; $\bar{x}_{\mathrm{East(XI-XIII)}}$ versus $\bar{x}_{\mathrm{East(XIV-XX)}} = 1.22 \pm 0.49$ ($n = 18$) versus 0.55 ± 0.29 ($n = 42$); $\bar{x}_{\mathrm{West(I-III)}}$ versus $\bar{x}_{\mathrm{West(IV-X)}} = 1.61 \pm 0.76$ ($n = 18$) versus 0.52 ± 0.25 ($n = 42$)]. Crab mean CW did not vary significantly over any source of variation ($P > 0.07$). Size–frequency distribution of green crabs (Fig. 18) was not different between the sides of the river (2 × 5 G-test of independence; $G = 5.9$, df = 4, $P = 0.2045$), or among treatments (Fisher's exact test; $P = 0.3472$); however, crabs >32-mm CW were found only in EU covered with the larger exclusion netting.

Green crab presence in recruitment boxes affected the number of clam recruits per EU that decreased logarithmically with crab biomass ($Y = 3.58e^{-0.614x}$, $r^2 = 0.337$, $n = 58$, $P < 0.0001$); however, analysis of covariance on the ln(number of recruits + 1) versus ln(crab mass) ($F = 14.6$, df = 1, 30, $P = 0.0006$) demonstrated that the recruit number for a common crab biomass was significantly higher on the east (64.7 ± 2.9 recruits, $n = 27$) versus west (19.8 ± 3.0 recruits, $n = 25$) of the river (Fig. 19). Of the 8 EU with zero clam recruits, seven contained individuals of *Carcinus maenas* ≥30-mm CW ($n = 10$ crabs). Of the 10 crabs with CW ≥30 mm, nine were recovered in EU designed to exclude the larger predators (CW range = 31.6–46.6 mm), and one was found in an EU with PS (no sand; 31.7-mm CW). Seven of the 58 recruitment boxes contained crabs ≥30-mm CW and 0-y class recruits of *Mya*; however, mean number of recruits in those 7 EU was 5.7 ± 12.1 ind. versus 275.4 ± 259.5 ind. in EU with crabs <30-mm CW [$n = 51$; $T_{\mathrm{obs}} = 2.09$, df = 47.2, (Satterthwaite method), $P = 0.0421$].

DISCUSSION

Effects of Post-settlement Mortality on Clam Recruitment Density

Results of four, short-term (4–7 mo) manipulative field trials conducted during 2 y, across two tidal estuaries in southern Maine, and over a geographic range of about 70 km (Exps. I and II) demonstrated that post-settlement mortality, rather than a limited supply of available larvae, is likely responsible for regulating densities of 0-y class individuals of *Mya arenaria* (Table 12). Repeated sampling of ambient, intertidal sediments demonstrated relatively low densities of *M. arenaria* (range = 0 ind. m^{-2} at WR and FR in May 2014 to 1.0 ind. m^{-2} at FR in April 2015) and no adults. The low clam densities could reflect a lack of available larvae or patchiness in larval supply because of a variety of biotic and abiotic factors (Morgan et al. 2009). In both years, deterring predators (>1.9 mm) from consuming 0-y class individuals resulted in enhanced densities (3–99×) of softshell clam juveniles compared with open controls that did not restrict predator access to post-settled individuals (Tables 2–5). Whereas no concomitant sampling for softshell clam larvae occurred in these studies, it was assumed that had larval supply been an important factor in regulating softshell clam

TABLE 5.

Experiment II. Mean number (± 95% CI) of 0-y class recruits of *Mya arenaria* at the WR (October 16, 2015) and FR (October 17, 2015) sites across two upper intertidal locations (100 m apart) and predator-exclusion treatments (see Table 1) after 144 days. At both sites, location I was closest to the upper portion of the estuary. Unit refers to a plastic horticultural pot (surface area = 0.0182 m^2 × 15 cm deep) (n = 6).

Site	Location	Treatment	Per unit	Per m^2
Webhannet	I	Open (control)	0.3 (0.5)	18.3 (29.7)
		Flexible netting	1.0 (1.8)	54.8 (96.2)
		Flexible and extruded	2.2 (3.5)	118.8 (193.9)
		PetScreen top only	8.3 (8.2)	456.9 (448.1)
		PetScreen top and bottom	6.5 (3.0)	356.4 (165.8)
	II	Open (control)	0.3 (0.8)	18.3 (46.9)
		Flexible netting	1.7 (2.9)	91.4 (157.2)
		Flexible and extruded	15.2 (24.5)	831.5 (1,342.6)
		PetScreen top only	2.7 (2.8)	146.2 (152.9)
		PetScreen top and bottom	18.7 (12.9)	1,023.4 (709.0)
Fore	I	Open (control)	6.3 (2.1)	347.2 (113.1)
		Flexible netting	9.5 (8.8)	520.8 (481.0)
		Flexible and extruded	16.0 (9.3)	877.2 (508.1)
		PetScreen top only	16.5 (9.9)	904.6 (541.9)
		PetScreen top and bottom	13.7 (13.5)	749.3 (738.3)
	II	Open (control)	7.0 (10.3)	383.8 (564.7)
		Flexible netting	19.8 (10.2)	1,085.5 (559.2)
		Flexible and extruded	28.3 (11.9)	1,553.2 (652.4)
		PetScreen top only	27.7 (13.6)	1,518.6 (745.6)
		PetScreen top and bottom	29.8 (12.7)	1,633.8 (696.3)

populations, or events that occur at settlement that reduce numbers of settling larvae (Clements & Hunt 2014), enhanced numbers of recruits in predator-exclusion treatments relative to controls would not have been observed. This was a risky assumption because recruits could have been missing from EU designed to protect settling clams because of at-settlement events such as lack of suitable settlement conditions (Green et al. 2009, 2013), micropredators (*sensu* Watzin 1986), ingestion of larvae (*sensu* André & Rosenberg 1991) by conspecific juveniles that were established in the EU at the beginning of each trial, or a number of abiotic factors related to the effect of protective netting on hydrodynamics within the protected unit; however, in every case where mean recruit density in control units without predator deterrent netting was compared with units protected with netting, significantly more individuals of *Mya* occurred in the protected EU, and no apparent differences were detected in sediments between the controls and protected treatments.

TABLE 6.

Experiment II. ANOVA on the mean SL of 0-y class individuals (recruits) of the softshell clam, *Mya arenaria*, per EU from the WR, Wells, ME (October 16, 2015) and FR, Portland, ME (October 17, 2015). Location refers to two upper intertidal sites approximately 100 m apart within each estuary (Fig. 1A, B). Treatment refers to predator-exclusion treatments (Table 1). Preplanned contrasts appear directly beneath the Treatment source of variation. At the WR site because only 36 of 60 EU contained *Mya* recruits, the data were unbalanced; hence, type III sums of squares are presented (Shaw & Mitchell-Olds 1993). At least one recruit occurred in each of the 60 EU at the FR site. Boldface *P* values indicate statistical significance. $\alpha' = 0.0127$ for all preplanned contrasts (n = 2).

	WR			FR		
Source of variation	df	MS	Pr > *F*	df	MS	Pr > *F*
Location	1	27.10	0.0615	1	78.87	0.0569
Block (location)	4	16.32	0.8723	4	11.22	0.1912
Treatment	4	445.83	**0.0048**	4	16.73	**0.0330**
Predation	1	127.04	0.0143	1	44.46	**0.0081**
Predator size	1	299.99	**0.0012**	1	3.25	0.4263
Deterrent type	1	11.83	0.3806	1	17.59	0.0756
Infaunal predation	1	6.96	0.4974	1	1.63	0.5709
Location × treatment	4	74.92	0.3231	4	5.21	0.4035
Treatment × block (location)	16	124.93	0.4728	16	4.78	0.7625
Experimental error	13	176.46	–	30	6.86	–
Total	35	865.56	–	59	–	–

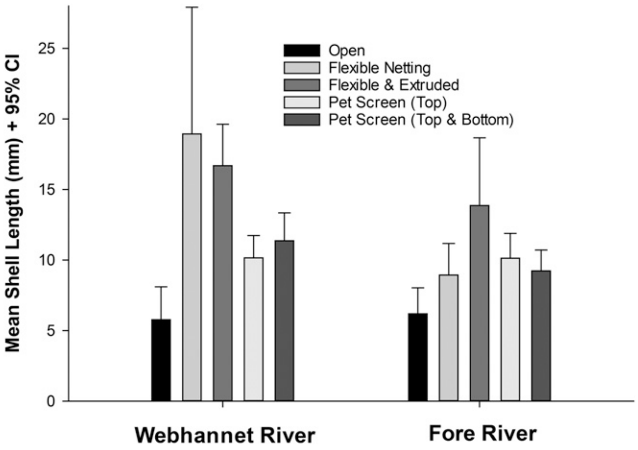

Figure 8. Experiment II. Mean SL of recruits of *Mya arenaria* per EU (0.0182 m^2) across both upper intertidal locations in the WR, Wells, ME, and FR, Portland, ME, on October 16 and 17, 2015, respectively. ANOVA (Table 6) indicated that the mean SL of clams in open units at the FR ($n = 12$) was significantly smaller (by nearly 30%) than the mean SL of animals in protected units (WR: $n_{\text{Open}} = 3$; $n_{\text{Flexible}} = 5$; $n_{\text{Flexible \& Extruded}} = 6$; $n_{\text{PetScreen (Top)}} = 10$; and $n_{\text{PetScreen (Top \& Bottom)}} = 12$).

In large-scale, netted field plots, the mean number of clam recruits varied greatly between the east (AR) and west (CC) side of the HR (Freeport, ME; Exp. III), but 4× to 899× more recruits occurred in benthic cores taken within plots that deterred predators versus cores taken adjacent (4 m away) to the netted plots in ambient sediments. Similarly, initially empty wooden recruitment boxes with various sizes of protective netting on the bottom and top placed on the sediment surface along 10 lower intertidal sites on each side of HR collected an average of 3–10× more clam recruits than from benthic cores taken from ambient sediments near the boxes. These are the first such observations of this phenomenon from the southern Maine coast, but were similar to those observed on intertidal flats in eastern Maine in some cases over a decade earlier where clam recruits were 3–4× more abundant in protected versus open EU (Beal & Kraus 2002, Beal 2006a, 2006b, Tan & Beal 2015) and on tidal flats on the north side of Cape Cod, MA, (Hunt & Mullineaux 2002) where densities of *Mya arenaria* recruits were ca. 5× higher in exclusion cages compared with uncaged plots after only 3 wk. In addition, recruits of *Mya* responded similarly to predator-exclusion caging in the mid-Northwest Atlantic region (Virnstein 1977, Bottom 1984), North Sea (Strasser 2002), Swedish west coast (Möller 1986), and Baltic Sea (Flach 2003). Collectively, the work presented here, from published results over a wide geographic range along the east coast of North America and in parts of northern Europe, provides convincing evidence that early post-settlement mortality due to predation is an important mechanism in regulating densities of 0-y class softshell clams and other bivalves.

TABLE 7.

Experiment II. Analysis of size–frequency distribution of 0-y class individuals (recruits) of the softshell clam, *Mya arenaria*, in EU located in (A) WR, Wells, ME on October 16, 2015), and (B) the FR, Portland, ME, on October 17, 2015. Shell lengths were divided into four size classes (<5.0, 5.1–10.0, 10.1–15.0, and >15.1 mm). Each source represents an orthogonal comparison of predator-exclusion treatments. Boldface *P* values indicate statistical significance. $\alpha' = 0.0127$.

Source	df	χ^2	*P*-value
(A)			
Predation	3	8.2025	0.0420
Predator size	3	32.8037	**<0.0001**
Deterrent type	3	1.7886	0.6174
Infaunal predation	3	27.3216	**<0.0001**
Total	12	70.1164	<0.0001
(B)			
Predation	3	42.2473	**<0.0001**
Predator size	3	18.7318	**<0.0001**
Deterrent type	3	11.2013	**0.0104**
Infaunal predation	3	2.1419	0.5435
Total	12	74.3223	<0.0001

Efforts in HR in 2014 (Exp. III) demonstrated how predators are responsible for patchiness in ambient recruit densities. Typically, densities of 0-y class clams in sediments adjacent to field plots varied from 4.5 to 57 ind. m^{-2}, with most benthic cores yielding <15 ind. m^{-2}. Recruits at AR in predator-deterrent plots averaged ca. 14,800 ind. m^{-2} (and nearly 20,000 ind. m^{-2} in plots seeded initially at a density of 320 ind. m^{-2} with cultured clams), whereas ambient densities within 4 m of the same plots averaged 16.5 ind. m^{-2}. Only 600 m away from the netted plots at AR, on the opposite side of the river at CC, a completely different scenario occurred. Whereas it is unclear how most of the netted plots were compromised, the overall effect of the ripped and dislodged nets can be viewed as an unintentional netted control. That is, a treatment where abiotic conditions such as shading, flow, and sedimentation are altered because of the presence of the net, but that concomitantly allows predators to access the area. At CC, 15 of 17 samples containing wild recruits (ca. 88%) were taken from plots with intact nets, and most of the compromised plots had no recruits. It is possible that factors other than predators were responsible for the low densities of 0-y class clams outside the plots at AR and CC, and in the compromised nets at CC such as differential larval settlement or behavior (Butman 1987, Snelgrove et al. 1999), potential differences in carbonate saturation state at the sediment–water interface between protected plots and the ambient mudflats (*sensu* Green et al. 2003), or differences in chemical cues by other species that settle at higher densities into protected plots and facilitate local conditions for settling *Mya arenaria* (*sensu* van der Heide et al. 2014), but these remain untested.

It is also noteworthy that whereas no cage controls were used at WR or FR in 2014 and 2015, green crabs averaged between 0.35 and 1.3 individuals per EU (19.2–71.2 crabs m^{-2}) during the October sampling, and most were recovered in EU designed to exclude predators. Many crabs were small (<10-mm CW), and likely entered EU with exclusion netting after clams had settled because most crabs overwinter at sizes between 5- and 10-mm CW, and megalopae and stage I crabs (ca. 1 mm CW) typically settle in August (Berrill 1982); however, crabs recovered in some of the protected EU's had CW ≥20 mm (Figs. 6 and 10), suggesting that they entered the EU earlier in the field study than most of the other crabs. These crabs likely molted to a size that was too large to escape the aperture of the netting, and remained in the EU until the end of the study. When that

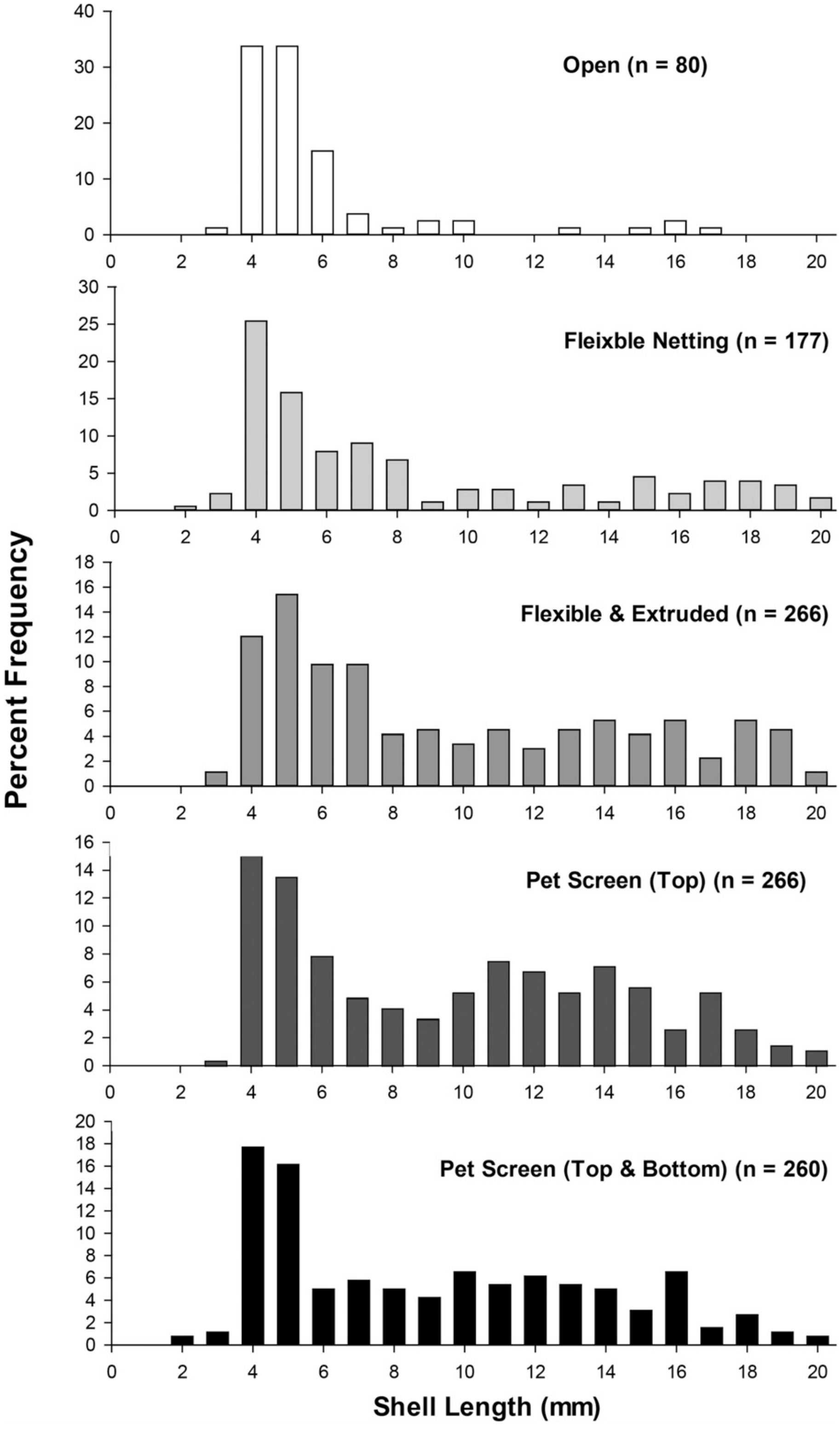

Figure 9. Experiment II. Size–frequency distribution of 0-y class recruits of softshell clams in EU pooled across location at the FR, Portland, ME, on October 17, 2015.

occurred, mean clam recruit densities were similar to those observed in open controls (Table 13). That is, relatively large crabs likely were responsible for reducing 0-y class clam densities in open controls because enhanced densities of clams occurred in protected units containing small crabs. Also, because netting on the 19 protected EU containing large crabs (Table 13) remained intact throughout the experimental period at both sites in both years, these units could be considered a type

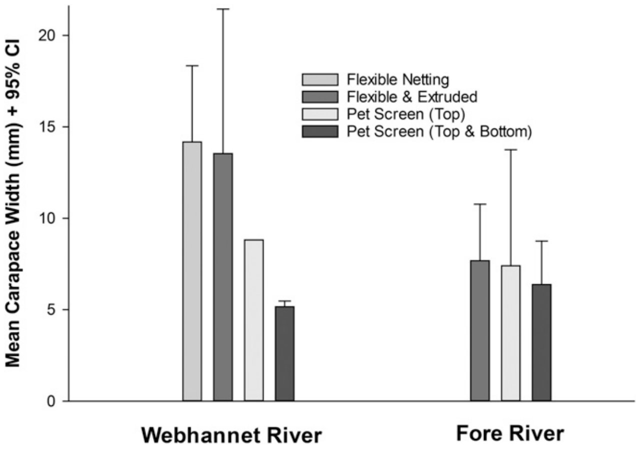

Figure 10. Experiment II. Mean CW of green crabs within EU pooled across locations at the FR, Portland, ME, on October 17, 2015. ANOVA indicated a significant treatment and treatment × location effect. No crabs were recovered from control units (*n* varies from 1 to 4, and represents the number of EU from which crabs were recovered).

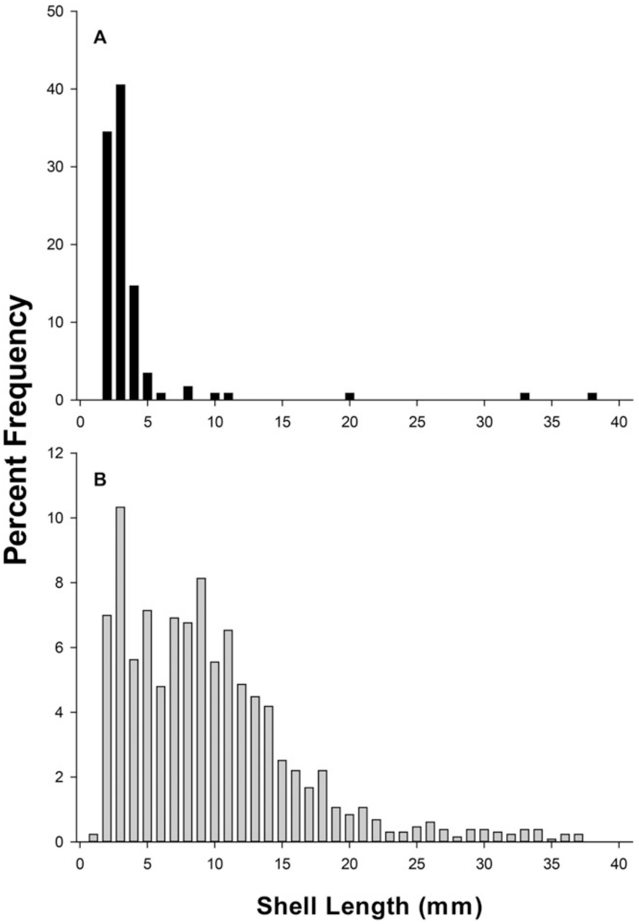

Figure 11. Experiment III. Size–frequency distribution of 0-y class recruits of *Mya arenaria* from netted plots in the HR (November 8–10, 2014). (A) CC ($n = 76$); (B) AR ($n = 1316$).

of cage control showing that the effects of excluding predators, rather than other potential factors associated with deterrent netting such as shading, temperature, sediment grain size, and water flow are paramount in understanding the post-settlement mortality in the early life history of *Mya* at these estuarine locations.

In 2015, epibenthic recruitment boxes (Exp. IV) at 5 of 10 lower intertidal locations on the east side of HR contained, on average, >100 *Mya arenaria* recruits per EU (i.e., >660 ind. m^{-2}; sites XIII–XV, Fig. 14). At those locations, mean recruit density in the 12 boxes excluding the smaller predators using PS was 1,220 ± 1,084 ind. (8,079 ± 7,176 ind. m^{-2}), whereas the six boxes that excluded the larger predators contained a mean approximately 10× lower—126 ± 176 ind. (= 834 ± 1,165 ind. m^{-2}). The difference in the two means, which is statistically significant [$T_{obs} = 2.20$, df = 11.42, (Satterthwaite method), $P = 0.0493$], is likely because of the fact that three of the six large-mesh recruitment boxes each contained an individual of *Carcinus maenas* >37-mm CW. Collectively, these results and those from the other field trials suggest that larval supply and at-settlement processes are much less important than immediate and longer term post-settlement processes that result in high mortalities typically seen in invertebrate bivalve populations (Gosselin & Qian 1997, Tezuka et al. 2012).

TABLE 8.

Experiment III. ANOVA on the square root–transformed mean number of 0-y class individuals (recruits) of the softshell clam, *Mya arenaria*, per benthic core ($A = 0.0182\ m^2$) from AR, HR, Freeport, ME (November 8–10, 2014; site XIII, Fig. 1C) ($n = 2$).

Source of variation	df	SS	MS	*F*	Pr > *F*
Block	4	559.83	139.96	2.43	0.0817
Trapping	1	1.36	1.36	0.02	0.8794
Block × trapping	4	423.71	105.93	1.84	0.1615
Intraspecific density	1	437.19	437.19	7.58	**0.0123**
Block × intraspecific density	4	634.25	158.56	2.75	0.0569
Trapping × intraspecific density	1	46.16	46.16	0.80	0.3817
Block × trapping × intraspecific density	4	356.03	89.01	1.54	0.2281
Net (block, trapping, intraspecific density)	20	1,153.92	57.69	0.70	0.8061
Experimental error	40	3,315.12	82.88	–	–
Total	79	6,927.58	–	–	–

Given that predators were observed in many of the small EU (FR and WR) and recruitment boxes (HR), a conservative estimate for post-settlement mortality (mean number of *Mya* juveniles in protected versus control EU and mean number in all recruitment boxes versus ambient sediments) would be between 99.1% (Fig. 2A) and 99.4% (Fig. 13) in the lower intertidal and between 92.7% (Fig. 7) and 97.4% (Fig. 2B) in the upper intertidal. These rates are similar to those observed at the three intertidal sites in Barnstable Harbor, MA, in 1998–1999 (Hunt et al. 2003).

Effects of Predator Size on Post-settlement Success

The aperture size of the exclusion netting was varied in Exps. I, II, and IV to examine the effects of predator size on softshell clam post-settlement mortality. An earlier study (Beal & Kraus

TABLE 9.

Experiment IV. Species list of invertebrate juveniles recovered from recruitment boxes on both east and west side of the HR, Freeport, ME (April 9–12 to November 3–6, 2015). The initially empty boxes were placed on the surface of intertidal flats. World Register of Marine Species was consulted on February 22, 2018 as the authority (www.marinespecies.org).

Phylum	Class	Order	Family	Genus	Species	Author
Annelida	Polychaeta	Phyllodocida	Glyceridae	*Glycera*	*dibranchiata*	Ehlers
Annelida	Polychaeta	Phyllodocida	Nereididae	*Alitta*	*virens*	M. Sars
Arthropoda	Malacostraca	Decapoda	Carcinidae	*Carcinus*	*maenas*	Linnaeus
Arthropoda	Malacostraca	Decapoda	Crangonidae	*Crangon*	*septemspinosa*	Say
Mollusca	Bivalvia	Adapedonta	Pharidae	*Ensis*	*leei*	Huber
Mollusca	Bivalvia	Cardiida	Tellinidae	*Limecola*	*balthica*	Linnaeus
Mollusca	Bivalvia	Myida	Myidae	*Mya*	*arenaria*	Linnaeus
Mollusca	Bivalvia	Mytilida	Mytilidae	*Mytilus*	*edulis*	Linnaeus
Mollusca	Bivalvia	Nuculanida	Yoldiidae	*Yoldia*	*limatula*	Say
Mollusca	Bivalvia	Nuculida	Nuculidae	*Nucula*	*proxima*	Say
Mollusca	Bivalvia	Ostreida	Ostreidae	*Crassostrea*	*virginica*	Gmelin
Mollusca	Bivalvia	Ostreida	Ostreidae	*Ostrea*	*edulis*	Linnaeus
Mollusca	Bivalvia	Venerida	Mactridae	*Mulinia*	*lateralis*	Say
Mollusca	Bivalvia	Venerida	Mactridae	*Spisula*	*solidissima*	Dillwyn
Mollusca	Bivalvia	Venerida	Veneridae	*Mercenaria*	*mercenaria*	Linnaeus
Mollusca	Bivalvia	Venerida	Veneridae	*Petricolaria*	*pholadiformis*	Lamarck
Mollusca	Bivalvia	Venerida	Veneridae	*Pitar*	*morrhuanus*	Dall
Mollusca	Gastropoda	Littorinimorpha	Hydrobiidae	*Ecrobia*	*truncata*	Vanatta
Mollusca	Gastropoda	Littorinimorpha	Littorinidae	*Littorina*	*littorea*	Linnaeus
Mollusca	Gastropoda	Littorinimorpha	Littorinidae	*Littorina*	*obtusata*	Linnaeus
Mollusca	Gastropoda	Neogastropoda	Muricidae	*Urosalpinx*	*cinerea*	Say
Mollusca	Gastropoda	Neogastropoda	Nassariidae	*Tritia*	*obsoleta*	Say

2002) at an intertidal flat in eastern Maine discovered that over a 1-y period density of *Mya arenaria* recruits was nearly twice that in EU that excluded large versus small predators (630 versus 326 ind. m^{-2}, respectively) when mesh sizes varied between 6.4 and 12.7 mm versus 4.2 mm, respectively. Because the smaller aperture netting became heavily fouled by species of red and brown macroalgae, it was presumed that the combination of small aperture and fouling restricted flow enough to negatively affect clam settlement. No similar fouling was observed in the present study, and the results of predator size on clam recruitment (Tables 2, 4, and 10) generally were opposite to what was predicted (Table 12). That is, in Exps. I and II, significantly more 0-y class *Mya* occurred in EU excluding smaller (treatments: PS_{top} and $PS_{top\ \&\ bottom}$) versus larger (treatments: Flexible, and Flexible and Extruded) predators. For example, in 2014 at both WR and FR, recruits were observed more frequently in lower versus upper intertidal EU; however, only in lower intertidal blocks did significantly more wild juveniles occur in units excluding the smaller (with PS) versus the larger predators (with 4.2 mm aperture netting; WR = 5.6×, FR = 9.4×; Fig. 2). In 2015, the same pattern occurred only at WR where nearly twice as many recruits occurred in treatments with smaller versus larger aperture netting. In addition, recruits of *Mya* at HR (Exp. IV) were about 3.5× more abundant in recruitment boxes covered on the top and bottom with PS (regardless of whether these had sand as an initial settlement substrate) versus boxes with the larger aperture extruded netting (Fig. 13).

Several reasons may help explain the disparity in results between the studies conducted in eastern Maine during the early 1990s versus the present field trials, but each relates to predators. First, no green crabs were recovered from any of the EU in the earlier study (Beal & Kraus 2002). In that experiment, survival rates of *Mya arenaria* juveniles (8.5–11.8 mm SL) in unprotected control units were relatively high, ranging from 64% to 78%, whereas in predator-exclusion treatments the survival rates were enhanced only 12.1%–26.1% more than controls. In 2014 at WR and FR, similar size juvenile clams were added to all EU, and mean survival rates in the unprotected units ranged from 0% to 3.1% compared with 71.0%–77.9% in protected units (Munroe et al. 2015). In 2015, no cultured juveniles of *M. arenaria* survived in open controls at WR, whereas mean survival in protected units was 74.1%, and similar results were observed at FR (B. Beal unpublished). Predation, especially by crustaceans such as green crabs, caused proportionately more clam deaths in the recent trials in southern Maine versus those carried out in eastern Maine during the early 1990s. Second, the smaller aperture PS netting (1.7 mm × 0.9 mm) may have permitted fewer (and smaller) green crabs to enter the EU compared with the larger aperture flexible netting (4.2 mm—WR and FR, 2014–2015; 6.4 mm—HR, 2015). Whereas this was not observed either in 2014 or 2015 at WR, it did occur in 2015 at FR (Fig. 10). At HR in 2015, green crabs were 4× more abundant in recruitment boxes with the larger netting versus PS, and the largest individuals of *Carcinus maenas* (32–46 mm) were recovered from boxes with the large, extruded netting. Third, it may be possible for *C. maenas* and other large crustaceans such as *Cancer irroratus* Say (that were observed in the intertidal during 2014 and 2015 at HR—C. Coffin and C. Goodenow, personal observation) to consume juveniles of *Mya* in EU protected with the largest aperture netting without entering the unit. Tan and Beal (2015) demonstrated in the laboratory that male individuals of *C. maenas* (69.9–71.7 mm) can crush juveniles of *M. arenaria*

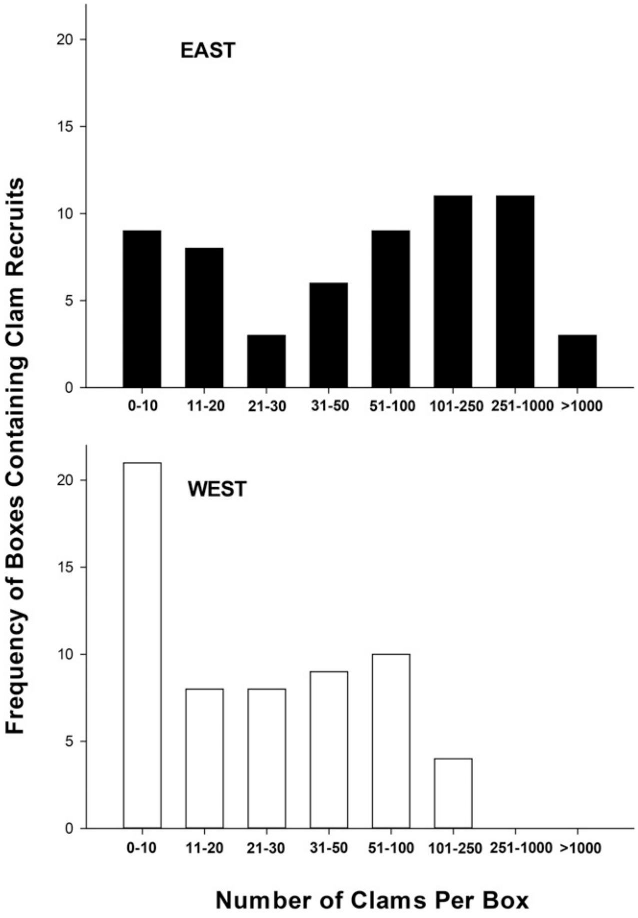

Figure 12. Experiment IV. Frequency of recruitment boxes (EU) containing 0-y class individuals of *Mya arenaria* on the east (N = 60) and west sides (N = 60) of the HR (November 3–6, 2015). A 2 × 8 *G*-test of independence indicated that the number of recruits per EU was not independent of side of river ($G = 30.8$, df = 7, $P < 0.0001$).

($\bar{x}_{SL}$= 14.8 mm) in EU completely covered with a piece of plastic, flexible netting (aperture = 6.4 mm). Whether crabs grasp clam siphons that extend through the netting apertures during feeding, pull them to the netting–sediment interface, and then consume them through the netting remains unclear.

Spatial Variation in Clam Recruitment within and between Tidal Heights

The field experiments demonstrated large spatial variability in abundance patterns of *Mya arenaria* recruitment, especially at scales ≥100 m (Table 12). For example, in 2014 at both WR and FR, more recruits were observed in lower versus upper intertidal blocks (Fig. 2; a result contrary to predictions—Table 12), but the effect depended on the particular treatment as proportionately more recruits were observed in EU excluding smaller versus larger predators. Previous studies in southern Maine (Vassiliev et al. 2010), the northwest Bay of Fundy in Atlantic Canada (LeBlanc & Miron 2006, Bowen & Hunt 2009), and in the Wadden Sea (Günther 1992, Strasser et al. 1999) have demonstrated similar results across the tidal gradient, whereas others (Beal 2006b, Landry & Miron 2011) have found the opposite, with more recruits occurring consistently along the upper shore. Morse and Hunt (2013) tracked the movement of colored sand in the intertidal in the southern Bay of Fundy (New Brunswick, Canada), and noted a shoreward migration regardless of tidal height, with rates 2–4× faster in the lower zone. This could mean that as a result of post-settlement dispersal, timing of sampling is critical in understanding distribution and abundance patterns of intertidal populations of juvenile *Mya*.

TABLE 10.

Experiment IV. Mixed-model nested ANOVA on the ln(number of *Mya* recruits +1) from the HR (April to November 2015). Side refers to east versus west side of the river. Treatment refers to epibenthic wooden boxes (57 cm × 26.5 cm × 7.6 cm) completely protected with predator-exclusion netting on the top and bottom [Trt. 1 = PS sand (Pet Screening with 1 L of sand added as a substrate); Trt. 2 = PS no sand (Pet Screening with no substrate); Trt. 3 = extruded (an extruded polyethylene netting with 6.4 mm aperture)]. Location refers to ten lower intertidal locations situated 200–300 m apart on both sides of the river (Fig. 1C). All three factors are fixed. *A priori* contrasts are indented, appearing below the Treatment source of variation, and use an adjusted type I error rate (α') = 0.0253. Sources of variation listed as location (side) and location × treatment (side) are decomposed into their respective east and west side components. Boldface *P* values indicate statistical significance ($n = 2$).

Source of variation	df	SS	MS	*F*	Pr > *F*
Side	1	54.71	54.71	47.18	**<0.0001**
Treatment	2	28.96	14.48	12.49	**<0.0001**
Predator size	1	28.85	28.85	24.88	**<0.0001**
Sediment	1	0.12	0.12	0.10	0.7539
Side × treatment	2	2.13	1.06	0.92	0.4052
Location (side)	18	116.38	6.47	5.58	**<0.0001**
East side	9	76.46	8.49	7.33	**<0.0001**
West side	9	39.92	4.44	3.83	**0.0007**
Location × treatment (side)	36	101.29	2.81	2.43	**0.0012**
East side	18	66.49	3.69	3.19	**0.0004**
West side	18	34.79	1.93	1.67	0.0713
Experimental error	60	69.57	1.16	–	–
Total	119	373.03	–	–	–

We observed significant spatial variation in recruit abundance within the same tidal height at scales of ca. 100 m (FR in 2015; Table 4) to 300 m (HR in 2015; Table 4), but did not see significant differences in mean recruit densities at scales <20 m (i.e., between blocks and plots) as had been predicted (Table 12). In Cobscook Bay and Passamaquoddy Bay (extreme eastern Maine; southern Bay of Fundy), recruitment of *Mya arenaria* individuals varied significantly over scales from 5 m to >10,000 m (Beal 2006b). Densities of 0-y class individuals varied significantly between blocks that were 5 m apart, between sites within embayments on the scale of 1–2 km, and between embayments that were 10 km apart. Spatial variation in clam recruitment also may occur because of bedload transport within a tidal height (Emerson & Grant 1991, Jennings & Hunt 2009, Hunt 2005). It is possible that this phenomenon could explain partly results from studies at WR and FR (Exps. I and II, 2014 and 2015), and from HR (Exp. III, 2014) because EU and netted plots were flush with sediments, but is less likely to have

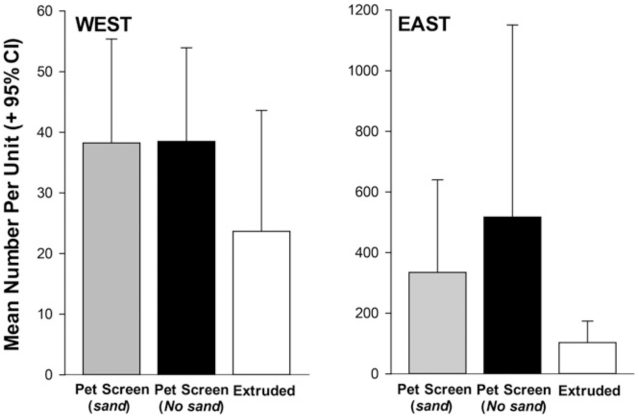

Figure 13. Experiment IV. Mean number (+95% CI) of 0-y class recruits of *Mya arenaria* per EU (0.15 m^2 recruitment box) on the west and east sides of the HR (November 3–6, 2015). Units were either covered on top and bottom with PS (that would exclude predators >1.9 mm) or with an extruded, thick, hard polyethylene mesh (that excludes predators >5.9 mm; see Table 1). Sand refers to the addition of 1 L of play sand per box to provide a settlement substrate. Note that *Y*-axis scaling differs for each graph ($n = 20$).

TABLE 11.

Experiment IV. Mixed-model nested ANOVA on the mean SL of 0-y class individuals (recruits) of *Mya arenaria* from epibenthic recruitment boxes deployed along the lower intertidal in the HR (April to November 2015). See Table 10 for a description of side, treatment, and location. All three factors are fixed. *A priori* contrasts are indented, appearing below the treatment source of variation, and use an adjusted type I error rate (α') = 0.0253. Source of variation listed as location (side) is decomposed into its respective east and west side components. Type III sums of squares are used for each hypothesis test (Shaw & Mitchell-Olds 1993) because of unbalanced data because only 112 of the 120 boxes contained live recruits. Boldface *P* values indicate statistical significance ($n = 2$).

Source of variation	df	SS	MS	*F*	Pr > *F*
Side	1	85.99	85.99	15.66	**0.0002**
Treatment	2	54.93	27.46	4.74	**0.0128**
Predator size	1	52.48	52.48	9.06	**0.0039**
Sediment	1	2.45	2.45	0.42	0.5184
Side × treatment	2	0.71	0.36	0.06	0.9404
Location (side)	18	573.21	31.85	5.50	**<0.0001**
East side	9	232.75	25.86	4.46	**0.0002**
West side	9	340.46	37.83	6.53	**<0.0001**
Location × treatment (side)	35	376.49	10.76	1.86	**0.0204**
Experimental error	53	306.99	5.79	–	–
Total	111	1,398.32	–	–	–

influenced results from the recruitment boxes (Exp. IV, 2015) because these were situated on top of the sediments in such a way that settlers would most likely have entered via the water column. Kube (1996) discovered large spatial variability in population structure of *M. arenaria*, including 0-y class individuals, in the subtidal region of Pomeranian Bay in the southern Baltic Sea. Clam densities ranged from <100 to >4,000 ind. m^{-2} over a north–south distance of about 100 km. Bedload transport and other physical forcing variables (e.g., erosion processes) were primarily responsible for the differences across sampling stations; however, differential predation by sea ducks (*Melanitta nigra* [L.] and *Clangula hyemalis* [L.]), especially on clams <10 mm SL, across the study area may have added to the observed differences in density. Surprisingly, little spatial variation in number of 0-y class individuals of *M. arenaria* occurred between the two southerly sites (distance ca. 45 km apart) in either year (Figs. 2 and 7). Conversely, density of recruits at CC and AR in the HR in 2014 differed by three orders of magnitude. Compromised netting at CC likely allowed predators access to the area beneath most of the nets, and this may have led to the high spatial variability in clam recruits between sites located only 600 m apart; however, a similar pattern of lower recruitment at CC versus AR occurred in 2015 (Fig. 14). Local hydrodynamics may help to explain this phenomenon. A dye/dilution study at HR (True 2013) indicated that tidal currents tend to push seawater toward the east side of the river on each flood tide. This scenario is heightened between June and September when southwest winds prevail in this area, and when clam larvae are settling from the water column (Ropes & Stickney 1965). That is, supply of larval clams or resuspension of recent post-settlers may be enhanced along the east versus the west side of HR. Armonies (1996) observed that large-scale distribution patterns of five byssus-drifting benthic bivalves, including *M. arenaria*, in the northern Wadden Sea was related to hydrographic conditions.

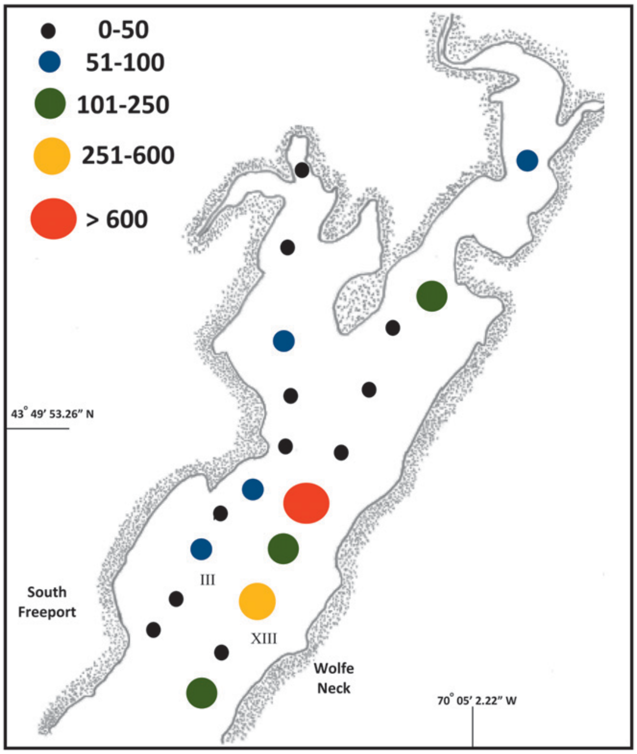

Figure 14. Experiment IV. Mean number of 0-y class individuals per recruitment box (EU with internal dimensions of 57 cm × 26.5 cm × 7.6 cm) located near the low-water mark on east (South Freeport) and west side (Wolfe Neck) of the HR, Freeport, ME (Fig. 1c). Units were deployed from April 9 to 12, 2015, and sampled from November 3 to 6, 2015. Each dot represents six EU. III = CC; XIII = AR, sites where Exp. III was conducted in 2014.

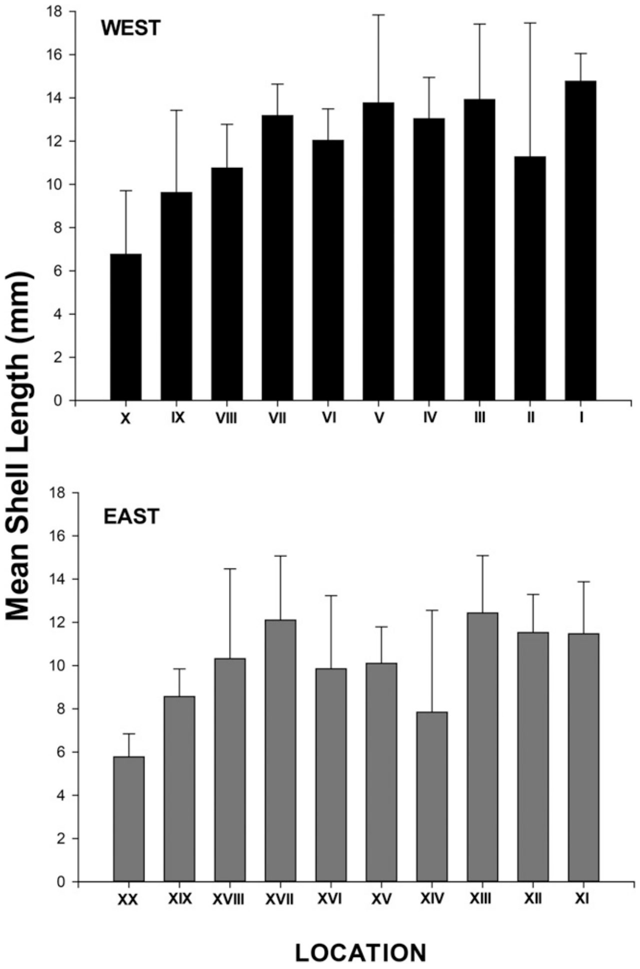

Figure 15. Experiment IV. Mean SL (+95% CI) of 0-y class recruits of *Mya arenaria* at each location on each side of the HR [pooling all EU; the *X*-axes are arranged from head (left) to mouth (right) of the river; see Fig. 1C] (*n* = 3–6).

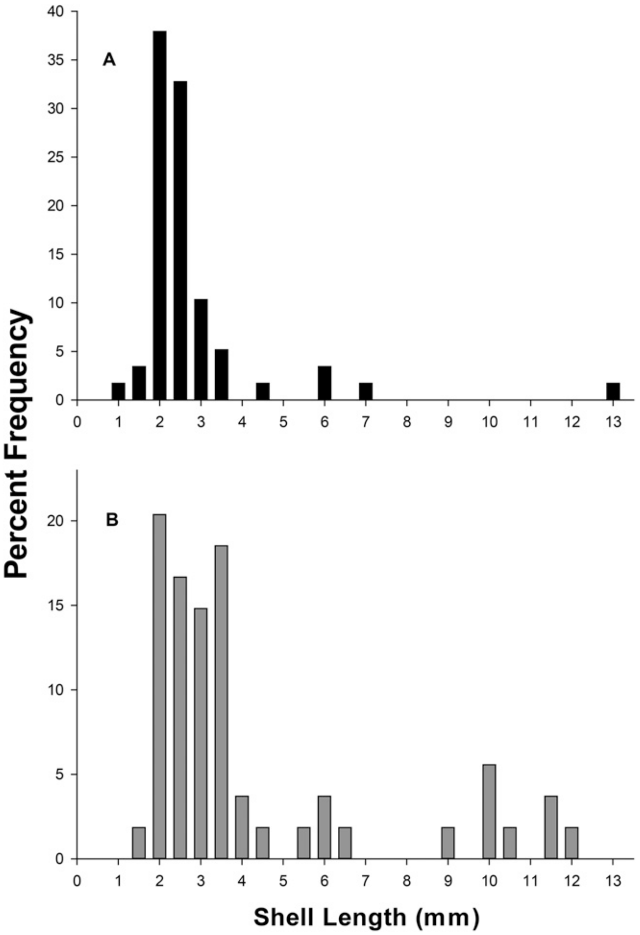

Figure 16. Experiment IV. Size–frequency distribution of the smallest clams recovered from recruitment EU during November 3–6, 2015, on the (A) east (N = 58) and (B) west (N = 54) side of the HR. A 2 × 5 *G*-test of independence (*G* = 22.8, df = 4, *P* = 0.0001) indicated that a higher proportion of clams <5-mm SL occurred on the east side of the river.

Effects of Intraspecific Density on Clam Recruitment

Infaunal suspension-feeding bivalve adults or juveniles may play a role in establishing 0-y class populations of conspecifics by ingesting planktonic larvae before settlement (Woodin 1976, Peterson 1982, Thrush et al. 1996, Whitlach et al. 1997), but no consistent pattern has emerged from field trials. Conversely, gregarious settlement in infaunal suspension-feeding bivalves is rare (but see Peterson & Black 1993, Gribben & Wright 2006). Increasing intraspecific densities of juveniles of *Mya* from 160 to 320 ind. m^{-2} resulted in an 85% enhancement of clam recruits at AR over a 6-mo period (Exp. III—HR in 2014). This result was opposite to the prediction (Table 12) based on field experiments in eastern Maine where experimental densities of softshell clam juveniles were varied between 660 and 1,320 ind. m^{-2} with no concomitant effect on clam recruits (Beal 2006b). Similarly, André and Rosenberg (1991) demonstrated that the number of *Mya* recruits was independent of adult densities ranging from 0 to 400 ind. m^{-2} in a field experiment on the Swedish west coast. If future studies find that gregarious settlement of *Mya* does occur elsewhere at these or larger scales, this could be a tool used by shellfish managers and aquaculturists to enhance large intertidal tracks (*sensu* Beal et al. 2016) without having to rely on procuring and deploying cultured individuals.

Relative Importance of Epibenthic versus Infaunal Predation on Clam Recruitment

Predation, especially by the invasive green crab, *Carcinus maenas*, rather than by infauna such as the nemertean, *Cerebratulus lacteus*, is likely to have played a key role in helping establish and maintain large variations in distribution and abundance of softshell clam recruits (Tables 2 and 4). Whereas significant enhancement of *Mya* recruits occurred in 2015 at WR in EU that excluded both predatory epifauna and infauna compared with similar units that excluded only epifauna, the effect occurred only once, and at only one location (Fig. 7A). The largest infaunal predator observed in this study, *C. lacteus*, has been responsible for limiting populations of *Mya arenaria* in Atlantic Canada (Rowell & Woo 1990, Bourque et al. 2001). The most ubiquitous predator in this study was *C. maenas* that has occurred in southern Maine for over a century (Rathbun 1905). Green crabs prey on all sizes of *Mya* (Ropes 1968, Whitlow 2010, Tan & Beal 2015), and crab population densities

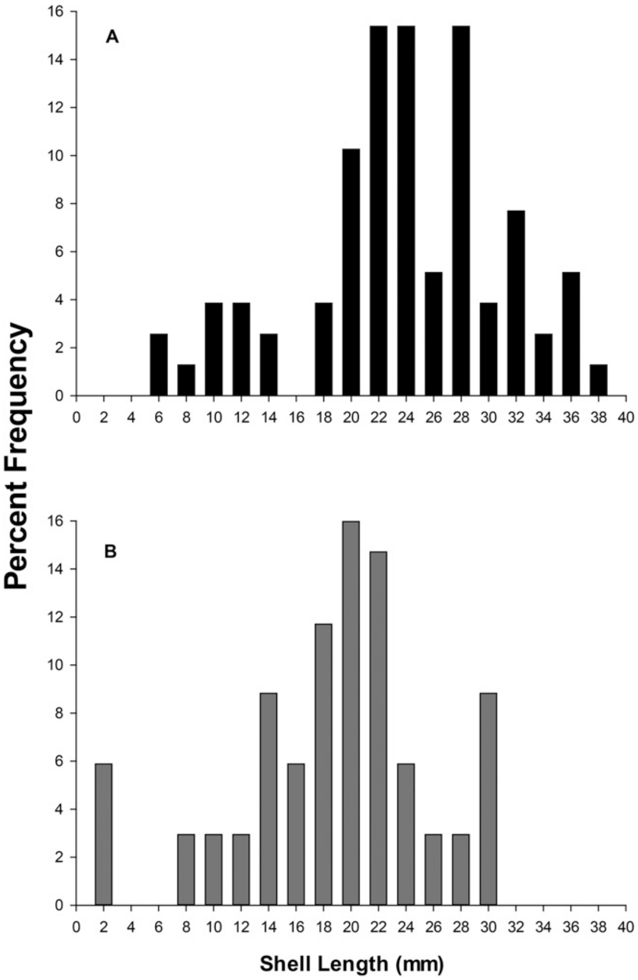

Figure 17. Experiment IV. Size–frequency distribution of the largest clams recovered from recruitment EU in the HR during November 3–6, 2015, that were covered with (A) PS (N = 78) and (B) extruded netting (N = 34). A 2 × 5 *G*-test of independence (*G* = 11.9, df = 4, *P* = 0.0177) indicated that proportionately more clams <20-mm SL occurred in EU covered with extruded netting.

are directly related to seawater temperature (Welch 1968). Over the past decade, sea surface temperatures in the Gulf of Maine have been warming rapidly, by an average of 0.13°C year^{-1}, which is faster than 99% of the global ocean (Pershing et al. 2015). During this period, an explosion in numbers and biomass of *C. maenas* has occurred, especially in southern Maine (McClenachan et al. 2015). Long-term observational studies in the Wadden Sea (Beukema & Dekker 2014) have shown direct linkages between the severity of winters and subsequent summer abundance of recruits of *M. arenaria* and three other soft-bottom bivalves. Cold winters result in a reduction of clam and other bivalve predators such as green crabs and shrimp (*Crangon crangon* [L.]) that, otherwise, keep bivalve populations below their carrying capacity. Similar patterns have been observed by Strasser (2002) and Strasser and Günther (2001). Green crabs were relatively abundant at WR and FR in both 2014 and 2015, averaging 1.04 and 0.32 ind. per EU over both years, respectively, and 0.80 ind. per EU at HR (2015). Whereas other invertebrate predators were observed across the three estuaries such as the milky ribbon worm, *C. lacteus*, and rock crab, *Cancer irroratus*, neither was as numerous as *C. maenas*. Other studies have shown unequivocally that green crabs have the ability to prey heavily on juvenile bivalve populations causing patchiness in distribution and abundance (Richards et al. 1999, Hiddink et al. 2002).

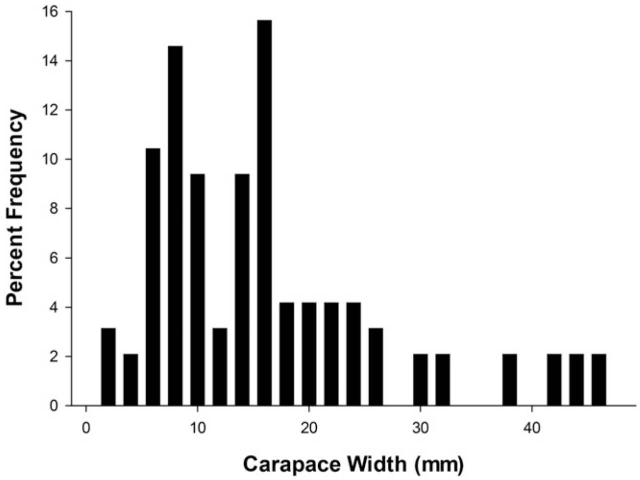

Figure 18. Experiment IV. Size–frequency (CW) distribution of green crabs, *Carcinus maenas*, in recruitment EU in the HR (pooling all EU) from November 3 to 6, 2015. Frequencies did not vary significantly between sides of river (2 × 5 *G*-test, *P* = 0.2405) or among treatments (Fisher's exact test, *P* = 0.3472) (N = 96).

Size of Mya Recruits and Green Crabs

In the two southernmost tidal estuaries in 2014 and 2015, softshell clam recruits generally were smaller in open EU and in units covered with PS (to deter predators >1.9 mm) than in EU protected from larger predators with the flexible netting (to deter predators >5.9 mm; Table 12). A similar result occurred in HR in 2015 (Exp. IV) where recruits in EU protected from the smaller predators were 15% larger than those protected from

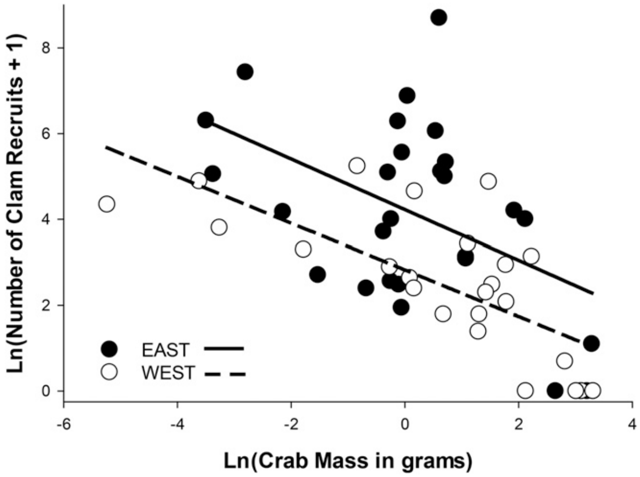

Figure 19. Experiment IV. ln–ln relationship between number of 0-y class individuals of *Mya arenaria* and mass of green crabs, *Carcinus maenas*, for *n* = 30 and 28 EU containing crabs on the east and west side of the HR (November 3–6, 2015), respectively. Analysis of covariance demonstrated that for a common crab mass, number of recruits was significantly higher in EU on the east versus west side of the river.

TABLE 12.

Results of the tests of hypotheses for each field trial. "+" refers to a statistically significant test of the hypothesis in a direction that was predicted—see Introduction; "–" refers to a statistically significant test of the hypothesis in an unpredicted direction; "ns+" refers to not statistically significant, as predicted; "ns–" refers to not statistically significant that was not predicted. The results are integrated across all main and interactive effects. "0" indicates no test was conducted.

	Field trials						
Hypotheses	**Exp. IV (HR—2015)**	**Exp. II (FR—2015)**	**Exp. III (HR/AR—2014)**	**Exp. III (HR/CC—2014)**	**Exp. II (WR—2015)**	**Exp. I (WR—2014)**	**Exp. I (FR—2014)**
(1) Predation (recruit density)	+	+	+	+	0	0	0
(1) Predation (recruit size)	–	+	+	ns±	0	0	0
(2) Predator size (recruit density)	–	–	–	ns–	0	0	–
(2) Predator size (recruit size)	+	+	+	+	0	0	–
(3) Deterrent type	ns+	ns+	ns+	ns+	0	0	0
(4) Infaunal predation	ns+	ns+	–	ns+	0	0	0
(5) Tidal height (recruit density)	–	–	0	0	0	0	0
(5) Tidal height (recruit size)	ns–	ns–	0	0	0	0	0
(6) Spatial variation (≤20 m spacing)	ns–	ns–	ns–	ns–	ns–	ns–	0
(6) Spatial variation (≥100 m spacing)	0	0	+	+	ns–	ns–	+
(7) Intraspecific density	0	0	0	0	ns+	–	0

larger predators (>9.1 mm). Small recruit size may have occurred in exclusion treatments and recruitment boxes with the smaller aperture netting (PS) because of the possible reduction in flow and/or a density-dependent effect on growth related to enhanced numbers of clams in EU covered by the PS netting (Figs. 2, 7, and 13).

Also, predation is a likely mechanism to help explain the small sizes of clams in the open EU at WR and FR. At those locations, *Mya arenaria* recruits in October ranged in SL from 2 to 25 mm (Figs. 3, 5, and 9) suggesting a protracted settlement event (although an alternative hypothesis is that the different sizes represent a brief settlement event, and the variation in SL among recruits is due to differential growth). If settlement occurs over the span of months, then it is likely that predators consume most 0-y class clams through the warm summer months. Clams settling later in the season benefit from a temporal refuge, as predation decreases with falling seawater temperatures after September. At HR, clams from ambient cores taken in April and November 2014 had similar ranges in SL from 3.2 to 13.9 mm, whereas recruits from netted plots ranged in SL from 1.7 to 38.3 mm. A similar pattern was observed from the epibenthic recruitment boxes in 2015, where the largest recruit attained a SL of 38.8 mm. Together, the data suggest that predation is severe on small *M. arenaria* and that those individuals that settle late in the year (September to October), and survive the winter, have a much greater probability of growing to a reproductive size (ca. 25 mm SL; Brousseau 1978) than those clams that settle earlier in the year (May to June) when predation may be more intense because of the combination of warmer seawater temperatures and relatively high abundance of *Mya* (and other bivalve) recruits. The sharp contrast in the distribution of clam SL at CC (2014), where predators gained access to the benthos due to the compromised nets, versus AR, 600 m away (Fig. 1C) where

TABLE 13.

Mean (± 95% CI) number of recruits of *Mya arenaria* (WR, FR; 2014–2015) per EU in: (A) open controls; (B) protected units containing no green crabs; (C) protected units with at least one green crab (CW < 20 mm); and (D) protected units with at least one green crab (CW ≥ 20 mm). Data is pooled across tidal heights (2014) and locations (2015). In each combination of location and year, means of A and D are similar, and significantly lower than the means of B and C which are similar (ANOVA; $P < 0.05$).

	WR		**2014**		**FR**		
A	**B**	**C**	**D**	**A**	**B**	**C**	**D**
(*n* = 8)	**(*n* = 15)**	**(*n* = 23)**	**(*n* = 2)**	**(*n* = 12)**	**(*n* = 33)**	**(*n* = 11)**	**(*n* = 4)**
0.3 ± 0.5	37.1 ± 26.6	34.5 ± 28.0	0.5 ± 6.3	1.9 ± 1.7	53.5 ± 31.5	36.9 ± 40.3	3.3 ± 3.8
	WR		**2015**		**FR**		
A	**B**	**C**	**D**	**A**	**B**	**C**	**D**
(*n* = 10)	(*n* = 18)	(*n* = 23)	(*n* = 9)	(*n* = 12)	(*n* = 33)	(*n* = 11)	(*n* = 4)
0.1 ± 0.2	8.8 ± 6.9	7.4 ± 4.3	0.0 ± 0.0	6.9 ± 4.3	23.0 ± 4.8	22.1 ± 5.8	1.5 ± 3.7

the exclusion nets were intact (Fig. 11), demonstrates the important role predators play in controlling clam sizes leading into and through the winter. Similarly, the largest clams in recruitment boxes were significantly smaller in EU with the larger aperture (and where green crab density was 4× higher) than in EU with the smaller (PS) aperture netting (Fig. 17).

Green crab CW were highly variable, ranging from 3 to 25 mm across sites and predator-exclusion treatments in Exps I and II (Figs. 6 and 10, respectively). In 2015, crabs size, pooled across all EU (Exp. IV), ranged in CW from 1.8 to 46.6 mm (Fig. 18; mean CW of 16.4 ± 2.3 mm, $N = 96$), with the largest animals and fewest clam recruits occurring in recruitment boxes with the larger aperture regardless of location or side of the river they were deployed (Fig. 13). Because sediments were not added to recruitment boxes, and none of the deterrent netting on any of the boxes was compromised, crabs could only have been a certain minimum size on entering a box. That is, crabs no larger than 9.1 and 1.9 mm could have entered boxes through the larger and smaller exclusion netting, respectively. This suggests that the largest crab (46.6-mm CW) from a box with extruded mesh (aperture = 6.4 mm) grew at least 37.5 mm in CW over the 211 days from April to November 2015. The largest individual in boxes protected with PS was 31.7 mm in CW, suggesting a growth rate of at least 29.8 mm in CW over that same period. These growth rates are much faster than those observed by Berrill (1982) during a time when coastal seawater temperatures in Maine were cooler than at present (Drinkwater & Petrie 2011), suggesting that increasing seawater temperatures along the Maine coast during the past decades could have resulted in an increase in the growth rate of a major predator of *Mya arenaria* and/or that physiological plasticity (Tepolt & Somero 2014) has enabled green crabs to become more tolerant/better adapted to the warmer seawater conditions that now exist along the southern Maine coast.

Management Considerations

Softshell clams are commercially harvested in the soft-bottom intertidal zone in Maine and northern New England (Hanna 1998) where they are associated with an annual, multimillion fishery (Maine Department of Marine Resources 2017). Commercial clam landings in Maine have dropped precipitously during the last decade, especially in southern Maine where green crab densities have increased (McClenachan et al. 2015) to levels similar to those observed in the early 1950s when coastwide landings dropped 78% (15,500 to 3,400 mt) from 1950 to 1959 (Glude 1955). Results from field experiments presented here suggest that current predation rates are so severe that they limit recruitment success to such a degree that less than 0.01% of 0-y class individuals survive beyond their first year. Coastal communities manage clam populations within their geographic and political jurisdiction cooperatively with the state of Maine through its Department of Marine Resources. A number of management tools are used by Maine communities, but these are no different than those used in the 1960s and 1970s when clam populations were historically high, seawater temperatures were significantly lower, and invasive green crab populations were scarce or totally absent along most of the Maine coast (Welch 1968). These tools vary from restricting all harvesting in defined areas for 6 mo or longer ("conservation closures"), erecting structures to slow currents in hopes that clams will settle in those areas (known as "brushing"—see Beal et al. 2016), to transplanting small clams (<30 mm SL) from areas of high densities (typically in the high intertidal) to the mid and lower intertidal where growth rates are faster (Beal et al. 2001). As seawater temperatures in the Gulf of Maine continue to warm, unless some disease or other invasive species reduces green crab numbers significantly, this species will continue to be the major predator of softshell clams, and impediment to increasing commercial harvests. Current co-management efforts must adapt to present environmental and biological conditions or risk watching the fishery decline to levels that are no longer commercially viable. Allowing flats to fallow for conservation purposes, erecting structures to enhance recruitment or transplanting clams without subsequently protecting them are exercises that benefit predators rather than sustain or enhance the fishery for harvesters. For example, core samples taken from ambient sediments in the HR (2014–2015) demonstrate clearly the effectiveness of traditionally managed areas. Few adult clams (on average, <1 ind. m^{-2}) were found in over 250 core samples, yet similar size core samples contained, on average, as many as 19,000 recruits of *Mya* (Exp. III), and recruitment boxes protected with PS on the east side of HR (Exp. IV) contained as many as 2,300 recruits/0.15 m^2. These observations provide clarity on two important aspects of current management practices. First, recruitment is independent of local adult clam biomass, suggesting that limiting effort by restricting access to intertidal flats (either through licensing or conservation closures) should not be a primary focus of co-management practices. Second, if results presented here from the three tidal estuaries are generalizable and scalable to larger areas, then with some effort, communities could discover local areas of intense natural recruitment, and then transplant the recruits in small, protected, manageable plots (*sensu* Beal et al. 2016) that could then be harvested sometime within the following 2 y. Whereas these activities would be untraditional in the sense of current management practices, and, perhaps socially unacceptable, it is clear the status quo, at least along the southern Maine coast, likely will result in an unsustainable fishery.

CONCLUSIONS

Few studies have investigated mechanisms in the field to help explain the observed patterns of both juvenile and adults of *Mya arenaria* in the Northwest Atlantic (but see Hunt & Mullineaux 2002, Green et al. 2009, 2013). The work presented here extends knowledge about the role that post-settlement events such as predation play in shaping distribution and abundance patterns of softshell clam recruits in three tidal estuaries in southern Maine. In addition to traditional predator-exclusion studies, a novel method (completely protected, initially empty epibenthic settlement traps—recruitment boxes) was used that integrated the settlement and recruitment of as many as 18 molluscan species, including *M. arenaria*, over 6 mo. Results from all six field experiments provide convincing evidence that predation on small recruits, especially by green crabs, is an important post-settlement process that helps explain the nature of spatial and temporal variation of 0-y class cohorts of the softshell clam. Predation on 0-y class individuals ultimately affects distribution and abundance of older animals, but can be offset or ameliorated by high levels of recruitment; however, recruitment rates of *Mya* as high as nearly 20,000 ind. m^{-2} were observed in protected field plots in the HR (Freeport) that occurred next to unprotected, ambient sediments containing fewer than 20 ind. m^{-2}. This suggests that mortality rates approaching >99.9% reduce annual cohort strength well below carrying capacity, and limit greatly the extent of ecosystem services (e. g., reducing turbidity that enhances water clarity, producing biodeposits that contain nutrients and organic carbon that induce denitrification, and other biogeochemical functions that couple the water column to the bottom), that otherwise would be provided by this suspension feeder. Losses of this magnitude, that likely are not limited to softshell clams but other intertidal organisms as well, can initiate a cascade effect with negative consequences on biodiversity and ecosystem function similar to that described by Van Colen et al. (2015) and Beukema and Dekker (2006). Traditional management practices with the goal of sustaining or enhancing the softshell clam fishery along the southern Maine coast require severe modifications that are adaptive with respect to current environmental and biological parameters.

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LITERATURE CITED

Abbott, R. T. 1974. American seashells, 2nd edition. New York, NY: Van Nostrand Reinhold. 663 pp.

Ambrose, W. G. 1984. Role of predatory infauna in structuring marine soft-bottom communities. *Mar. Ecol. Prog. Ser.* 17:109–115.

André, C. & R. Rosenberg. 1991. Adult-larval interactions in the suspension-feeding bivalves *Cerastoderma edule* and *Mya arenaria*. *Mar. Ecol. Prog. Ser.* 71:227–234.

Andresen, H. & J. van der Meer. 2010. Brown shrimp (*Crangon crangon* L.) functional response to density of different sized juvenile bivalves *Macoma balthica* (L.). *J. Exp. Mar. Biol. Ecol.* 390:31–38.

Armonies, W. 1996. Changes in distribution patterns of 0-group bivalves in the Wadden Sea: byssus-drifting releases juveniles from constraints of hydrography. *J. Sea Res.* 35:323–334.

Beal, B. F. 2006a. Biotic and abiotic factors influencing growth and survival of wild and cultured individuals of the softshell clam (*Mya arenaria* L.) in eastern Maine. *J. Shellfish Res.* 25:461–474.

Beal, B. F. 2006b. Relative importance of predation and intraspecific competition in regulating growth and survival of juveniles of the softshell clam, *Mya arenaria* L., at several spatial scales. *J. Exp. Mar. Biol. Ecol.* 336:1–17.

Beal, B. F., R. Bayer, M. G. Kraus & S. R. Chapman. 1999. A unique shell marker in juvenile, hatchery-reared individuals of the softshell clam, *Mya arenaria* L. *Fish Bull.* 97:380–386.

Beal, B. F. & M. G. Kraus. 2002. Interactive effects of initial size, stocking density, and type of predator deterrent netting on survival and growth of cultured juveniles of the softshell clam, *Mya arenaria* L., in eastern Maine. *Aquaculture* 208:81–111.

Beal, B. F., D.-M. Nault, H. Annis, P. Thayer, H. Leighton & B. Ellis. 2016. Comparative, large-scale field trials along the Maine coast to assess management options to enhance populations of the commercially important softshell clam, *Mya arenaria* L. *J. Shellfish Res.* 35:711–727.

Beal, B. F., M. R. Parker & K. W. Vencile. 2001. Seasonal effects of intraspecific density and predator exclusion along a shore-level gradient on survival and growth of juveniles of the softshell clam, *Mya arenaria* L., in Maine, USA. *J. Exp. Mar. Biol. Ecol.* 264:133–169.

Berrill, M. 1982. The life cycle of the green crab *Carcinus maenas* at the northern end of its range. *J. Crustac. Biol.* 2:31–39.

Beukema, J. J. & R. Dekker. 2006. Annual cockle *Cerastoderma edule* production in the Wadden Sea usually fails to sustain both wintering birds and a commercial fishery. *Mar. Ecol. Prog. Ser.* 309:189–204.

Beukema, J. J. & R. Dekker. 2014. Variability in predator abundance links winter temperatures and bivalve recruitment: correlative evidence from long-term data in a tidal flat. *Mar. Ecol. Prog. Ser.* 513:1–15.

Bottom, M. L. 1984. The importance of predation by horseshoe crabs, *Limulus polyphemus*, to an intertidal sand flat community. *J. Mar. Res.* 42:139–161.

Bourque, D., G. Miron & T. Landry. 2001. Predation on softshell clams (*Mya arenaria*) by the nemertean *Cerebratulus lacteus* in Atlantic Canada: implications for control measures. *Hydrobiologia* 456:33–44.

Bowen, J. E. & H. L. Hunt. 2009. Settlement and recruitment patterns of the softshell clam, *Mya arenaria*, on the northern shore of the Bay of Fundy, Canada. *Estuaries Coasts* 32:758–772.

Brousseau, D. J. 1978. Spawning cycle, fecundity, and recruitment in a population of softshell clam, *Mya arenaria*, from Cape Ann, Massachusetts. *Fish Bull.* 76:155–166.

Butman, C. A. 1987. Larval settlement of soft-sediment invertebrates—the spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. *Oceanogr. Mar. Biol.* 25:113–165.

Carlton, J. T. & J. Hodder. 2003. Maritime mammals: terrestrial mammals as consumers in marine intertidal communities. *Mar. Ecol. Prog. Ser.* 256:271–286.

Castorani, M. C. N., R. N. Glud, H. Hasler-Sheetal & M. Holmer. 2015. Light indirectly mediates bivalve habitat modification and impacts on seagrass. *J. Exp. Mar. Biol. Ecol.* 472:41–53.

Clements, J. C. & H. L. Hunt. 2014. Influence of sediment acidification and water flow on sediment acceptance and dispersal of juvenile softshell clams (*Mya arenaria* L.). *J. Exp. Mar. Biol. Ecol.* 453: 62–69.

Commito, J. A. 1982. Effects of *Lunatia heros* predation on the population dynamics of *Mya arenaria* and *Macoma balthica* in Maine, USA. *Mar. Biol.* 69:187–193.

Commito, J. A. & E. M. Boncavage. 1989. Suspension-feeders and coexisting infauna: an enhancement counterexample. *J. Exp. Mar. Biol. Ecol.* 125:33–42.

Degraer, S., P. Meire & M. Vincx. 2007. Spatial distribution, population dynamics and productivity of *Spisula subtruncata*: implications for fisheries in seaduck wintering areas. *Mar. Biol.* 152:863–875.

Dekker, R. & J. J. Beukema. 2007. Long-term and large-scale variability in productivity of the tellinid bivalve *Macoma balthica* on Wadden Sea tidal flats. *Mar. Ecol. Prog. Ser*. 337:117–134.

de Montadouin, X. & G. Bachelet. 1996. Experimental evidence of complex interactions between biotic and abiotic factors in the dynamics of an intertidal population of the bivalve *Cerastoderma edule*. *Oceanol. Acta* 19:449–463.

Dethier, M. N., J. Ruesink, H. Berry & A. G. Sprenger. 2012. Decoupling of recruitment from adult clam assemblages along an estuarine shoreline. *J. Exp. Mar. Biol. Ecol*. 422–423:48–54.

Doering, P. H., J. R. Kelly, C. A. Oviatt & T. Sowers. 1987. Effect of the hard clam *Mercenaria mercenaria* on benthic fluxes of inorganic nutrients and gases. *Mar. Biol*. 94:377–383.

Donadi, S., J. Westra, E. J. Weerman, T. van der Heide, E. M. van der Zee, J. van de Koppel, H. Olff, T. Piersma, H. W. van der Veer & B. K. Eriksson. 2013. Non-trophic interactions control benthic producers on intertidal flats. *Ecosystems (N. Y.)* 16:1325–1335.

Drinkwater, K. F. & B. Petrie. 2011. A note on the long-term sea surface temperature records at Boothbay Harbor, Maine. *J. Northwest Atl. Fish. Sci*. 43:93–101.

Dunn, R., L. S. Mullineaux & S. W. Mills. 1999. Resuspension of postlarval softshell clams *Mya arenaria* through disturbance by the mud snail *Ilyanassa obsoleta*. *Mar. Ecol. Prog. Ser*. 180:223–232.

Emerson, C. W. & J. Grant. 1991. The control of softshell clam (*Mya arenaria*) recruitment on intertidal sandflats by bedload transport. *Limnol. Oceanogr*. 36:1288–1300.

Fernandez, I. J., C. V. Schmitt, S. D. Birkel, E. Stancioff, A. J. Pershing, J. T. Kelley, J. A. Runge, G. L. Jacobson & P. A. Mayewski. 2015. Maine's climate future: 2015 update. Available at: http://cci.siteturbine.com/uploaded_files/climatechange.umaine.edu/files/MainesClimateFuture_2015_Update2.pdf.

Flach, E. C. 2003. The separate and combined effects of epibenthic predation and presence of macro-infauna on the recruitment success of bivalves in shallow soft-bottom areas on the Swedish west coast. *J. Sea Res*. 49:59–67.

Folk, R. L. 1980. Petrology of sedimentary rocks, 3rd edition. Austin, TX: Hemphill Publishing Co. 185 pp.

Gerasimova, A. V., N. V. Maximovich & N. A. Filippova. 2015. Cohort life tables for a population of the softshell clam, *Mya arenaria* L., in the White Sea. *Helgol. Mar. Res*. 69:147–158.

Glude, J. B. 1955. The effects of temperature and predators on the abundance of the softshell clam, *Mya arenaria*, in New England. *Trans. Am. Fish. Soc*. 84:13–26.

Gosselin, L. A. & P. Y. Qian. 1997. Juvenile mortality in benthic marine invertebrates. *Mar. Ecol. Prog. Ser*. 146:265–282.

Green, M. A., M. E. Jones, C. L. Boudreau, R. L. Moore & B. A. Westman. 2003. Dissolution mortality of juvenile bivalves in coastal marine deposits. *Limnol. Oceanogr*. 49:727–734.

Green, M. A., G. G. Waldbusser, L. Hubazc, E. Cathcart & J. Hall. 2013. Carbonate mineral saturation state as the recruitment cue for settling bivalves in marine muds. *Estuaries Coasts* 36:18–27.

Green, M. A., G. G. Waldbusser, S. L. Reilly, K. Emerson & S. O'Donnell. 2009. Death by dissolution: sediment saturation state as a mortality factor for juvenile bivalves. *Limnol. Oceanogr*. 54:1037–1047.

Gribben, P. E. & J. T. Wright. 2006. Invasive seaweed enhances recruitment of a native bivalve: role of refuge from predation and the habitat choice of recruits. *Mar. Ecol. Prog. Ser*. 318:177–185.

Günther, C.-P. 1992. Settlement and recruitment of *Mya arenaria* L. in the Wadden Sea. *J. Exp. Mar. Biol. Ecol*. 159:203–215.

Hanna, S. S. 1998. Managing for human and ecological context in the Maine soft shell clam fishery. In: Berkes, F., C. Folk & J. Colding, editors. Linking social and ecological systems: management practices and social mechanisms for building resilience. Cambridge, UK: Cambridge University Press. pp. 190–211.

Hiddink, J. G., R. ter Hofstede & W. J. Wolff. 2002. Predation of intertidal infauna on juveniles of the bivalve *Macoma balthica*. *J. Sea Res*. 47:141–159.

Hunt, H. L. 2005. Effects of sediment source and flow regime on clam and sediment transport. *Mar. Ecol. Prog. Ser*. 296:143–153.

Hunt, H. L., A. D. McLean & L. S. Mullineaux. 2003. Post-settlement alteration of spatial patterns of soft shell clam (*Mya arenaria*) recruits. *Estuaries* 26:72–81.

Hunt, H. L. & L. S. Mullineaux. 2002. The roles of predation and postlarval transport in recruitment of benthic marine invertebrates. *Limnol. Oceanogr*. 47:151–164.

Irlandi, E. A. 1994. Large- and small-scale effects of habitat structure on rates of predation: how percent coverage of seagrass affects rates of predation and siphon nipping on an infaunal bivalve. *Oecologia* 98:176–183.

Jennings, L. B. & H. L. Hunt. 2009. Distances of dispersal of juvenile bivalves (*Mya arenaria* Linnaeus), *Mercenaria mercenaria* (Linnaeus), *Gemma gemma* (Totten). *J. Exp. Mar. Biol. Ecol*. 376:76–84.

Jones, H. F. E., C. A. Pilditch, K. R. Bryan & D. P. Hamilton. 2011. Effects of infaunal bivalve density and flow speed on clearance rates and near-bed hydrodynamics. *J. Exp. Mar. Biol. Ecol*. 401:20–28.

Kelso, W. E. 1979. Predation on softshell clams, *Mya arenaria*, by the common mummichog, *Fundulus heteroclitus*. *Estuaries* 2:249–254.

Kenaya, G. 2014. Effects of infaunal bivalves on associated macrozoobenthic communities in estuarine soft-bottom habitats: a bivalve addition experiment in a brackish lagoon. *J. Exp. Mar. Biol. Ecol*. 457:180–189.

Komorita, T., R. Kajihara, H. Tsutsumi, S. Shibanuma, T. Yamada, N. Higaki & S. Montani. 2010. Reevaluation of the nutrient mineralization process by infaunal bivalves (*Ruditapes philippinarum*) in a shallow lagoon in Hokkaido, Japan. *J. Exp. Mar. Biol. Ecol*. 383:8–16.

Kotta, J., K. Herkul, I. Kotta, H. Orav-Kotta & V. Lauringson. 2009. Effects of the suspension feeding mussel *Mytilus trossulus* on a brackish water macroalgal and associated invertebrate community. *Mar. Ecol. (Berl.)* 30:56–64.

Kube, J. 1996. Spatial and temporal variations in the population structure of the softshell clam *Mya arenaria* in the Pomeranian Bay (southern Baltic Sea). *J. Sea Res*. 35:335–344.

Landry, S. & G. Miron. 2011. Effect of vertical planktonic distribution of competent larvae on spat location in a soft-bottom intertidal zone: a case study for the softshell clam (*Mya arenaria*) and the blue mussel (*Mytilus edulis*). *J. Exp. Mar. Biol. Ecol*. 410:87–100.

Larsen, J. K. & M. Guillemette. 2000. Influence of annual variation in food supply on abundance of wintering common eiders *Somateria mollissima*. *Mar. Ecol. Prog. Ser*. 201:301–309.

LeBlanc, S. & G. Miron. 2006. Bentho-pelagic distribution of early stages of softshell clams (*Mya arenaria*) in tidally contrasted regimes. *Can. J. Zool*. 84:459–472.

MacKenzie, R. A. & M. Dionne. 2008. Habitat heterogeneity: importance of salt marsh pools and high marsh surfaces to fish production in two Gulf of Maine salt marshes. *Mar. Ecol. Prog. Ser*. 368:217–230.

Maine Department of Marine Resources. 2017. Marine resources. Available at: http://www.maine.gov/dmr/commercial-fishing/landings/index.html.

McClenachan, L., G. O'Connor & T. Reynolds. 2015. Adaptive capacity of co-management systems in the face of environmental change: the softshell clam fishery and invasive green crabs in Maine. *Mar. Policy* 52:26–32.

Michaud, E., G. Desrosiers, F. Mermillod-Blondin, B. Sundby & G. Stora. 2006. The functional group approach to bioturbation: II. The effects of the *Macoma balthica* community on fluxes of nutrients and dissolved organic carbon across the sediment-water interface. *J. Exp. Mar. Biol. Ecol*. 337:178–189.

Miller, C. A. & G. G. Waldbusser. 2016. A post-larval stage-based model of hard clam *Mercenaria mercenaria* development in response to multiple stressors: temperature and acidification severity. *Mar. Ecol. Prog. Ser.* 558:35–49.

Möller, P. 1986. Physical factors and biological interactions regulating infauna in shallow boreal areas. *Mar. Ecol. Prog. Ser.* 30:33–47.

Morgan, P. A., M. Dionne, R. MacKenzie & J. Miller. 2015. Exploring the effects of shoreline development on fringing salt marshes using nekton, benthic invertebrate, and vegetation metrics. *Estuaries Coasts* 38:1274–1287.

Morgan, S. G., J. L. Fisher & A. J. Mace. 2009. Larval recruitment in a region of strong, persistent upwelling and recruitment limitation. *Mar. Ecol. Prog. Ser.* 394:79–99.

Morse, B. L. & H. L. Hunt. 2013. Impact of settlement and early post-settlement events on spatial distribution of juvenile *Mya arenaria* on an intertidal shore. *J. Exp. Mar. Biol. Ecol.* 448:57–65.

Munroe, D., J. Kraeuter, B. Beal, K. Chew, M. Luckenbach & C. P. Peterson. 2015. Clam predator protection is effective and necessary for food production. *Mar. Pollut. Bull.* 100:47–52.

Munroe, D. & R. S. McKinley. 2007. Effect of predator netting on recruitment and growth of manila clams (*Venerupis philippinarum*) on soft substrate intertidal plots in British Columbia, Canada. *J. Shellfish Res.* 26:1035–1044.

Neter, J., W. Wasserman & M. H. Kutner. 1990. Applied linear statistical models: regression, analysis of variance, and experimental designs, 3rd edition. Homewood, IL: Richard D. Irwin, Inc. 1181 pp.

Newell, C. R. & H. Hidu. 1986. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic)—softshell clam. U.S. Fish Fish Wildl. Serv. Biol. Rep. 82 (11.53). U.S. Army Corps of Engineers, TR EL-82-24. 17 pp.

Ólafsson, E. B., C. H. Peterson & W. G. Ambrose, Jr. 1994. Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: the relative significance of pre- and post-settlement processes. *Oceanogr. Mar. Biol. Annu. Rev.* 32:65–109.

Pershing, A. J., M. A. Alexander, C. M. Hernandez, L. A. Kerr, A. Le Bris, K. E. Mills, J. A. Nye, N. R. Record, H. A. Scannell, J. D. Scott, G. D. Sherwood & A. C. Thomas. 2015. Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. *Science* 350:809–812.

Peterson, B. J. & K. L. Heck, Jr. 1999. The potential for suspension feeding bivalves to increase seagrass productivity. *J. Exp. Mar. Biol. Ecol.* 240:37–52.

Peterson, C. H. 1982. The importance of predation and intra- and interspecific competition in the population biology of two infaunal suspension-feeding bivalves, *Protothaca staminea* and *Chione undatella. Ecol. Monogr.* 52:437–475.

Peterson, C. H. & R. Black. 1993. Experimental tests of the advantages and disadvantages of high density for two coexisting cockles in a Southern Ocean lagoon. *J. Anim. Ecol.* 62:614–633.

Polyakov, O., J. N. Kraeuter, E. E. Hofmann, S. C. Buckner, V. M. Bricelj, E. N. Powell & J. M. Klinck. 2007. Benthic predators and northern quahog (= hard clam) (*Mercenaria mercenaria* Linnaeus, 1758) populations. *J. Shellfish Res.* 26:995–1010.

Rathbun, M. J. 1905. Fauna of New England. Crustacea. *Occ. Papers Boston Soc. Nat. Hist.* 7:1–117.

Richards, M. G., M. Huxham & A. Bryant. 1999. Predation: a causal mechanism for variability in intertidal bivalve populations. *J. Exp. Mar. Biol. Ecol.* 241:159–177.

Ropes, J. W. 1968. The feeding habits of the green crab, *Carcinus maenas* (L.). *Fish Bull.* 67:183–203.

Ropes, J. W. & A. P. Stickney. 1965. Reproductive cycle of *Mya arenaria* in New England. *Biol. Bull.* 128:315–327.

Rowell, T. W. & P. Woo. 1990. Predation by the nemertean worm, *Cerebratulus lacteus* Verrill, on the softshell clam, *Mya arenaria* Linnaeus, 1758, and its apparent role in the destruction of a clam flat. *J. Shellfish Res.* 9:291–297.

Sandwell, D. R., C. A. Pilditch & A. M. Lohrer. 2009. Density dependent effects of an infaunal suspension-feeding bivalve (*Austrovenus stutchburyi*) on sandflat nutrient fluxes and microphytobenthic productivity. *J. Exp. Mar. Biol. Ecol.* 373:16–25.

Seitz, R. D., R. N. Lipcius & A. H. Hines. 2016. Consumer versus resource control and the importance of habitat heterogeneity for estuarine bivalves. *Oikos* 126:121–135.

Shaw, R. G. & T. Mitchell-Olds. 1993. ANOVA for unbalanced data: an overview. *Ecology* 74:1638–1645.

Snelgrove, P. V. R., J. Grant & C. A. Pilditch. 1999. Habitat selection and adult-larvae interactions in settling larvae of softshell clam *Mya arenaria. Mar. Ecol. Prog. Ser.* 182:149–159.

Stickney, A. P. 1964. Salinity, temperature, and food requirements of softshell clam larvae in laboratory culture. *Ecology* 45:283–291.

Strasser, M. L. 2002. Reduced epibenthic predation on intertidal bivalves after a severe winter in the European Wadden Sea. *Mar. Ecol. Prog. Ser.* 241:113–123.

Strasser, M., R. Dekker, K. Essink, C.-P. Günther, S. Jacklin, I. Kröncke, P. Brinch Madsen, H. Michaelis & G. Vedel. 2003. How predictable is high bivalve recruitment in the Wadden Sea after a severe winter? *J. Sea Res.* 49:47–57.

Strasser, M. & C.-P. Günther. 2001. Larval supply of predator and prey: temporal mismatch between crabs and bivalves after a severe winter in the Wadden Sea. *J. Sea Res.* 46:57–67.

Strasser, M., M. Walensky & K. Reise. 1999. Juvenile-adult distribution of the bivalve *Mya arenara* on intertidal flats in the Wadden Sea: why are there so few year classes? *Helgol. Mar. Res.* 53:45–55.

Tan, E. B. P. & B. F. Beal. 2015. Interactions between the invasive European green crab, *Carcinus maenas* (L.), and juveniles of the softshell clam, *Mya arenaria* L., in eastern Maine. *J. Exp. Mar. Biol. Ecol.* 462:62–73.

Tepolt, C. K. & G. N. Somero. 2014. Master of all trades: thermal acclimation and adaptation of cardiac function in a broadly distributed marine invasive species, the European green crab, *Carcinus maenas. J. Exp. Biol.* 217:1129–1138.

Tezuka, N., S. Kamimura, M. Hamaguchi, H. Saito, H. Iwano, J. Egashira, Y. Fukudu, T. Tawaratsumida, A. Nagamoto & K. Nakagawa. 2012. Settlement, mortality and growth of the asari clam (*Ruditapes philippinarum*) for a collapsed population on a tidal flat in Nakatsu, Japan. *J. Sea Res.* 69:23–35.

Thrush, S. F., J. E. Hewitt, M. Gibbs, C. Lundquist & A. Norkko. 2006. Functional role of large organisms in intertidal communities: community effects and ecosystem function. *Ecosystems (N. Y.)* 9:1029–1040.

Thrush, S. F., J. E. Hewitt, R. D. Pridmore & V. J. Cummings. 1996. Adult/juvenile interactions of infaunal bivalves: contrasting outcomes in different habitats. *Mar. Ecol. Prog. Ser.* 132: 83–92.

True, E. D. 2013. Tracking the discharge of a waste water treatment plant in Casco Bay, Maine with a numerical coastal model. Available at: http://casconorwich.org/pdf/Har2.pdf.

Underwood, A. J. 1997. Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge, UK: Cambridge University Press. 504 pp.

Van Colen, C., S. F. Thrush, S. Parkes, R. Harris, S. A. Woodin, D. S. Wethey, C. A. Pilditch, J. E. Hewitt, A. M. Lohrer & M. Vincx. 2015. Bottom-up and top-down mechanisms indirectly mediate interactions between benthic biotic ecosystem components. *J. Sea Res.* 98:42–48.

van der Heide, T., E. Tielens, E. M. van der Zee, E. J. Weerman, S. Holthuijsen, B. Klemens Eriksson, T. Piersma, J. van de Koppel & H. Olff. 2014. Predation and habitat modification synergistically interact to control bivalve recruitment on intertidal flats. *Biol. Conserv.* 172:163–169.

Vassiliev, T., S. R. Fegley & W. R. Congleton. 2010. Regional differences in initial settlement and juvenile recruitment of *Mya arenaria* L. (softshell clam) in Maine. *J. Shellfish Res.* 29:337–346.

Virnstein, R. W. 1977. The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. *Ecology* 58:1199–1217.

Watzin, M. 1986. Larval settlement into marine soft-sediment systems: interactions with the meiofauna. *J. Exp. Mar. Biol. Ecol.* 98:65–113.

Welch, W. R. 1968. Changes in abundance of the green crab, *Carcinus maenas* (L.), in relation to recent temperature changes. *Fish Bull.* 67:337–345.

Whitlach, R. B., A. H. Hines, S. F. Thrush, J. E. Hewitt & V. Cummings. 1997. Benthic faunal responses to variation in patch density and patch size of a suspension-feeding bivalve. *J. Exp. Mar. Biol. Ecol.* 216:171–189.

Whitlow, W. L. 2010. Changes in survivorship, behavior, and morphology in native softshell clams induced by invasive green crab predators. *Mar. Ecol. (Berl.)* 31:418–430.

Whitlow, W. L. & J. H. Grabowski. 2012. Examining how landscapes influence benthic community assemblages in seagrass and mudflat habitats in southern Maine. *J. Exp. Mar. Biol. Ecol.* 411:1–6.

Winer, B. J., D. R. Brown & K. M. Michels. 1991. Statistical principles in experimental design, 3rd edition. New York, NY: McGraw-Hill. 1057 pp.

Woodin, S. A. 1976. Adult-larval interactions in dense infaunal assemblages: patterns of abundance. *J. Mar. Res.* 34:25–41.