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Interactive effects of tidal height and predator exclusion on growth and survival of wild and cultured juveniles of the soft-shell clam, *Mya arenaria* L., at two intertidal flats in southern Maine



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10 February 2015

Summary

A comparative field experiment was initiated at two intertidal flats in southern Maine (Wells – Webhannet River; Portland – Fore River) in May 2014 to examine the interactive effects of tidal height and predator exclusion on the growth and survival of cultured individuals of the soft-shell clam, *Mya arenaria* L. ($\bar{x}_{\text{Shell length}} = 12.95 \pm 0.20$ mm). Experimental units (0.018 m²) were placed near the upper and lower intertidal and filled with ambient sediments at both sites. Clams were added to units at a density of 660 ind. m⁻². Predator exclusion included five treatments: 1) none (controls); 2) flexible netting (4.2 mm aperture); 3) flexible and rigid netting (6.4 mm); 4) Pet screen over the top of the units; and 5) Pet screen over the top and bottom of the units. Netting was designed to exclude green crabs, *Carcinus maenas*, whereas Pet screen was designed to exclude crabs and nemertean worms, *Cerebratulus lacteus*. Experimental units at each site were collected in October 2014, after 151 days in the field.

Survival did not vary significantly across tidal heights at either site. Less than 5% of clams in control units were recovered vs. > 50% survival in protected units at both sites. Pet screen did not enhance survival at either site compared with flexible netting. Growth was faster at the lower vs. upper intertidal at one site (by ca. 20%), but not at the other, and was depressed between 50-60% in units protected with Pet Screening compared to open and netted units. Mean final shell length in open and netted units pooled across sites ranged from 25-40 mm. Wild, 0-year class recruits of *Mya* were observed at both sites, and were generally more abundant in lower vs. upper intertidal units. Few recruits occurred in control units, but mean abundance of recruits was an order of magnitude greater in units protected with Pet screen (3843.9 ± 1737.9 , n = 44) vs. flexible netting (726.4 ± 400.5 , n = 44) pooled across both sites.

These results suggest that predation on small clams (both cultured and wild) is intense, and can easily explain the recent decline in wild clam populations in many intertidal areas in southern Maine. In this region, most commercial densities of *Mya* occur in narrow bands near the upper intertidal because: 1) this is an area that historically was not harvested due to slow growth rates and small adult size; and 2) predation is less intense at this tidal level since most predators are waterborne and prey mostly during tidal inundation. Large tracts of the intertidal are not amenable to netting and other deterrent measures to reduce predation; however, it is possible for

individuals to manage small areas (ca. 1-3 acres) where either wild or cultured clams can be farmed. Netting applied to small intertidal plots can be used to protect 0-year class wild clams that settle during the late summer into the fall. Data from this study suggests that these plots be deployed below the upper intertidal to maximize numbers of wild seed and their growth.

Introduction

Since 2009, annual landings of soft-shell clams, *Mya arenaria* L., in Maine have averaged 10.6 million pounds worth an average of \$14.6 million. During that period, the fishery has been the second or third most valuable of all commercially-important marine species after lobsters (*Homarus americanus*) and elvers (*Anguilla rostrata*) (ME DMR, 2015). The fishery is co-managed by the State of Maine in cooperation with individual coastal communities that elect a stewardship committee or council to help make management decisions (Beal, 2002).

Recently, traditional clam management activities along the entire coast of Maine have been hampered somewhat due to a population explosion of green crabs, *Carcinus maenas* (L.) (Tan and Beal, 2015) that has been noted coastwide (Webber, 2014). This invasive species was first observed in Maine around 1905 (Scattergood, 1952), and its population numbers correlate directly with seawater temperatures (Glude, 1955; Welch, 1968). Green crabs are eurythermic, and can survive temperatures $< 0^{\circ}\text{C}$ to $> 35^{\circ}\text{C}$ (Hidalgo et al., 2005), but prefer temperatures between $3\text{-}26^{\circ}\text{C}$ (Kern, 2002). In Maine, clam management programs depend on natural recruitment to populate intertidal beds. Depending on tidal height and geographic location along the coast, after 2-5 years these clams can be harvested commercially (clams must first attain a shell length, SL, of 50.8 mm, or 2-inches, before they are considered legal to possess). Although it is not practical to exclude green crabs from large intertidal tracts, to date, most of Maine's coastal communities either have ignored the fact that green crab numbers are high or have decided that there is nothing that can be done to protect their clam resources. The result of this decision has been the loss, in most communities, of commercial clam densities from the mid- to lower intertidal. A recent soft-shell clam population survey in the town of Yarmouth, Maine (MER, 2013) exemplifies the plight of many coastal communities with clamming resources. That study showed a lack of natural recruitment in all but the upper intertidal, and that a subsidy of large, commercial clams are restricted along the upper shore where predation (both by humans

and other predators) is less intense than areas lower in the intertidal. Results from the survey are similar to those from a field experiment in eastern Maine (Beal et al., 2001) demonstrating that juvenile clams are more susceptible to predation along a tidal gradient from the lower shore, where clam mortality is relatively high, to the upper shore, where the opposite is observed.

Repeated, small-scale studies in eastern Maine since the mid-1980's have demonstrated the importance of predators in controlling populations of both wild and cultured soft-shell clams (Beal, 2005, 2006a; Beal and Kraus, 2002; Tan and Beal, 2015). These investigations have shown that flexible netting (polypropylene; 4.2 mm and 6.4 mm aperture) can deter crustacean predators in most habitats resulting in improved survival by as much as 80% over control plots where predators have limitless access to clam juveniles. In addition, the use of netting can result in an enhancement of wild soft-shell clam recruits (0-year class individuals; Beal and Kraus, 2002). Results of these small-scale studies have been applied at larger scales with similar results (Beal, 2014).

Here, a manipulative field experiment was conducted from May to October 2014 in the Webhannet River, Wells, Maine and the Fore River, Portland, Maine to examine the fate of cultured and wild soft-shell clam juveniles at two tidal heights where four different predator exclusion treatments and a control (no predator exclusion) were arrayed in small-scale experimental units.

Methods

A comparative field experiment was deployed at two intertidal locations in southern Maine (Figs. 1-2) to determine the interactive effects of tidal height and different types of predator exclusion on the fate of cultured individuals of the soft-shell clam, *Mya arenaria* L., as well as on the size and density of wild, 0-year class *Mya* recruits (sensu Hunt and Mullineaux, 2002; Beal, 2006a).

At each location, a series of plastic horticultural pots (experimental units – 15 cm diameter x 15 cm deep – as described in Beal et al., 2001) were arrayed at the upper and lower intertidal in three 2 x 5 matrices (1 m spacing between rows and columns) that were 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

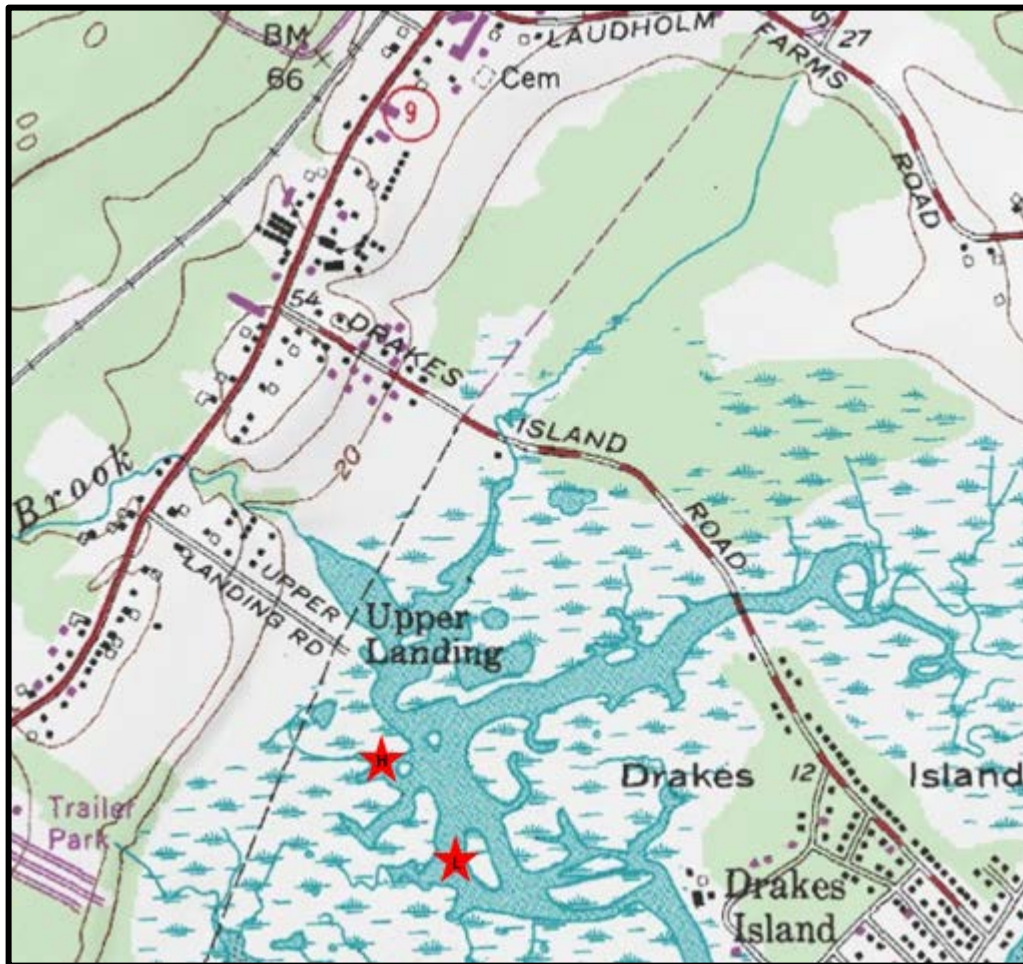


Figure 1. Topographic map showing the approximate areas of the high ($43^{\circ}19'39.1811''\text{N}$; $70^{\circ}33'57.9888''\text{W}$) and low ($43^{\circ}19'37.5900''\text{N}$; $70^{\circ}33'50.4704''\text{W}$) tide blocks in the Webhannet River, Wells, Maine. Experiment was initiated on 12 May 2014, and was carried out until 10 October 2014 (151 days).

ambient sediments (Fig. 3). Twelve cultured individuals of *Mya arenaria* (mean shell length, SL, \pm 95% CI = 12.95 ± 0.20 mm, $n = 451$) from the Downeast Institute for Applied Marine Research & Education (DEI; Great Wass Island, Beals, ME) were added to each experimental unit and gently pushed with fingers 4-6 mm below the sediment surface.

Two replicates of each of five predator exclusion treatments were randomly assigned positions within each matrix (block) at each site and tidal height (Table 1; Fig. 4). Units remained in place for ca. 150 days until each was removed from the sediments and the contents of each washed through a 2 mm sieve (Fig. 5). It was possible to distinguish cultured clams from wild clams because of a distinct disturbance line that forms in the valves of cultured clams upon

placing them in sediments (Fig. 6; see Beal et al., 1999). The “hatchery mark” also allows one to determine an individual growth rate for each whole (live or dead) clam. Therefore, the initial and final SL of each live clam was measured to the nearest 0.01 mm using digital calipers and the final SL of each wild clam was measured similarly. Cultured clams from each experimental unit were placed into four categories: Alive, Dead with undamaged valves, Dead with crushed or chipped valves, or missing. In addition, all wild clams from each experimental unit were enumerated and measured (SL as described above). When number of wild clams per unit exceeded 50, a representative sample of 20 individuals was selected for measurement. Finally, all live green crabs from each unit were enumerated, and the carapace width (CW) of each was measured to the nearest 0.01 mm using digital calipers.

Table 1. Description of the five predator exclusion treatments used in the field experiments (May to October 2014 in the Webhannet and Fore River)

Predator Exclusion Treatment	Description
1) Control	Open unit with piece of 4.2 mm flexible netting ¹ around periphery to keep clams from moving outside of unit. Predators are not excluded (see Tan and Beal, 2015).
2) Flexible Netting	Unit covered completely with a piece of 4.2 mm flexible netting ¹ to exclude large predators.
3) Flexible Netting with VEXAR	Top of unit covered with a piece of 6.4 mm extruded netting ² that was held in place by a piece of 4.2 mm flexible netting ¹ that covered the entire unit. Double layered protection to exclude large predators.
4) Pet screen	Unit covered completely with a piece of Pet screen ³ . Aperture ca. 1.8 mm. Designed to keep out large predators as well as nemertean worms such as <i>Cerebratulus lacteus</i> .
5) Pet screen top & bottom	Unit covered completely with piece of Pet Screen ³ . A circular piece of the same material was inserted into the bottom of the unit prior to adding sediments. This prohibits nemertean and other worms from entering the unit from the bottom.

¹ Polypropylene (OV7100; Industrial netting; <http://www.industrialnetting.com/ov7100.html>).

² Polyethylene (XV1170; Industrial netting; <http://www.industrialnetting.com/xv1170.html>)

³ Pet screen (<http://www.phifer.com/consumerdiy/product/62/petscreen-pet-resistant-screen>)

Analysis of variance was performed on the arcsine-transformed mean percent survival data from both locations separately (to meet assumptions of variance homogeneity) and on the untransformed mean absolute growth (Final SL – Initial SL). In both instances, the following linear model was used:

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

Y_{ijkl} = Dependent variable (survival; growth);

μ = theoretical mean;

A_i = Tidal height ($a = 2$; high vs. low; 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).

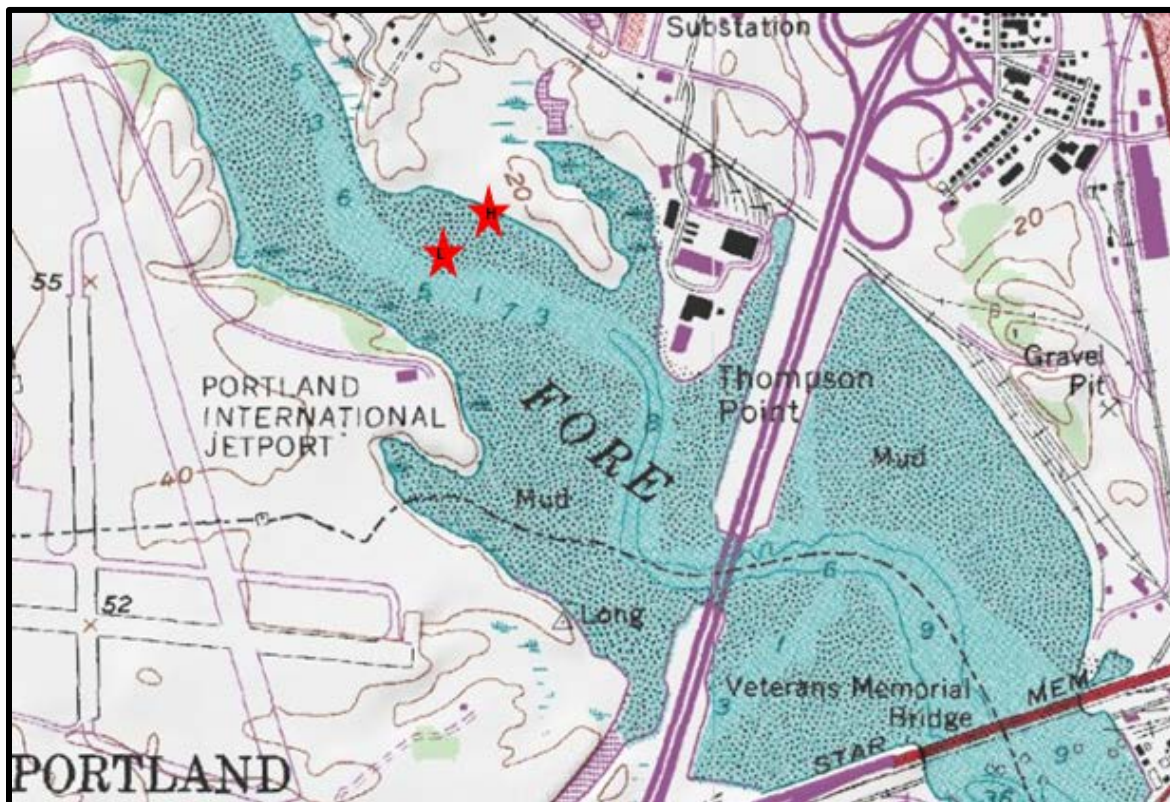


Figure 2. Topographic map showing the approximate areas of the high ($43^{\circ}39'07.4657''N$; $70^{\circ}17'50.5932''W$) and low ($43^{\circ}39'04.0003''N$; $70^{\circ}17'53.2176''W$) tide blocks in the Fore River, Portland, Maine. Experiment was initiated on 13 May 2014, and was carried out until 11 October 2014 (151 days).

Pre-planned, single degree-of-freedom orthogonal contrasts were used to better understand differences in survival and growth among the predator exclusion treatments as defined below:

- 1) Open vs. Protected (examines the importance of predator exclusion netting by comparing the mean of protected vs. control [unnetted] units);
- 2) Pet screen vs. Flexible Netting (examines the mean of the two treatments in which Pet screening is use to exclude predators [> 2.5 mm – distance of the diagonal] vs. the mean of the two treatments in which Flexible Netting is use to exclude larger predators [> 5.9 mm – distance along the diagonal]).
- 3) Flexible vs. Flexible & VEXAR (examines the importance of adding a rigid piece of plastic mesh to units protected with the flexible netting [4.2 mm aperture] vs. units without the rigid mesh netting but that are protected with flexible netting).
- 4) Pet screen vs. Pet screen & Bottom screen (examines the importance of excluding worms such as the nemertean, *Cerebratulus lacteus* from both top and bottom of experimental units vs. excluding worms from entering through the top of the unit).

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 used to determine appropriate mean square estimates for each source of variation.



Figure 3. Setting out experimental units near the upper intertidal in the Webhannet River, Wells, Maine – 12 May 2014.

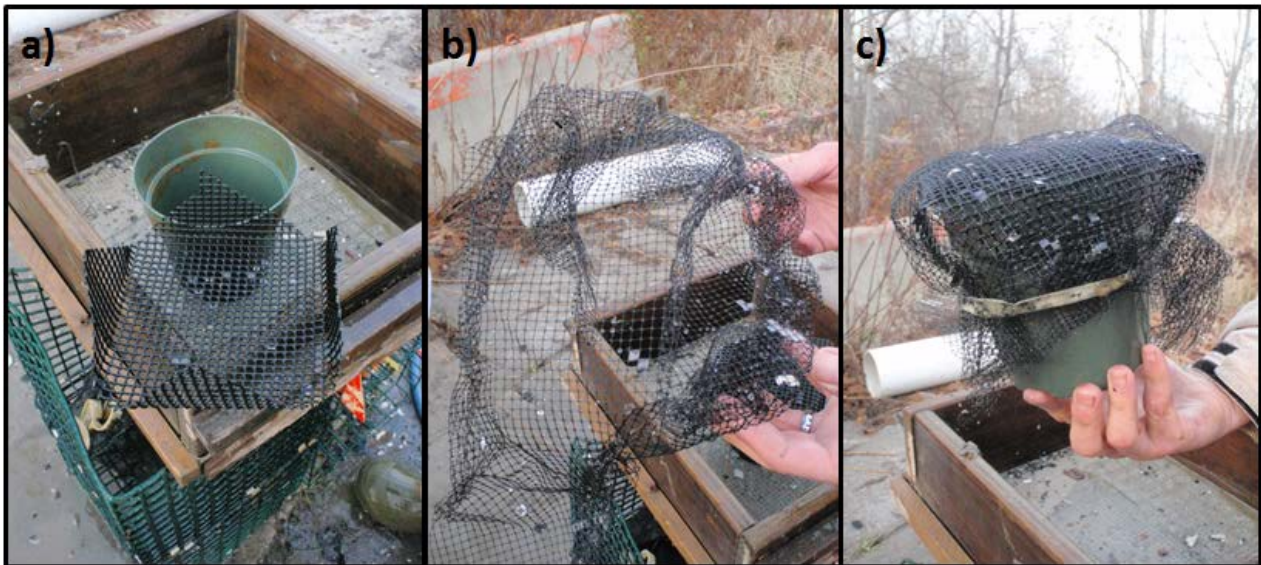


Figure 4. Predator exclusion treatments: a) VEXAR piece (ca. 15 cm x 15 cm); b) Piece of flexible netting; c) Experimental unit with VEXAR and flexible netting (Treatment #3, Table 1).



Figure 5. A sieve with 2 mm mesh used to retain wild and cultured clams from each experimental unit at the end of the field experiment (10-11 October 2014).



Figure 6. The “hatchery mark” that appears in the valves of cultured individuals of the soft-shell clam upon placing them into sediments. The mark allows one to determine the size of an individual at the beginning of the experiment so that an individual growth rate can be estimated for all live individuals at the end of the field trial. Wild clams do not produce as distinct a mark.

Results

Wells (Webhannet River; 12 May to 10 October – 151 days)

A number of experimental units were lost ($n_{\text{high}} = 1$; $n_{\text{low}} = 11$) during the experimental period apparently due to several severe storms and their accompanying tidal surges. Some units that remained through the end of the study, especially those in the lower intertidal, were difficult to find because they were buried under 2-5 cm of sediment. None of the netting on the remaining units was lost or ripped, however.

Mean percent survival (Table 2) did not vary significantly across tidal height ($P = 0.1903$, Table 3; $\bar{x}_{\text{High}} = 63.5 \pm 13.3\%$, $n = 29$; $\bar{x}_{\text{Low}} = 53.9 \pm 18.0\%$, $n = 19$), but did according to predator exclusion treatment (Fig. 7). Only one of the four pre-planned contrasts for the exclusion treatment was statistically significant (Open vs. Protected; Table 3). Mean survival in the protected units ($71.0 \pm 8.8\%$, $n = 40$) was ca. 22x higher than in the open units ($3.1 \pm 5.2\%$, $n = 8$). Milky ribbon worms were found in three of the 48 (6.3%) experimental units retrieved. A single nemertean occurred in one unit at the upper (Flex Net & VEXAR: 2 dead undamaged and 10 live clams) and one in the lower intertidal (Flexible Net: 11 dead undamaged and 1 live clam). One unit in the lower intertidal contained two individuals of *Cerebratulus lacteus* (Flexible Net: 11 dead undamaged, and 1 live clam). No nemerteans were observed in any of the units with Pet screening or the Open (control) units.

Mean absolute shell growth (Table 4) was not affected by tidal position ($P = 0.2725$; Table 5), but the presence of Pet screen depressed growth by ca. 50% from 19.5 ± 3.8 mm ($n = 22$) in open units and those covered with flexible netting vs. 9.8 ± 1.8 mm ($n = 19$) in units protected with the Pet screen (Fig. 8). Mean final SL (Table 4; Fig. 9) was 32.5 ± 1.1 mm ($n = 22$) for clams in the open and flexible netted units vs. 22.0 ± 1.6 mm ($n = 19$) in units with Pet screen.

The effect of predator exclusion on recruitment of 0-year class wild clam juveniles (Table 6) was not the same across tidal heights ($P = 0.0204$; Table 7). Although there was an enhancement of *Mya* recruits in the protected vs. control units at both tidal heights, the effect was more dramatic at the low tide level (Fig. 10). For example, in upper intertidal experimental units, a mean enhancement of nearly 40% occurred between control and protected units (10.9 ± 30.4 ind. m^{-2} , n

= 5 vs. 415.8 ± 137.9 ind. m^{-2} , $n = 24$), whereas in the low intertidal, the mean enhancement was ca. 115% (control = 36.5 ± 157.3 ind. m^{-2} , $n = 3$; protected = 4310.6 ± 3354.1 ind. m^{-2} , $n = 16$). In upper intertidal blocks, no differences were observed in mean numbers of recruits among the protected treatments. In the lower intertidal blocks, however, units protected with Pet screening had approximately 5.5x as many recruits, on average, as units protected with flexible netting ($\bar{x}_{Pet} = 7312.2 \pm 6590.7$ ind. m^{-2} ; $\bar{x}_{Flex} = 1308.9 \pm 1228.2$ ind. m^{-2} ; $n = 8$).

Mean recruit size varied along the tidal gradient ($P < 0.0001$). Mean SL of wild clams in upper intertidal experimental units (14.2 ± 0.92 mm, $n = 181$) was ca 12% smaller than in the lower intertidal (16.1 ± 1.02 mm, $n = 330$). In addition, size distributions of recruits between tidal heights were significantly different (Fig. 11) with a disproportionate percentage of animals > 25 mm SL in the low vs. upper intertidal. Clams in units protected with Pet screen were ca. 40% smaller (11.9 ± 0.6 mm, $n = 270$) than those protected with flexible netting (19.3 ± 1.3 mm, $n = 241$). Distribution of recruit sizes between the two types of netting (Fig. 12) shows that most (81.1%) animals were < 15 mm SL in units covered with Pet screen whereas only 44.8% of recruits in units protected with flexible netting were in this size range.

A total of 62 green crabs occurred in the 48 experimental units recovered at the end of the study. Crabs were found in 29 of the units (ca. 60%). ANOVA on the square root-transformed mean number per unit (Table 8) demonstrated no significant tidal height or treatment effect (mean density per unit = 1.3 ± 0.4 ind., $n = 48$). Mean CW of green crabs varied significantly by tidal height ($P = 0.013$; $\bar{x}_{Upper} = 9.4 \pm 2.4$ mm, $n = 22$; $\bar{x}_{Lower} = 7.8 \pm 3.5$ mm, $n = 7$) but not by predator exclusion treatment ($P = 0.706$). CW size-frequency distribution (Fig. 13) did not differ significantly across tidal heights ($G = 2.8$, $df = 2$, $P = 0.2461$).

Table 2. Cultured individuals of the soft-shell clam, *Mya arenaria*. Mean percent (\pm 95% confidence interval) alive (A), dead individuals with undamaged valves (DU), dead individuals with chipped or crushed valves (DC), and missing individuals (M) at two tidal heights and five predator exclusion treatments in the Webhannet River, Wells, Maine over a 151-day period from 12 May to 10 October 2014. Number of replicates per treatment varies because some experimental units were lost during the experimental period.

Tidal Height	Treatment	n	A	DU	DC	M
	Open (control)	5	5.0(9.3)	1.7(4.6)	0.0(0.0)	93.3(8.7)
	Flexible netting	6	59.7(20.3)	18.1(12.9)	8.3(13.6)	13.9(10.6)
HIGH	Flex net & VEXAR	6	80.6(14.3)	6.9(8.6)	1.4(6.6)	11.1(13.2)
	Pet screen	6	72.2(38.9)	15.3(22.4)	2.8(7.1)	9.7(13.9)
	Pet screen & Bottom	6	90.3(12.9)	2.8(7.1)	0.0(0.0)	6.9(10.2)
	Open (control)	3	0.0(0.0)	0.0(0.0)	0.0(0.0)	100.0(0.0)
	Flexible netting	4	50.0(77.3)	45.8(84.2)	2.1(6.6)	2.1(6.6)
LOW	Flex net & VEXAR	4	95.8(13.3)	4.2(13.3)	0.0(0.0)	0.0(0.0)
	Pet screen	4	62.5(13.3)	20.8(27.6)	4.2(13.3)	1.6(7.1)
	Pet screen & Bottom	4	76.4(23.7)	6.9(11.6)	6.9(17.9)	9.8(11.1)

Table 3. Analysis of variance on the arc sine-transformed mean percent survival of cultured individuals of the soft-shell clam, *Mya arenaria*, in the Webhannet River, Wells, Maine over a 151-day period from 12 May to 10 October 2014. Pre-planned, single degree-of-freedom contrasts appear directly beneath the Treatment source of variation. Boldface P-values are considered statistically significant. Type III sums of squares are used because some treatments were lost causing an unbalanced design (n = 3 to 6). $\alpha' = 0.0127$ for all pre-planned contrasts.

Source of Variation	df	SS	MS	F	Pr > F
Tidal Height	1	849.14	849.14	2.48	0.1903
Treatment	4	22682.85	5670.71	10.93	0.0003
Open vs. Protected	1	20698.61	20698.61	39.89	<.0001
Pet screen vs. Flexible Net	1	252.81	252.81	0.49	0.4966
Flexible vs. Flexible & VEXAR	1	2859.28	2859.28	5.51	0.0341
Pet screen vs. Pet screen & Bottom	1	247.63	247.63	0.48	0.5009
Tidal Height x Treatment	4	2615.29	653.82	1.26	0.3315
Block(Tidal Height)	4	1368.43	342.11	1.48	0.2470
Treatment x Block(Tidal Height)	14	7264.03	518.86	2.214	0.0488
Experimental Error	20	4637.67	231.88		
Total	47	40811.09			

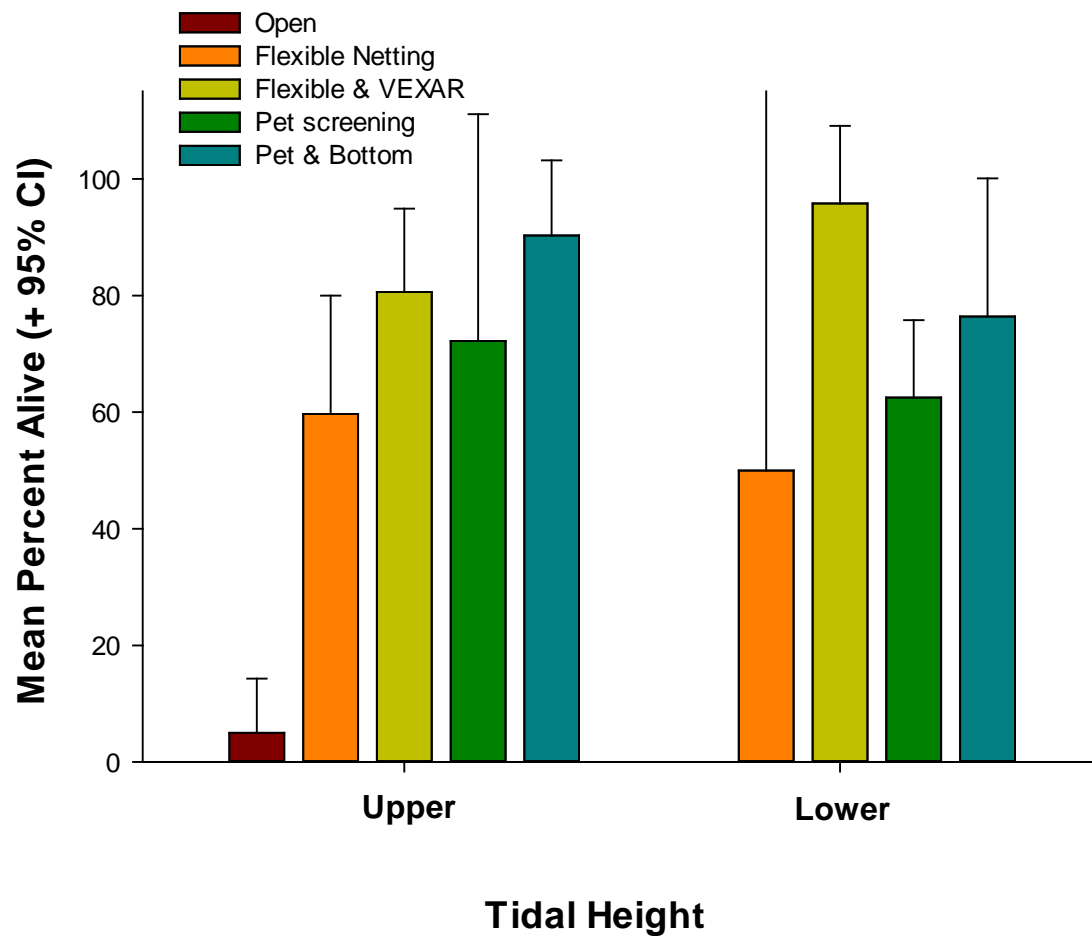


Figure 7. Mean survival of juvenile soft-shell clams (initial mean SL = 12.95 ± 0.20 mm, n = 451) at two tidal heights and five predator exclusion treatments from 12 May to 10 October in the Webhannet River, Wells, Maine. (n = 3 to 6; see Table 2).

Table 4. Cultured individuals of the soft-shell clam, *Mya arenaria*. Mean (\pm 95% confidence interval) absolute growth (final length – initial length) and final shell length of clams in five predator exclusion treatments and at two tidal heights in the Webhannet River, Wells, Maine over a 151-day period from 12 May to 10 October 2014. Due to differential survival across treatments (see Table 2), sample size (n) varied from 2 to 6 for each mean estimate. - indicates no survivors.

<u>Tidal Height</u>	<u>Treatment</u>	<u>n</u>	<u>Absolute Growth (mm)</u>	<u>Final Shell length (mm)</u>
HIGH	Open (control)	2	21.3(6.8)	35.1(7.6)
	Flexible netting	6	18.5(2.1)	32.2(3.0)
	Flex net & VEXAR	6	18.8(2.7)	31.7(2.2)
	Pet screen	5	7.1(1.2)	19.7(1.6)
	Pet screen & Bottom	5	12.2(3.6)	23.9(3.9)
LOW	Open (control)	-	-	-
	Flexible netting	4	21.4(6.8)	33.1(5.5)
	Flex net & VEXAR	4	18.9(3.6)	31.9(2.4)
	Pet screen	4	9.7(5.5)	22.2(4.7)
	Pet screen & Bottom	4	9.7(7.6)	21.9(6.3)

Table 5. Analysis of variance on the mean absolute growth of cultured soft-shell clams in the Webhannet River, Wells, Maine from 12 May to 10 October 2014. Because sample size was not equal among treatments due to differential survival, Type III sums of squares was used for all hypothesis tests. Pre-planned contrasts appear below the Treatment source of variation. Boldface P-values are statistically significant. $\alpha' = 0.0127$ for all pre-planned contrasts.

Source of Variation	df	SS	MS	F	Pr > F
Tidal Height	1	7.40	7.40	1.62	0.2725
Treatment	4	791.97	197.99	14.93	0.0002
Open vs. Protected	1	82.70	82.70	6.24	0.0297
Pet screen vs. Flexible Net	1	870.61	870.61	65.64	<.0001
Flexible vs. Flexible & VEXAR	1	3.31	3.31	0.25	0.6272
Pet screen vs. Pet screen & Bottom	1	41.86	41.86	3.16	0.1033
Tidal Height x Treatment	3	34.06	11.35	0.86	0.4923
Block(Tidal Height)	4	18.31	4.58	0.69	0.6099
Treatment x Block(Tidal Height)	11	145.89	13.26	1.99	0.0974
Experimental Error	17	113.08	6.65		
Total	40	1339.36			

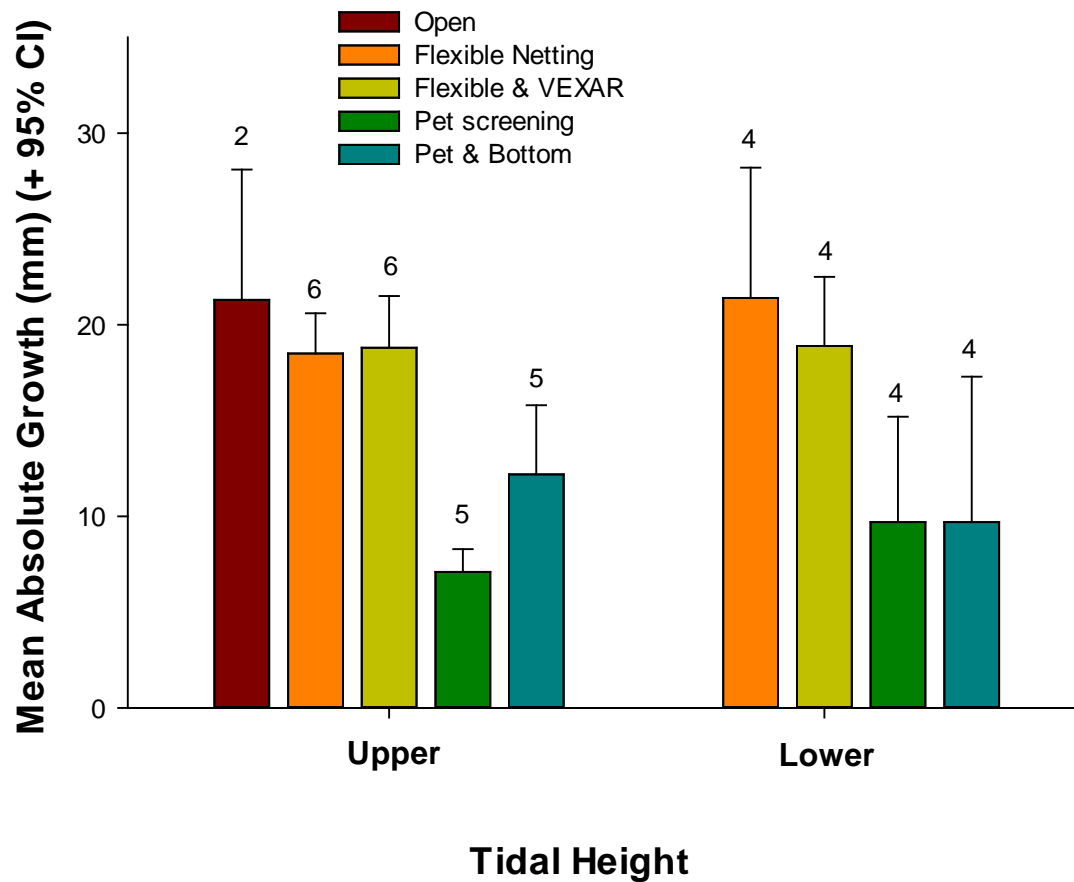


Figure 8. Mean absolute growth of juvenile soft-shell clams at two tidal heights and in five predator exclusion treatments from 12 May to 10 October 2014 in the Webhannet River, Wells, Maine. Number above each bar represents sample size.

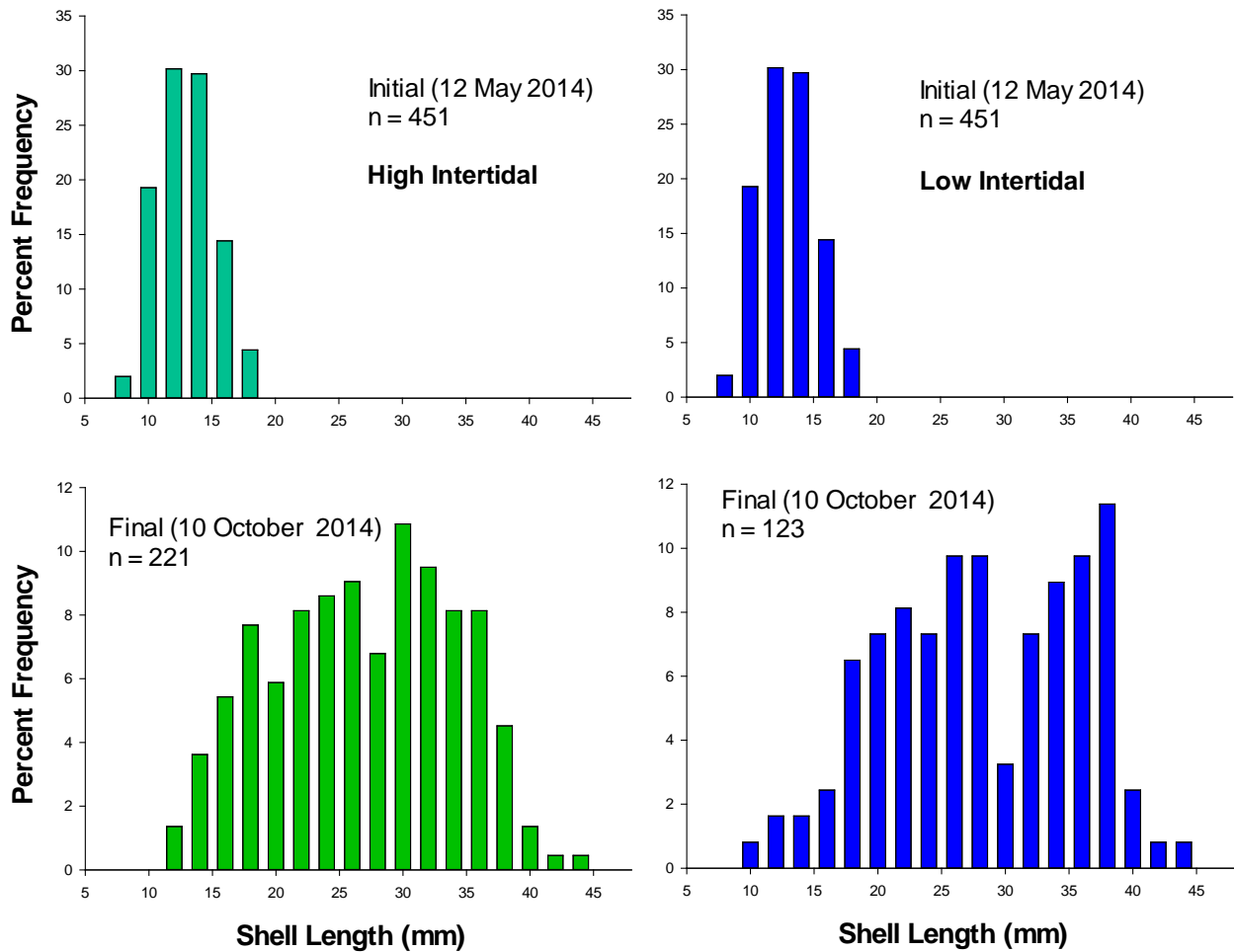


Figure 9. Initial and final size-frequency distribution of juvenile soft-shell clams at two tidal heights in the Webhannet River, Wells, Maine from 12 May to 10 October 2014.

Table 6. Mean number (\pm 95% confidence interval) of wild 0-year class recruits (i.e., individuals \leq 15.0 mm shell length) from experimental units (0.01824 m²) at both the high and low water mark at the Webhannet River, Wells, Maine on 10 October 2014. n = the number of experiment units for a given treatment.

<u>Tidal Height</u>	<u>Treatment</u>	<u>n</u>	<u>Per Unit</u>	<u>Per m²</u>
<i>HIGH</i>	Open (control)	5	0.2(0.6)	10.9(30.4)
	Flexible netting	6	7.5(6.5)	411.2(354.2)
	Flex net & VEXAR	6	4.8(2.8)	264.9(156.2)
	Pet screen	6	9.3(8.3)	511.7(456.9)
	Pet screen & Bottom	6	8.7(6.7)	475.1(366.9)
<i>LOW</i>	Open (control)	3	0.7(2.9)	36.5(157.2)
	Flexible netting	4	10.0(21.0)	548.2(1152.9)
	Flex net & VEXAR	4	37.8(50.0)	2069.6(2741.5)
	Pet screen	4	180.0(320.2)	9868.4(17556.9)
	Pet screen & Bottom	4	86.8(70.3)	4756.0(3848.6)

Table 7. Analysis of variance on the square root-transformed mean number of 0-year class individuals (recruits) of the soft-shell clam, *Mya arenaria*, per experimental unit from the Webhannet River, Wells, Maine (12 May to 10 October 2014). Pre-planned contrasts appear directly beneath the Treatment source of variation. Boldface P-values indicate statistical significance. n = variable depending on the number of recovered experimental units (see Table 6). $\alpha' = 0.0127$ for all pre-planned contrasts.

Source of Variation	df	SS	MS	F	Pr > F
Tidal Height	1	148.70	148.70	19.89	0.0112
Treatment	4	245.32	61.33	6.90	0.0028
Open vs. Protected	1	110.44	110.44	12.43	0.0034
Pet screen vs. Flexible Net	1	73.44	73.44	8.27	0.0122
Flexible vs. Flexible & VEXAR	1	6.41	6.41	0.72	0.4100
Pet screen vs. Pet screen & Bottom	1	6.06	6.06	0.68	0.4228
Tidal Height x Treatment	4	146.97	36.74	4.13	0.0204
Block(Tidal Height)	4	29.91	7.48	1.73	0.1821
Treatment x Block(Tidal Height)	14	124.42	8.89	2.06	0.0681
Experimental Error	20	86.25	4.31		
Total	47	788.15			

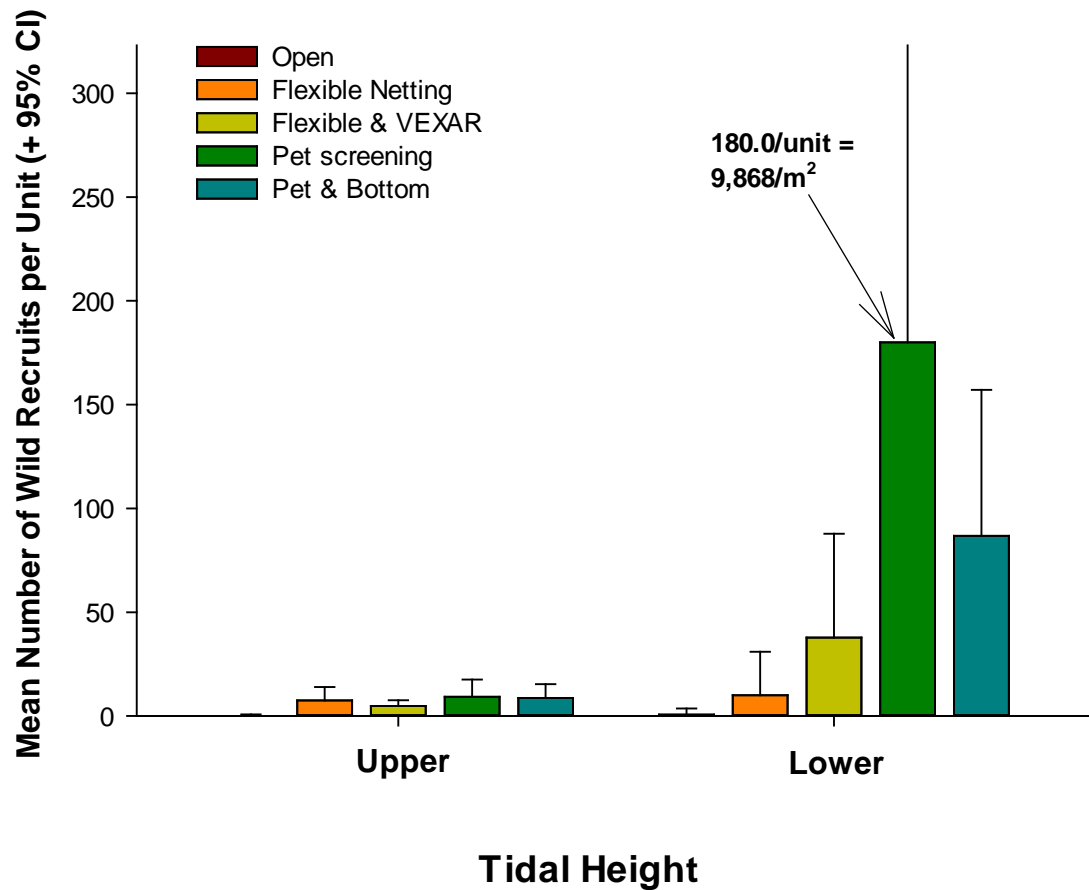


Figure 10. Mean number of wild recruits of the soft-shell clam at two tidal heights and in five predator exclusion treatments from 12 May to 10 October 2014 in the Webhannet River, Wells, Maine.

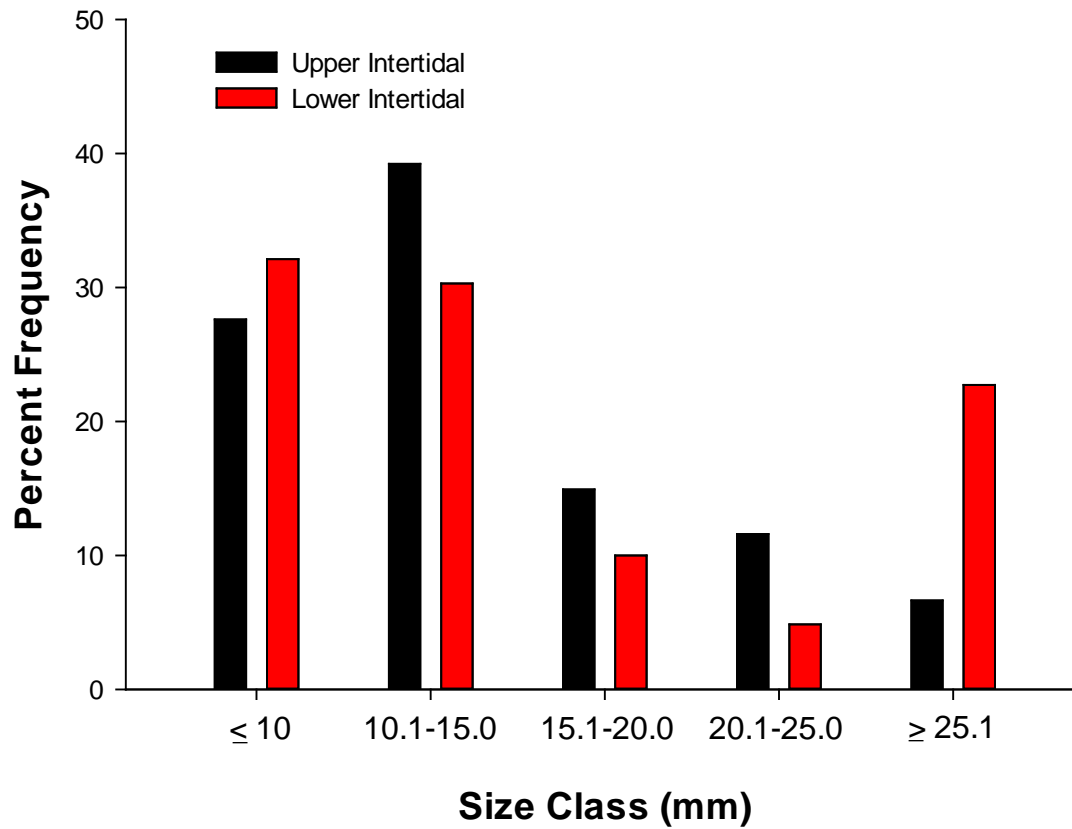


Figure 11. Distribution of sizes of *Mya* recruits across tidal heights at the Webhannet River, Wells, Maine on 10 October 2014. A G-test of independence indicated that the two distributions were not the same ($G = 33.5$, $df = 4$, $P < 0.0001$).

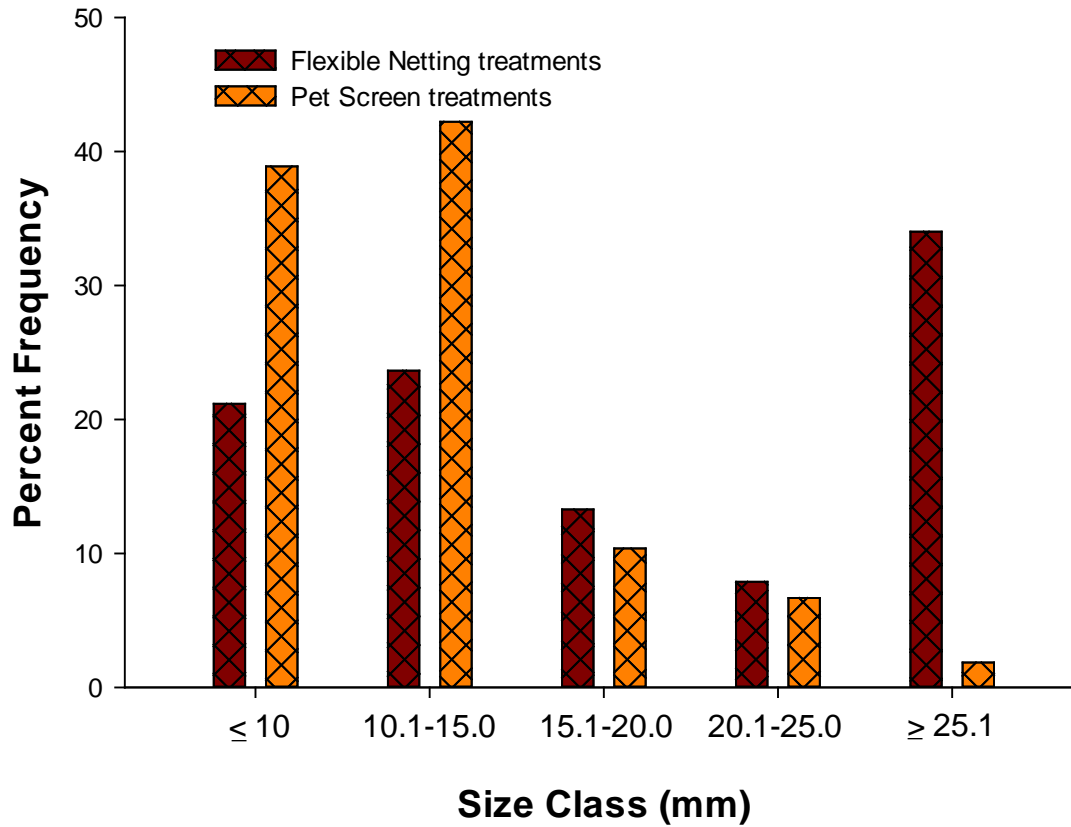


Figure 12. Distribution of sizes of *Mya* recruits across the two types of predator exclusion treatments at the Webhannet River, Wells, Maine on 10 October 2014. A G-test of independence indicated that the two distributions were not the same ($G = 119.4$, $df = 4$, $P < 0.0001$).

Table 8. Analysis of variance on the square root-transformed mean number of green crabs, *Carcinus maenas*, per experimental unit from the Webhannet River, Wells, Maine (12 May to 10 October 2014). n = variable depending on the number of recovered experimental units (see Table 6). Type III sums of squares were used.

Source of Variation	df	SS	MS	F	Pr > F
Tidal Height	1	2.74	2.74	6.63	0.0617
Treatment	4	1.11	0.28	0.63	0.6500
Tidal Height x Treatment	4	2.22	0.56	1.26	0.3331
Block(Tidal Height)	4	1.65	0.41	0.65	0.6330
Treatment x Block(Tidal Height)	14	6.19	0.44	0.70	0.7529
Experimental Error	20	12.69	0.63		
Total	47	26.72			

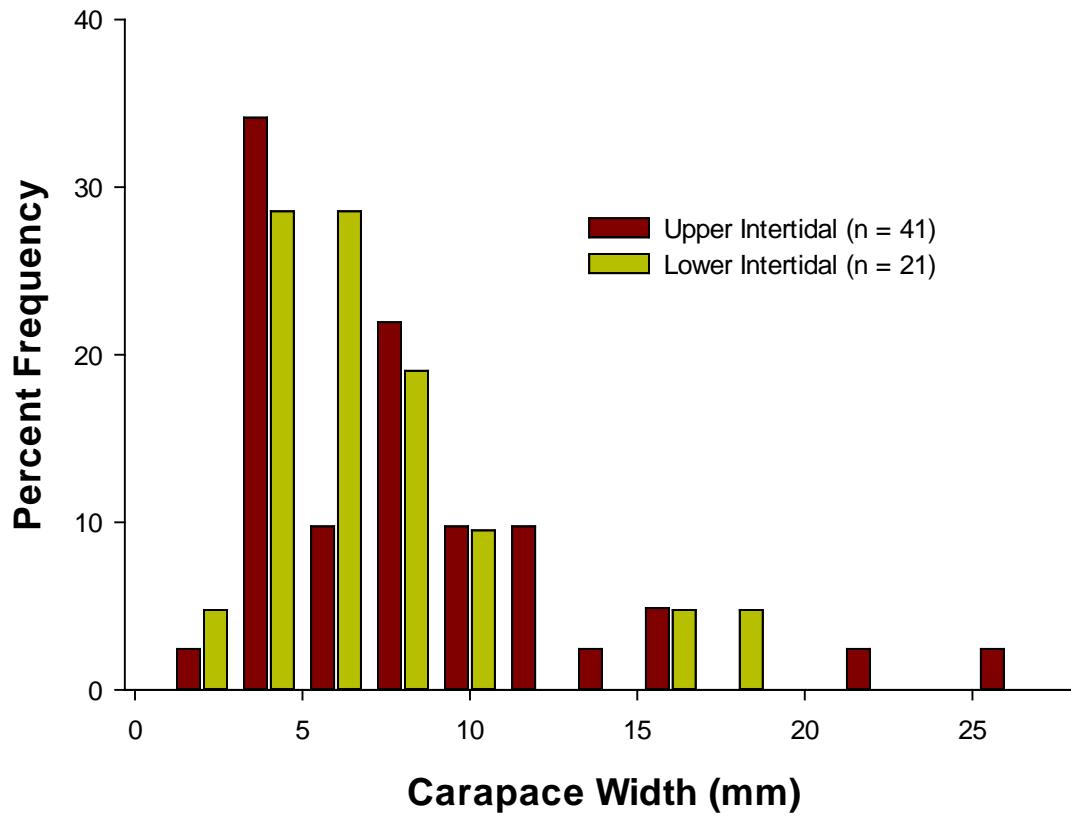


Figure 13. Size-frequency distribution of green crabs, *Carcinus maenas*, occurring in experimental units in the Webhannet River, Wells, Maine on 10 October 2014. A G-test of independence indicated that the two distributions were not significantly different ($G = 2.8$, $df = 2$, $P = 0.2461$).

Portland (Fore River; 13 May to 11 October – 151 days)

No clams were recovered alive in open (control) experimental units located in the upper intertidal blocks, and an average of only $2.8 \pm 4.5\%$ ($n = 6$) juveniles survived in the lower intertidal experimental units that were unprotected (Table 9). Survival in protected units was relatively high ($77.9 \pm 7.3\%$, $n = 48$) and did not vary between tidal heights (Table 10; Fig. 14). Greater than 85% of clams were missing from open units whereas less than 15% (pooled across both tidal heights) were missing from protected units. It appeared that fewer clams were missing from units protected with Pet screen vs. flexible netting (Table 9).

Growth varied significantly between the two tidal heights (Tables 11-12; Figs. 15-16) with clams in the lower intertidal blocks attaining a mean final SL (28.9 ± 2.5 mm, $n = 25$) that was approximately 20% greater than clams in the upper blocks (23.7 ± 1.5 mm, $n = 23$). A significant depression in mean absolute growth was observed between clams protected with flexible netting vs. Pet screening at both tidal heights (Table 12; Fig. 15). For example, clams in units protected with flexible netting added 15.8 ± 1.7 mm ($n = 23$) of new shell during the 151-day trial whereas those in units protected with Pet screening added 9.9 ± 1.5 mm ($n = 23$), a difference of nearly 60%.

Wild *Mya* recruits were observed in all experimental treatments at both tidal heights (Table 13; Fig. 17); however, the pattern of recruitment between treatments varied significantly across tidal height due mainly to the comparison between units protected with flexible netting vs. Pet screen in upper vs. lower intertidal blocks (Table 14). Generally, more recruits occurred in units protected with Pet screening vs. flexible netting, but the mean difference in abundance per unit between the two combined treatments varied significantly across tidal heights. For example, at the upper intertidal, the mean difference ($\pm 95\%$ CI) in recruitment between these treatments was 6.8 ± 5.3 ind. unit⁻¹ ($n = 12$) whereas in the lower intertidal, the mean difference was 126.3 ± 68.7 ind. unit⁻¹ (Fig. 17). Highest mean densities were observed in the Pet screening & Bottom screening treatment at the low intertidal (202.1 ind. unit⁻¹, or $11,028$ ind. m⁻²; Table 13).

Mean recruit size did not vary significantly between upper and lower intertidal blocks ($P = 0.0787$; $\bar{x}_{SL} = 9.8 \pm 1.2$ mm, $n = 53$), but did so among treatments ($P < 0.0001$); however, the

pattern varied between tidal heights ($P = 0.0009$; Fig. 18). In addition, size-frequency distribution varied significantly between tidal heights (Fig. 19). A higher percentage of clams < 5 mm SL occurred in upper vs. lower experimental units. The opposite pattern existed for clams in the 9.1-11.0 mm size class.

Green crabs occurred in 17 of the 60 (28.3%) of the experimental units (mean CW = 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 ($P > 0.40$). In addition, no other predator was encountered in the experimental units at the end of the experiment.

Table 9. Cultured individuals of the soft-shell clam, *Mya arenaria*. Mean percent (\pm 95% confidence interval) alive (A), dead individuals with undamaged valves (DU), dead individuals with chipped or crushed valves (DC), and missing individuals (M) at two tidal heights and five predator exclusion treatments in the Fore River, Portland, Maine over a 151-day period from 13 May to 11 October 2014. $n = 6$

<u>Tidal Height</u>	<u>Treatment</u>	<u>A</u>	<u>DU</u>	<u>DC</u>	<u>M</u>
	Open (control)	0.0(0.0)	0.0(0.0)	12.5(12.1)	87.5(12.1)
	Flexible netting	81.9(15.1)	0.0(0.0)	5.6(7.1)	12.5(10.7)
HIGH	Flex net & VEXAR	84.7(12.9)	1.5(3.6)	6.9(6.6)	6.9(10.2)
	Pet screen	88.9(10.6)	9.7(11.6)	0.0(0.0)	1.4(3.6)
	Pet screen & Bottom	69.4(41.9)	11.1(24.5)	16.7(33.3)	2.8(4.5)
	Open (control)	2.8(4.5)	0.0(0.0)	8.4(7.8)	88.8(4.5)
	Flexible netting	69.4(33.9)	1.4(3.6)	18.1(22.4)	11.1(23.9)
LOW	Flex net & VEXAR	68.1(12.9)	1.4(3.6)	16.7(17.5)	13.8(31.6)
	Pet screen	91.7(11.1)	6.7(13.5)	0.0(0.0)	1.6(7.1)
	Pet screen & Bottom	76.4(23.7)	6.9(11.6)	6.9(17.9)	9.8(11.1)

Table 10. Analysis of variance on the arc sine-transformed mean percent survival of cultured individuals of the soft-shell clam, *Mya arenaria*, at the Fore River, Portland, Maine from 13 May to 11 October 2014. Pre-planned, single degree-of-freedom contrasts appear directly beneath the Treatment source of variation. Boldface P-values are considered statistically significant. $\alpha' = 0.0127$ for all pre-planned contrasts.

Source of Variation	df	SS	MS	F	Pr > F
Tidal Height	1	41.24	41.24	0.20	0.6756
Treatment	4	40093.96	10023.49	0.94	<.0001
Open vs. Protected	1	38402.98	38402.99	142.07	<.0001
Pet screen vs. Flexible Net	1	319.69	319.69	1.18	0.2929
Flexible vs. Flexible & VEXAR	1	1.54	1.54	0.01	0.9408
Pet screen vs. Pet screen & Bottom	1	1369.75	1369.75	5.07	0.0388
Tidal Height x Treatment	4	1019.81	254.95	0.94	0.4644
Block(Tidal Height)	4	812.11	203.03	0.46	0.7651
Treatment x Block(Tidal Height)	16	4324.91	270.31	0.61	0.8499
Experimental Error	30	13268.39	442.27		
Total	59	59560.42			

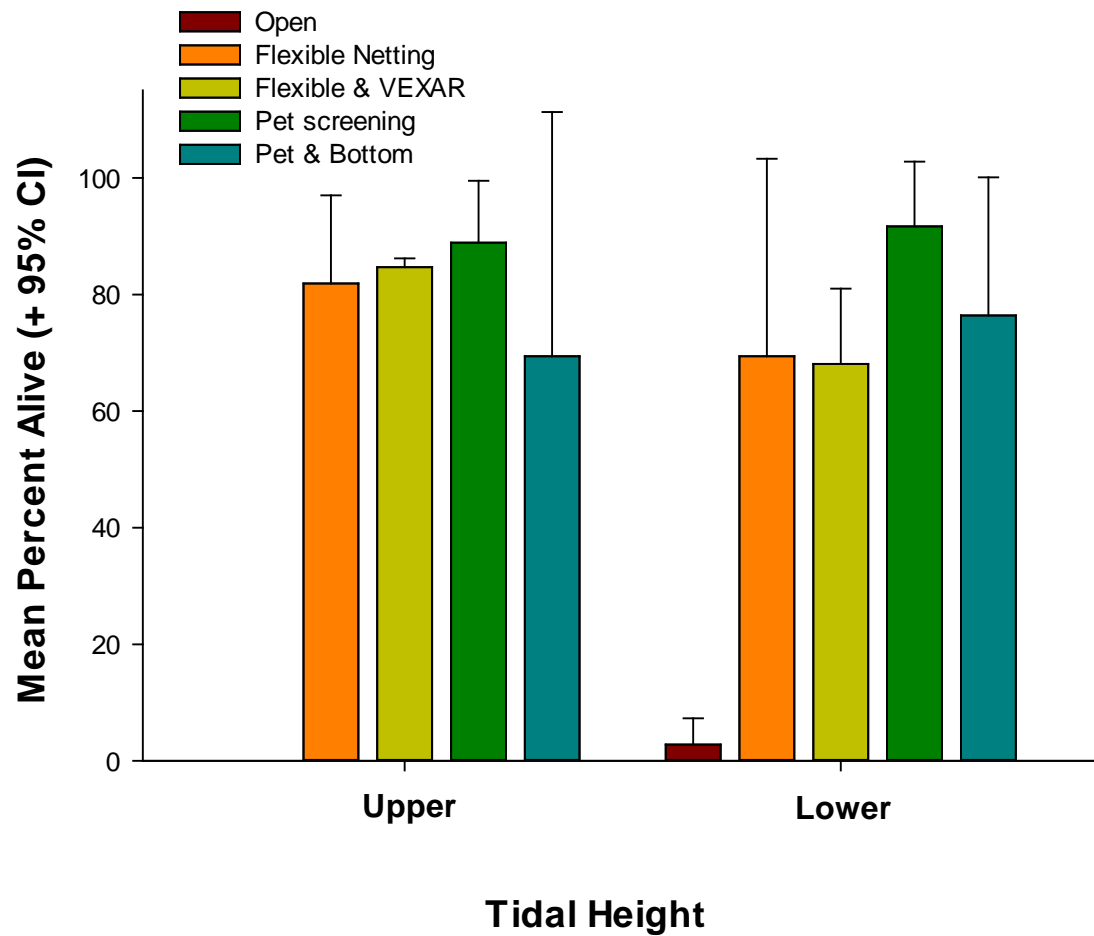


Figure 14. Mean survival of juvenile soft-shell clams (initial mean SL = 12.95 ± 0.20 mm, n = 451) at two tidal heights and in five predator exclusion treatments from 13 May to 11 October 2014 in the Fore River, Portland, Maine. (n = 6)

Table 11. Cultured individuals of the soft-shell clam, *Mya arenaria*. Mean (\pm 95% confidence interval) absolute growth (final length – initial length) and final shell length of clams in five predator exclusion treatments and at two tidal heights in the Fore River, Portland, Maine over a 151-day period from 13 May to 11 October 2014. Due to differential survival across treatments (see Table 9), sample size (n) varied from 2 to 6 for each mean estimate. - indicates no survivors.

<u>Tidal Height</u>	<u>Treatment</u>	n	Absolute Growth (mm)	Final Shell length (mm)
	Open (control)	-	-	-
	Flexible netting	6	13.6(1.3)	26.9(1.7)
<i>HIGH</i>	Flex net & VEXAR	6	12.5(1.4)	25.0(1.2)
	Pet screen	6	6.7(3.2)	19.3(2.9)
	Pet screen & Bottom	5	10.3(3.0)	23.4(3.6)
	Open (control)	2	28.0(29.9)	41.0(36.1)
	Flexible netting	6	21.3(1.4)	33.9(1.8)
<i>LOW</i>	Flex net & VEXAR	5	15.8(3.8)	29.4(3.8)
	Pet screen	6	10.9(3.9)	23.9(4.7)
	Pet screen & Bottom	6	11.7(3.2)	24.7(2.7)

Table 12. Analysis of variance on the mean absolute growth of cultured soft-shell clams at Fore River, Portland, Maine from 13 May to 11 October 2014. Because sample size was not equal among treatments due to differential survival, Type III sums of squares was used for all hypothesis tests. Pre-planned contrasts appear below the Treatment source of variation. Boldface P-values are statistically significant. $\alpha' = 0.0127$ for all pre-planned contrasts.

Source of Variation	df	SS	MS	F	Pr > F
Tidal Height	1	183.44	183.44	103.06	0.0005
Treatment	4	792.04	198.01	18.61	<.0001
Open vs. Protected	1	332.23	332.23	31.22	<.0001
Pet screen vs. Flexible Net	1	365.79	365.79	34.37	<.0001
Flexible vs. Flexible & VEXAR	1	67.87	67.87	6.38	0.0253
Pet screen vs. Pet screen & Bottom	1	26.15	26.15	0.31	0.5887
Tidal Height x Treatment	3	62.53	20.84	1.96	0.1701
Block(Tidal Height)	4	7.14	1.78	0.35	0.7651
Treatment x Block(Tidal Height)	13	138.34	10.64	2.06	0.0651
Experimental Error	22	113.59	5.16		
Total	47	1297.08			

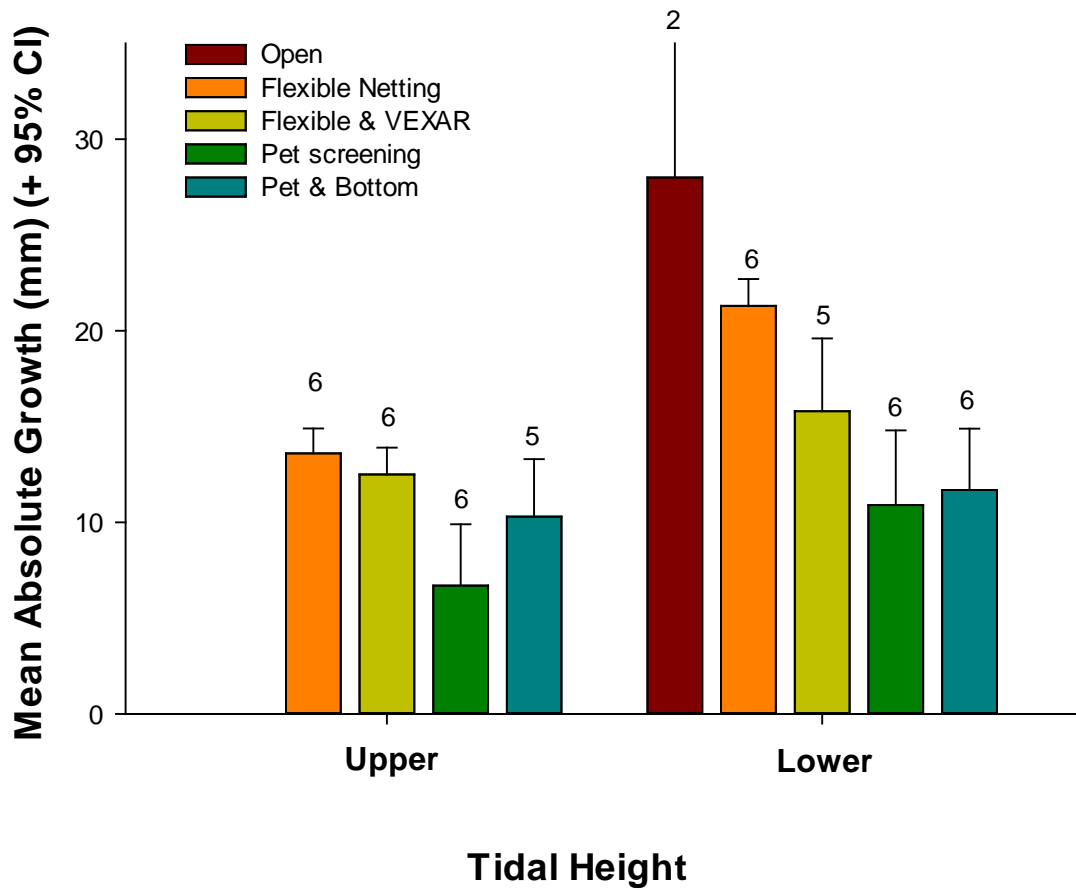


Figure15. Mean absolute growth of juvenile soft-shell clams at two tidal heights and in five predator exclusion treatments from 13 May to 11 October 2014 in the Fore River, Portland, Maine. Number above each bar represents sample size.

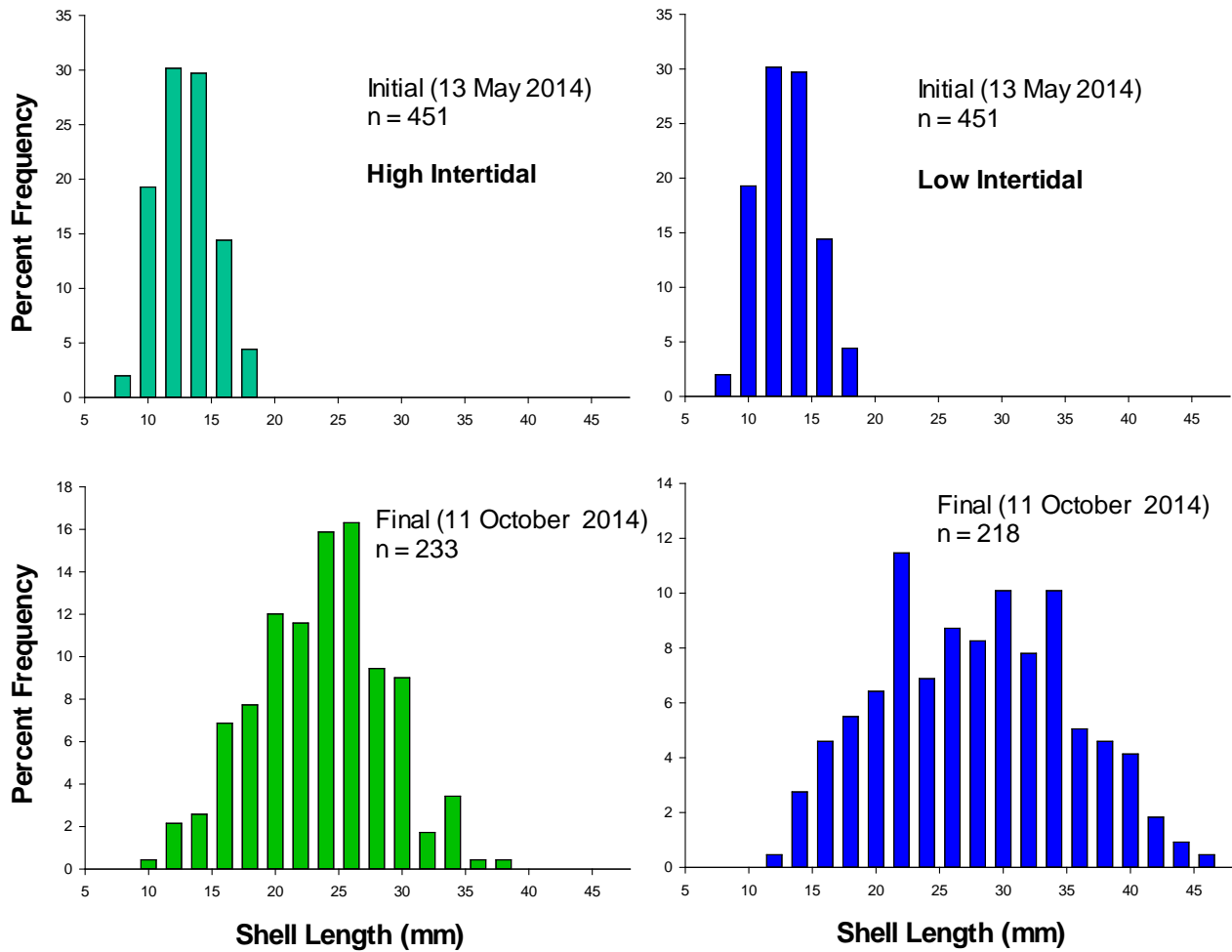


Figure 16. Initial and final size-frequency distribution of juvenile soft-shell clams at two tidal heights in the Fore River, Portland, Maine from 13 May to 11 October 2014.

Table 13. Mean number (\pm 95% confidence interval) of wild 0-year class recruits (i.e., individuals \leq 15.0 mm shell length) from experimental units (0.01824 m²) at both the high and low water mark at the Fore River, Portland, Maine on 11 October 2014. n = 6

<u>Tidal Height</u>	<u>Treatment</u>	<u>Per Unit</u>	<u>Per m²</u>
<i>HIGH</i>	Open (control)	1.2(1.2)	63.9(67.3)
	Flexible netting	6.7(7.2)	365.5(396.4)
	Flex net & VEXAR	2.0(1.3)	109.6(72.8)
	Pet screen	7.7(7.1)	420.3(389.7)
	Pet screen & Bottom	14.5(6.3)	794.9(346.7)
<i>LOW</i>	Open (control)	2.8(3.8)	155.3(210.4)
	Flexible netting	6.0(8.6)	328.9(468.8)
	Flex net & VEXAR	38.3(52.2)	2101.6(2860.9)
	Pet screen	95.7(80.7)	5244.9(4422.3)
	Pet screen & Bottom	201.2(121.0)	11028.9(6635.2)

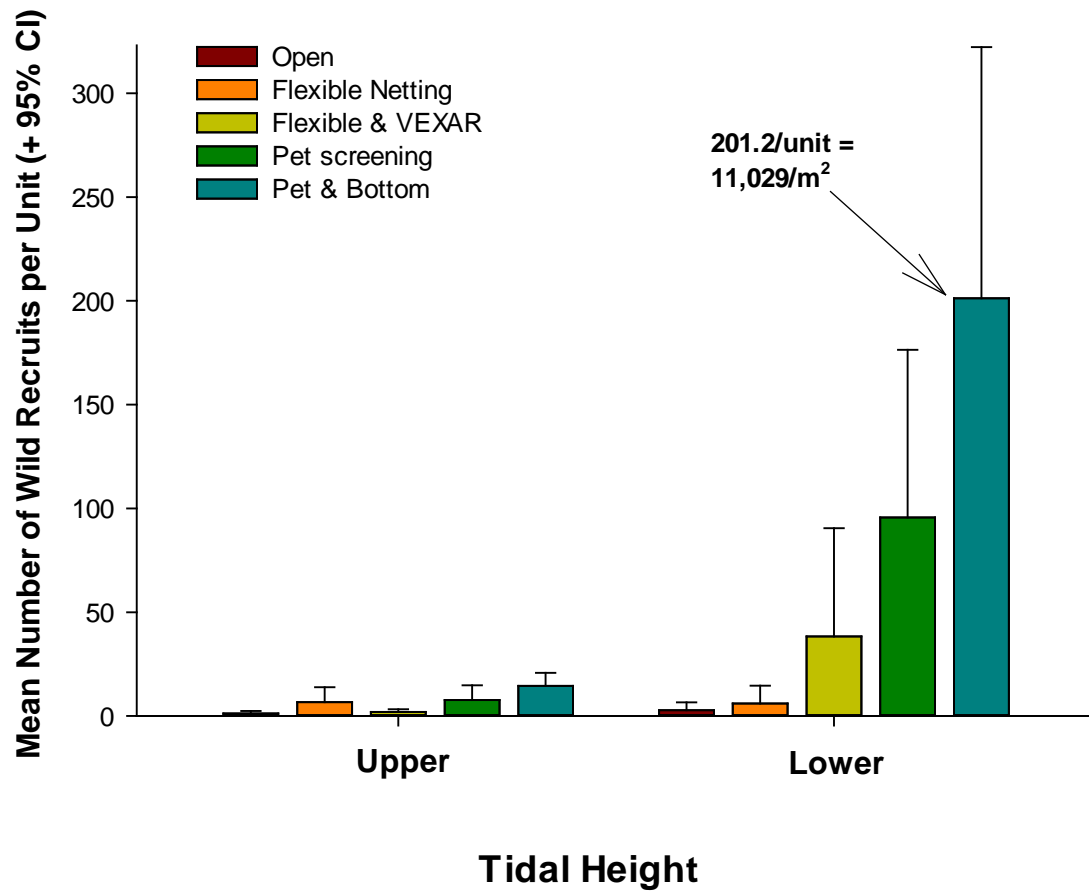


Figure 17. Mean number of wild recruits of the soft-shell clam at two tidal heights and in five predator exclusion treatments from 13 May to 11 October 2014 in the Fore River, Portland, Maine. (n = 6)

Table 14. Analysis of variance on the square root-transformed mean number of 0-year class individuals (recruits) of the soft-shell clam, *Mya arenaria*, per experimental unit from the Fore River, Portland, Maine (13 May to 11 October 2014). Pre-planned contrasts appear directly beneath the Treatment and Tide x Treatment source of variation. Boldface P-values indicate statistical significance. $\alpha' = 0.0127$ for all pre-planned contrasts. n = 6

Source of Variation	df	SS	MS	F	Pr > F
Tidal Height	1	236.97	236.97	94.70	0.0006
Treatment	4	426.72	106.68	11.55	0.0001
Open vs. Protected	1	137.80	137.80	14.92	0.0014
Pet screen vs. Flexible Net	1	238.32	238.32	25.80	0.0001
Flexible vs. Flexible & VEXAR	1	7.15	7.15	0.77	0.3921
Pet screen vs. Pet screen & Bottom	1	43.44	43.44	4.70	0.0455
Tidal Height x Treatment	4	207.54	51.88	5.62	0.0051
Tide x Open vs. Protected	1	48.24	48.24	5.22	0.0363
Tide x Pet vs. Flexible Net	1	122.45	122.45	13.26	0.0022
Tide x Flexible vs. Flex & VEXAR	1	26.51	26.51	2.87	0.1096
Tide x Pet vs. Pet & Bottom screen	1	10.33	10.33	1.12	0.3060
Block(Tidal Height)	4	10.01	2.50	0.33	0.8550
Treatment x Block(Tidal Height)	16	147.79	9.24	1.22	0.3083
Experimental Error	30	226.87	7.56		
Total	59	1255.90			

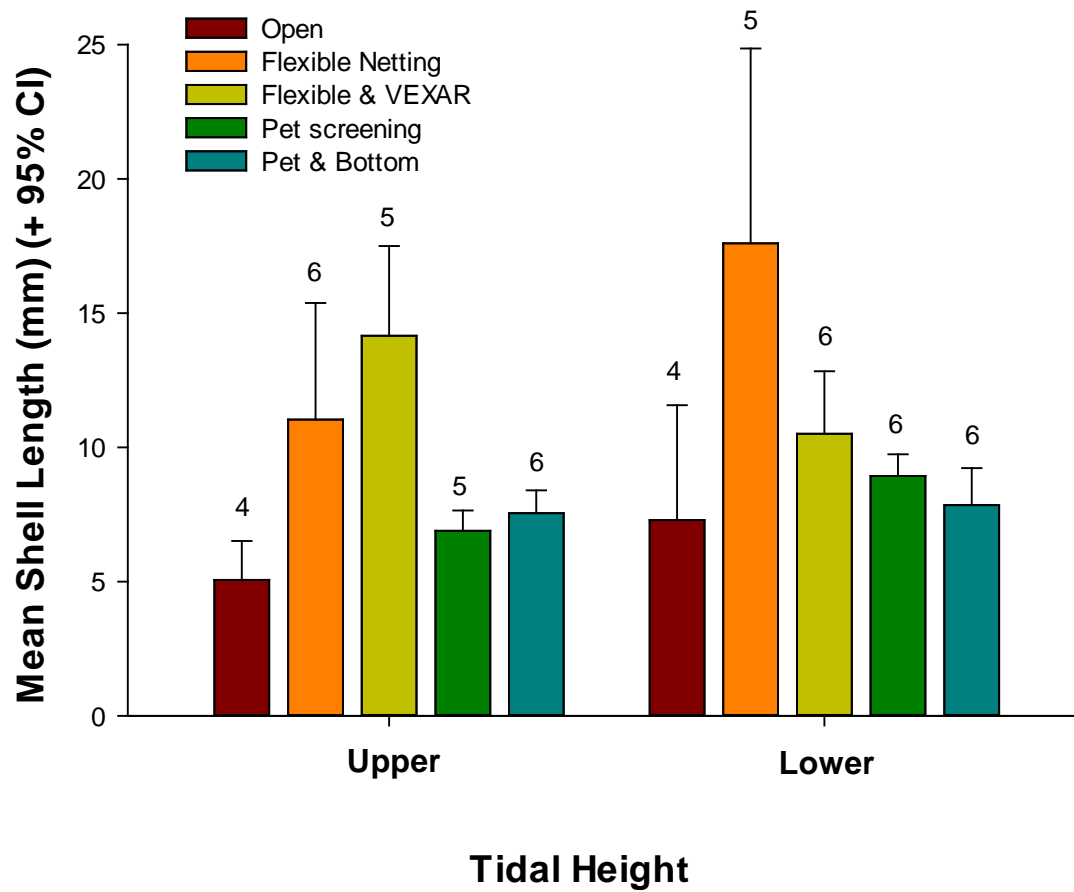


Figure 18. Mean shell length of wild recruits of *Mya arenaria* in experimental units at the Fore River (11 October 2015). Number above each bar reflects the number of experimental units in each treatment containing wild recruits.

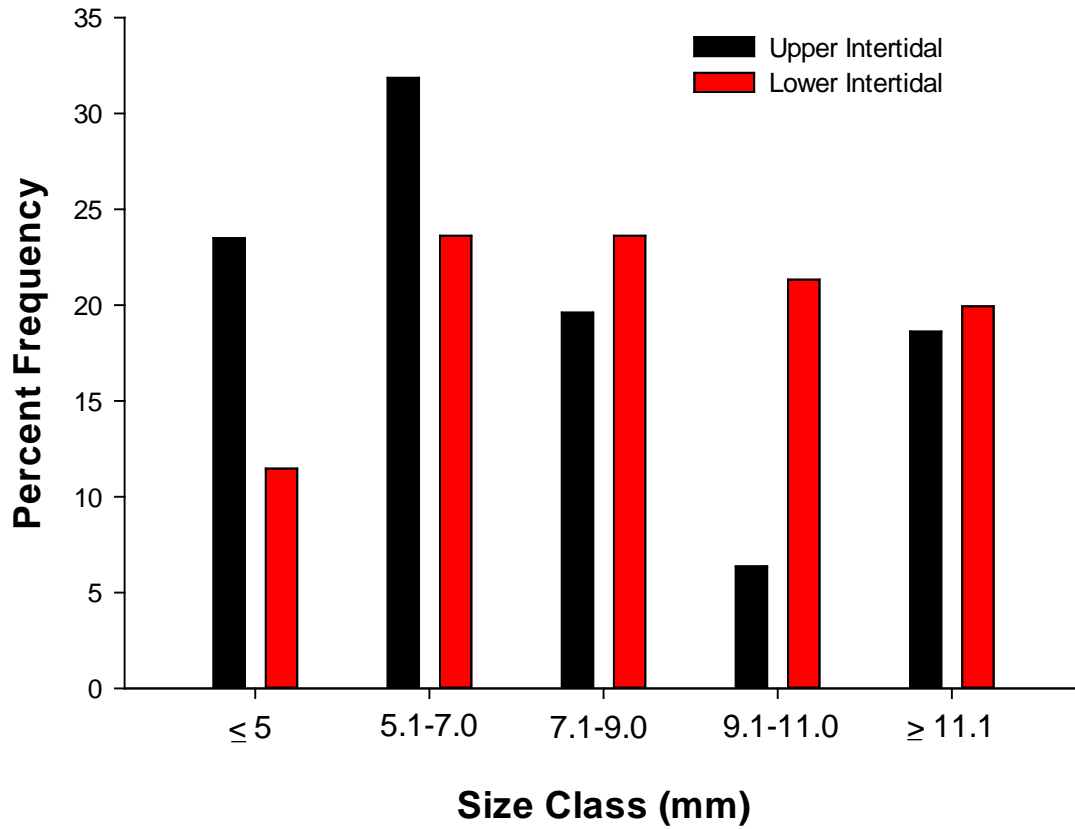


Figure 19. Size-frequency distribution of wild recruits of *Mya arenaria* from the Fore River (11 October 2015). $n_{\text{Upper}} = 209$, $n_{\text{Lower}} = 453$. A G-test of independence demonstrated that the two distributions were significantly different ($G = 39.2$, $df = 4$, $P < 0.0001$).

Discussion

Clams at both sites had relatively high recovery rates in protected vs. control units regardless of tidal position. For example, in Wells, mean percent alive in protected units ranged from 50.0-95.8% (overall mean = $71.0 \pm 8.8\%$, $n = 48$) whereas only $3.1 \pm 5.2\%$ ($n = 8$) were recovered in the open (control) units. No live clams were recovered in any of the open units in the lower intertidal blocks ($n = 3$). Similar results were obtained from the Portland site where $> 65\%$ of clams were recovered in protected units (overall mean = $77.9 \pm 7.3\%$, $n = 48$) vs. $1.4 \pm 2.1\%$ ($n = 12$). These dramatic differences in mean percent of clams recovered from predator exclusion treatments vs. controls underscore the importance of predation at both sites, and are remarkably similar to those obtained at two mid-intertidal sites in Freeport during the summer and fall of 2013 (Beal, 2014). At one site (Little River), mean survival of cultured clams (ca. 14 mm SL) from August to November was ca. 1% and no live clams were recovered at the other site (Recompence). Conversely, clams in units protected with flexible netting and with flexible netting plus VEXAR averaged $> 50\%$ at both sites. These mortality rates are greater than any observed in similar, small-scale studies in eastern Maine with similar size soft-shell clam juveniles (see Beal et al., 2001; Beal and Kraus, 2002; Beal, 2006a).

The assortment of predator exclusion treatments used in this study was designed to separate effects of crabs and nemertean worms. Flexible netting has been used to deter large predators such as green crabs, fish, and birds with varying degrees of success for years in both small- and large-scale studies (Beal, 2006b). Large green crabs have the ability to prey on clams in experimental units protected with flexible netting (Tan and Beal, 2015). Although the mechanism for this activity is not proven, the fact that netting can only deter crabs, not exclude them completely, suggests that it might be possible to improve the efficacy of flexible netting with the goal of increasing clam survival. The second netting treatment (Flex net & VEXAR) was an attempt to do this. That is, by adding a piece of heavy-duty (extruded) polyethylene netting directly over the top of experimental units, and held in place by a piece of the flexible netting (Fig . 4), it was thought that this combination of netting types would improve clam survival compared to the single layer of flexible netting. None of the a priori contrasts (Flexible net vs. Flexible net & VEXAR) at either site were statistically significant (Tables 3 & 10). At Wells, the addition of the VEXAR to units resulted in a 55% increase in mean percent of clams

recovered (Flexible netting: $55.8 \pm 22.8\%$, $n = 10$; Flexible netting & VEXAR: $88.7 \pm 11.8\%$, $n = 10$), but this comparison was not statistically significant ($P = 0.0341$; $\alpha' = 0.0127$). At Portland, both means were identical (75% , $n = 12$).

The two other exclusion treatments used Pet screening primarily to exclude nemerteans (e.g., *Cerebratulus lacteus*) that have been observed in many soft-bottom intertidal sites in southern Maine (Beal, pers. obs.). One treatment used a single piece of the fabric to cover the top of the experimental units (i.e., Pet screen; Tables 2 & 9). This should also have excluded green crabs and other large, epibenthic predators. The other nemertean exclusion treatment included a circular piece of Pet screen the same diameter as the bottom of the experimental unit (ca. 15 cm) that was added to the unit prior to filling with ambient sediments. The idea was that the bottom piece would exclude nemerteans from entering the unit through the 5-6 drainage holes in the bottom of each experimental unit. At Wells, where several nemerteans were encountered in October, but not in any of the Pet screen treatments, mean percent of clams recovered did not differ significantly between the screened treatments ($\bar{x}_{Pet\ screen} = 68.3 \pm 20.4\%$ vs. $\bar{x}_{Pet\ screen\ \&\ Bottom} = 73.3 \pm 19.2\%$, $n = 10$). At Portland where no nemerteans were observed in any of the October samples, the mean difference was about 20%, but this was not statistically significant ($\bar{x}_{Pet\ screen} = 88.9 \pm 6.5\%$ vs. $\bar{x}_{Pet\ screen\ \&\ Bottom} = 72.9 \pm 19.8\%$, $n = 12$).

These results provide an unambiguous picture of how cultured soft-shell clams should be used to enhance wild stocks. The mortality rate of unprotected clams at both sites in this study, at the two study sites in Freeport in 2013 (Beal, 2014), and from published accounts from intertidal sites in eastern Maine (Beal and Kraus, 2002; Beal, 2006a) is extremely high (> 90% in most cases) whereas mortality rates of protected clams typically are less than 50%. That is, it would not make sense economically to broadcast hatchery-reared seed clams on a mudflat then walk away without protecting them. Although netting is costly (ca. \$0.13 per square foot) and labor required to install and maintain it throughout the summer and fall, the enhanced survival of clams in netted plots would more than offset the additional costs and, more importantly, provide significantly more shellfish for clammers to harvest eventually.

Shell growth varied according to tidal height at Portland ($P = 0.0005$; Table 12), where the difference in mean absolute shell growth was approximately 50% ($\bar{x}_{Upper} = 10.8 \pm 1.5$ mm, $n = 23$ vs. $\bar{x}_{Lower} = 15.9 \pm 2.5$ mm, $n = 25$), but not at Wells ($P = 0.2725$; Table 5; $\bar{x}_{Upper\&Lower} = 14.9 \pm 1.8$ mm, $n = 41$). Predator exclusion treatments had significant effects on absolute shell growth and final mean length that were consistent between sites. For example, the comparison of the two flexible netting treatments and the two Pet screen treatments was highly significant ($P < 0.0001$) at both sites (Table 5 & 12), with significant growth depression occurring for clams in the Pet screen treatments. In the Webhannet River, mean final SL was 32.2 ± 1.1 mm ($n = 20$) in units with flexible netting, but only 22.0 ± 1.6 mm ($n = 19$) for units protected with Pet screen, a 46% difference. In the Fore River, the difference was 26% ($\bar{x}_{Flexible} = 28.8 \pm 1.7$ mm, $n = 23$; $\bar{x}_{Pet\ screen} = 22.8 \pm 1.6$ mm, $n = 23$). Because the Pet screen affected growth rates similarly at both sites, the mechanism is likely related to reduced flow due to the smaller aperture of the screening material. This hypothesis remains to be tested.

Density of wild clams in experimental units at the end of the experiment varied in a similar fashion at both sites. Mean recruitment per unit was ca. 10x greater in lower vs. upper blocks, and the densities were remarkably similar between sites ($\bar{x}_{Fore|Upper} = 6.4 \pm 2.5$ ind. unit⁻¹, $n = 30$; $\bar{x}_{Fore|Lower} = 68.8 \pm 36.3$ ind. unit⁻¹, $n = 30$; $\bar{x}_{Web|Upper} = 6.3 \pm 2.3$ ind. unit⁻¹, $n = 29$; $\bar{x}_{Web|Lower} = 66.3 \pm 52.4$ ind. unit⁻¹, $n = 19$). Although significant Tide x Treatment effects on clam recruitment occurred at both sites, enhanced numbers of wild clams occurred in units protected with Pet screening at both tidal heights at the Fore River site (Fig. 17) and at the low tidal height at the Webhannet Site (Fig. 10). It is unclear why this result occurred; however, the enhanced protection of small clams afforded by the Pet screen may be the reason. If Pet screen can be used on a larger scale to encourage survival of 0-year class soft-shell clams, this may be another tool that towns can use to enhance their flats.

These results also speak to the relative importance of predation vs. acidification of sediments (sensu Green et al., 2009, 2013) as a mechanism for declining soft-shell clam populations in the areas of the two study sites. Although neither sediment pH nor sediment saturation state was measured in this study, the mechanism relating to a general pattern of a lack of small clams in

the intertidal can be explained simply by predation. The difference in cultured clam survival and wild clam recruitment in unprotected vs. protected experimental units at both sites was strikingly stark. The use of flexible netting and Pet screening led to significant increases in survival of cultured clams and significant enhancement of wild 0-year class individuals. Dissolution as a mortality factor has been shown to be important in some coastal sediments (Green et al., 2009). It is likely that sediments at both sites were not undersaturated with respect to calcium carbonate. If they had been, then there would have been no enhancement of *Mya* recruits in protected vs. open/ control units.

In the recent past, the major predator of soft-shell clams of most sizes in southern Maine has been the invasive green crab, and this species was observed in relatively high densities in experimental units at both sites at the end of the study compared to other predators (e.g., nemertean, fish, other crustaceans). No clear pattern emerged for green crab abundance at either site relative to tidal height or treatment. At the Fore River study site, green crabs occurred at a mean density of 0.27 ± 0.13 ind. unit⁻¹ (14.6 ± 7.3 ind. m⁻², n = 60). Mean green crab density at the Webhannet River study site was 1.27 ± 0.40 ind. unit⁻¹ (69.67 ± 21.71 ind. m⁻², n = 48). Crabs were relatively small at each site (≤ 25.1 mm CW at the Wells site, n = 62; < 26.6 mm CW at the Portland site). Most crabs were < 10 mm CW suggesting that these were the 2014 year class recruits (Berrill, 1982). Because crab settlers can be as small as 1 mm CW when they reach the benthos, it is possible for crabs to enter into protected units or into larger plots protected with netting by crawling through the apertures and residing in those units or plots while escaping their own predators. It is likely that crabs > 20 mm are at least two years old, and many of the units containing crabs of those sizes were associated with high mortality rates (dead crushed category, see Tables 2 & 9) and low recruitment numbers. Miron et al. (2005) demonstrated that large green crabs (ca. 60 g) preferentially preyed on soft-shell clams < 15 mm SL under laboratory conditions when offered clams as large as 40 mm SL.

Conclusion

Maine's soft-shell clam resources have dwindled in recent years to the point where most of the harvestable biomass is located along the upper shore. In most towns, flats with tens to hundreds

of productive acres are a thing of the past. Clammers no longer spread out over these vast acres of intertidal flats, but instead, congregate along the upper intertidal where the last vestiges of commercial quantities of clams exist. Results from this and other studies (Beal, 2006a,b; 2014) suggest that predation is the mechanism primarily responsible for this scenario. Clammers are now harvesting the subsidy along the upper shore that, until recently, was largely ignored by commercial license holders. Typically, clams near the upper intertidal grow more slowly but have higher survival rates than conspecifics at lower tidal levels (Beal et al., 2001) because most predation on clams originates from the subtidal since most predators are mobile and prey during tidal inundation. It is also likely, but untested to date, that the upper intertidal subsidy may act as a spawning refuge (sanctuary) for *Mya* and that, in the past, these areas may have contributed disproportionately to the annual reproductive cycle that occurs along the Maine coast each May-July (Ropes and Stickney, 1965). What happens to Maine's clamming industry if/when fishing pressure lowers the upper shore clam subsidies to less than commercial densities? What tools do clammers have in their management arsenal to take control of what appears to be a downward spiral – shrinking productive intertidal flats and fewer harvestable clams? Results presented here suggest that on spatial scales a single clammer can manage (perhaps 1-3 acres near the mid intertidal) it is possible to grow cultured clam seed to commercial sizes within two years and/or encourage wild seed to settle into protected plots. Seed must be managed, too, and, when overwintered (see Beal et al., 1995), those small, 0-year class clams can be planted in protected plots the following spring with the goal of harvesting them within two years. Wild clams grow at rates similar to cultured stock.

The idea of farming clams, rather than hunting for them, is anathema to most clammers, who pride themselves in having acquired the skill and perseverance it takes to locate commercial quantities of clams from hundreds of intertidal acres day-after-day for week-upon-week from year-to-year. Perhaps the vagaries of several back-to-back cold winters that may act to reduce predators, combined with excellent wild clam recruitment, will re-populate flats so that the recent period of declining commercial clam stocks will be short-lived. If not, and commercial stocks continue to fall, those who refuse to put new ideas and new thinking into bold action steps to create new commercial opportunities for themselves will likely have to find alternative employment.

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